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A Psychophysical Approach to Touch: from Multi-sensory Processes to Body Representations

By

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Declaration

I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other university. This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and Acknowledgements.

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Last but not least: grazie Giacomo.

Abstract

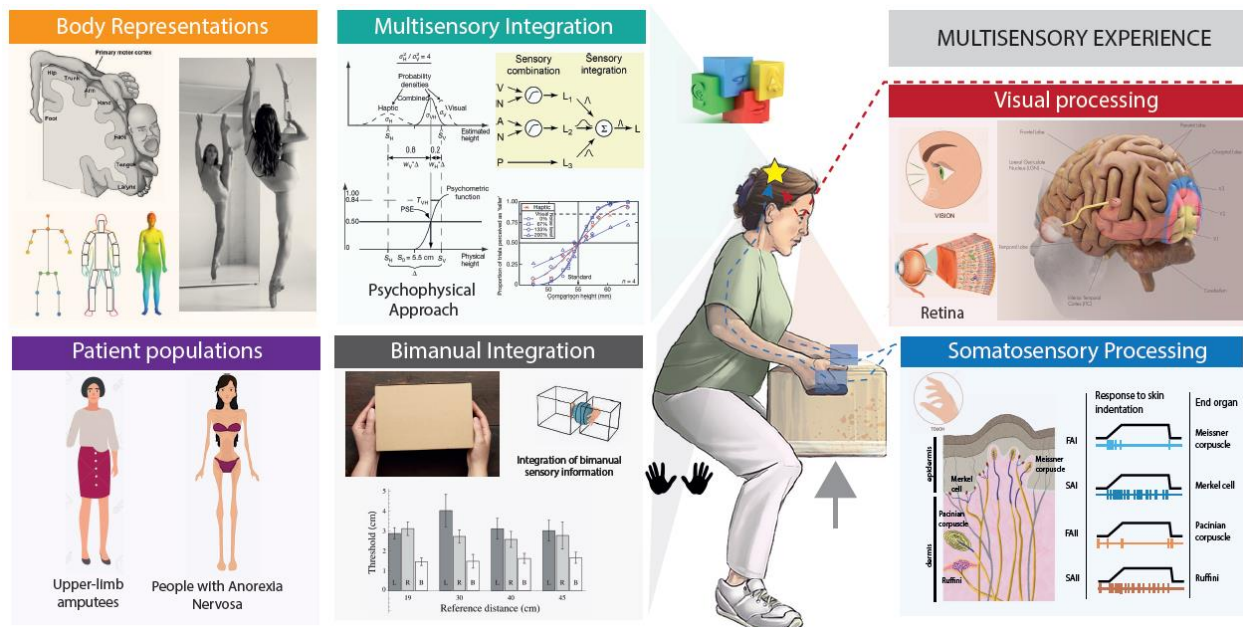
The goal of this PhD dissertation is to investigate the sense of touch in its complexity. The somatosensory system is made up of a number of submodalities, and it is a pivotal building block of our experience of the external world and the body itself. In a natural context, the somatosensory signals are continuously integrated with the signals coming from other sensory modalities, allowing to come up with unambiguous percepts of the world. When facing a somatosensory deficit, the benefits of such an optimal integration could be lost, with dramatic consequences. Due to the importance of these sensory processes, quantitative and rigorous psychophysical methods have to be carefully implemented and adopted to unveil crucial somatosensory processes. Therefore, to investigate multisensory integration in different clinical populations suffering from somatosensory deficits, two studies were conducted. In the first one, the integration of visual and artificial somatosensory information are investigated in an amputee provided with a sensorized bionic hand prosthesis. The results indicate that sensory substitution based on intraneural feedback can be integrated with natural visual feedback. The study opens encouraging scenarios in the development of increasingly sophisticated technology devoted to the restoration of lost limb functioning. The second study involves patients with Anorexia Nervosa (AN) and healthy individuals with and without body concerns. Its findings suggest that patients show visual and tactile objects shape distortion and lower sensory acuity. To a lesser extent, the biases in shape perception (i.e. width overestimation) were observed also in the other two healthy groups, and was more pronounced in women concerned about their bodies. These biases are interpreted as a reflection of proven distortions in the Mental Body Representations of the body (MBRs). Finally, our results do not support the multi-modal integration impairment hypothesis. The study encourages to evaluate the potential of perceptual indexes as a tool to support clinical practice.

Another fundamental feature of the somatosensory system is that the inputs can be static or dynamic, implying movement and an active interaction between the skin and the perceived objects. To analyze this important perceptual aspect in depth, I carried out two studies comparing bimanual performances in static and dynamic conditions. The first study investigated sensory integration mechanisms within the somatosensory modality (i.e. the integration of information coming from the two hands). The results showed that the information coming from the two hands are integrated in a statistically optimal fashion. Slightly better performances are observed in the dynamic conditions providing a little evidence of movements' benefits on the perceptual performances. This work confirms the importance of cognitive effects in bimanual integration processing. The second study targeted the effect of movement on lower-level information processing. A bimanual

manipulandum was used to measure size-change detection thresholds of a virtual bar at rest or during continuous movements. The results showed that the humans' ability to localize the relative positions of their upper-limbs decreases during movement. The existence of different processes underlying size discrimination in static and dynamic objects perception is suggested.

Finally, the sense of touch has an essential role in the constitution of our sense of-self. Different MBRs and their interaction provide a reference context to perceive our own body and the external objects. Accordingly, the last experiment presents a paradigm designed to investigate different cognitive maps of the body and their interaction in a complex task involving their synergy.

The figure below proposed a graphical abstract of this PhD dissertation, which is part of a research activity carried out in collaboration between different national and international Universities, Research Institutions and Hospitals. Overall, it provides an overview of the different peculiar aspects underlying the somatosensory experience by using a quantitative approach based on the methods of psychophysics.



Graphical Abstract. A psychophysical approach to Touch: From multi-sensory processes to body representations

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Chapter 1

Introduction

At the age of 19, I.W. suddenly caught a rare virus that eliminated all tactile and positional feedback from the neck down. I.W. was unable to perceive where his body was positioned in space or whether it was moving. Over a period of two years, he slowly relearned to walk, and dress himself, and even after decades of training he needed to follow every movement with his eyes in order to successfully carry out everyday actions (Cole, 1995; *The Man Who Lost His Body*, BBC Documentary, 1998). The case of I.W. highlights the critical role of somatosensory sensing for our experience of the world. Indeed, we are profoundly limited in our existence without touch. The sensory modality, which relates to the “body senses”, is often referred as somatosensory system. It is a complex system and it comprises several submodalities including the cutaneous senses (e.g. temperature, pain, etc.) or kinesthetic senses (i.e. the sense of limb position and the sense of limb movement; Jones, 2018; Proske & Gandevia, 2009). In order to come up with robust percepts of the external environment, the somatosensory system involves the integration of information from different sensory modalities (Ernst & Bühlhoff, 2004). However, it counts some important differences with the other senses.

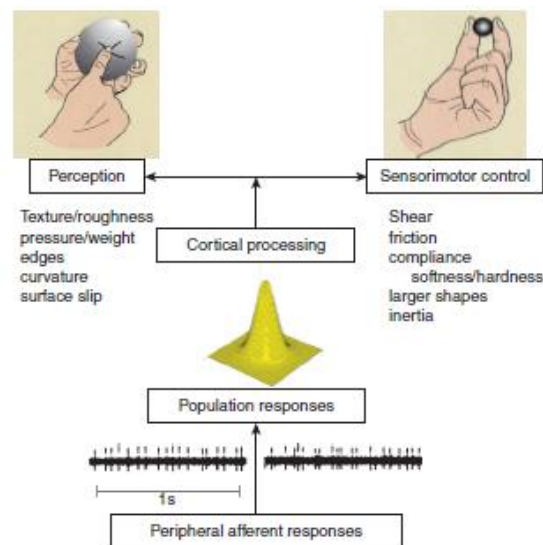


Figure 1. Pathway from skin mechanoreceptors to brain. Different signals coming from the receptors are used both for perception and sensorimotor control (taken from Jones & Smith, 2014).

The somatosensory system is bidirectional, in that there is a tight interaction between the touched object and the related somatosensory sensation. For example, during active objects exploration (i.e. haptic perception) the information we can extract about an object's properties is exquisitely linked to the movements performed. Sensory signals from somatosensory receptors are involved not only in passive tactile perception, but also in dynamic operations for force modulation and limbs control (Figure 1). Finally, the organ attached to the sense of touch is the skin, which is not only the largest among all the other sensory organs, but it also defines the physical limits of our body and acts as a barrier protecting it. The body is central to the construction of our sense of self. Furthermore, somatosensory signals have been demonstrated to play a crucial role in the constitution of the cognitive body maps, which shape our corporeal experience and provide a reference to perceive the objects of the external world (Figure 1.1) (Longo et al., 2010; Serino & Haggard, 2010).

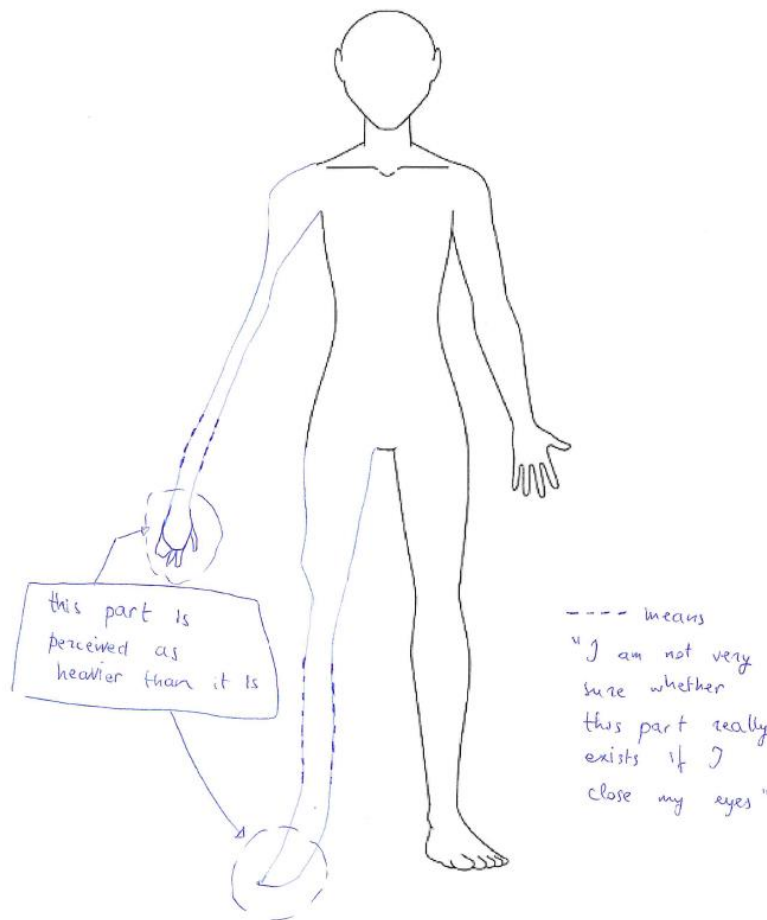


Figure 1.1. Graphic representation of the body as perceived by an individual chronically deafferented that I tested during my PhD. The subject suffers the loss of tactile and proprioceptive sensations on the right arm and leg after the removal of an osteochondroma. Her drawing gives a

hint of the strong link between the lack of somatosensory signal and the bodily self-consciousness. Indeed, the subject reported abnormal perceptions of the right side of the body: the limbs are perceived as much longer and thinner than the contralateral not affected ones. The limb extremities are also perceived as heavier, and as indicated by the dotted lines, the perception of some body parts is not completely clear, and she cannot say with confidence whether they exist or not.

This thesis investigates the somatosensory processing mechanisms related to these different aspects in both healthy individuals and different clinical populations suffering from somatosensory deficits. The following sections offer a closer look to the integration mechanisms occurring between the somatosensory signals and the visual sensory modality, and within the somatosensory modality itself. In particular, I will present the most influential model proposed to describe optimal integration of sensory information from different sensory modalities. Then, I will concentrate on the integration within the somatosensory modality, and I will review evidence related to the processing of information coming from the two hands, with particular attention to the effect of movement on such bimanual operations. Finally, I will focus on the importance of touch for the construction of the cognitive maps of the body, and I will present two models that have been proposed to describe the relation between the touch and the body. This introduction together with the [Thesis Outline \(Section 1.3, Chapter 1\)](#) should provide an exhaustive background for the comprehension of the studies that I have conducted during my PhD. The [Chapters 2](#) includes the investigations on multisensory integration processing in two clinical populations with somatosensory deficits, i.e. an amputee individual and women suffering from Anorexia Nervosa. [Chapters 3](#) is about sensory-motor integration of information involved in bimanual performances. Finally, [Chapter 4](#) presents the results of the last experiment in which we investigate the interaction between tactile and proprioceptive signals as a way to study the interaction between the different mental representations underlying somatosensory perception.

A final note related to the approach adopted in this work: the intent to investigate the fundamental relations of dependency between the body and the mind was a guiding thread along all the studies. Citing Fechner (1966;1860) “*As an exact science psychophysics, like physics, must rest on experience and the mathematic connection of those empirical facts that demand a measure of what is experienced or, when such a measure is not available, a search for it*”. Accordingly, in order to quantitatively investigate the alterations and perceptual distortions in the somatosensory information processing, we adopted the psychophysical method in all the studies presented in this thesis.

1.1 Sensory Integration

Humans perceive their own body and the surrounding environment through several sources of information. When a healthy individual judge the size of an object, often there is more than one sensory estimate available for perceiving the object property. For example, the individual can look at the object while manipulating it, thus both visual and tactile information are simultaneously available to the perception.

For a long time, vision has been considered as the dominant sense over the other sensory modalities. A classic case of visual capture was reported by Gibson (1933), who performed a series of eight experiments where participants wore prism spectacles that made vertical straight lines appear curved. Although kinesthetic information coming from the tactile exploration of the object, indicated that the line was straight, subjects experienced no conflict and the vertical straight lines felt curved. Coherently, Rock & Victor (1964) claimed that that "*conflict between visual and tactual size is... resolved more or less completely in favor of visual size*" (p. 595). They demonstrated that in drawing and matching tasks, unaware participants provided with conflicting visual and somatosensory information, tend to reproduce their visual impression of the object property with only a little contribution of tactile information. These and other studies strengthened the hypothesis that vision dominates touch (Miller, 1972; Power & Graham, 1976). However, despite being small, the contribution of the touch on the bimodal percept was always consistent, and subsequent studies started showing experimental situations in which the influence of touch on the integrated percept was considerable. In 1972, McDonnell & Duffett started conceiving the idea that the generalization of vision as a dominant modality may be premature. They found that in a matching task in which participants visually and tactually explored wooden blocks, there was a great variability in the response pattern and the participants' final judgment was a compromise between the available sensory signals (McDonnell & Duffett, 1972). The finding was replicated and confirmed by subsequent studies (e.g. Hershberger & Misceo, 1996; Klein, 1966). In a 2000 Shams et al., clearly showed an "auditory capture" effect in a study about the integration of audio and visual information. The participants was asked to report the number of visually perceived stimuli, while they were hearing to one or more auditory stimuli. Their responses were often incorrect, and the reported number was clearly biased towards the auditory information (Shams et al., 2000).

This new evidence raises the question of how does the brain integrates different sensory modalities and under what conditions one or the other dominates became of growing interest. Great credit was given to Welch & Warren's (1986) hypothesis, which proposed that discrepancies between

sensory signal were resolved in favor of the most appropriate modality, hence the name “Modality Precision Hypothesis”. The idea was that the dominance of one or the other sensory modality depends on the appropriateness of the available sensory modalities to determine the specific property of the object taken into consideration. For example, orientation is a mainly visual quality, and neurons in V1 were demonstrated to be selective for this feature (Hubel & Wiesel, 1959; Tootell et al., 1998). Accordingly, visual information is the most precise at determining such a property, and has been demonstrated as dominant over other modalities (Gori et al., 2008). In contrast, audition appears to be the most appropriate modality when considering temporal judgments (Shams et al., 2000). Accordingly, several studies have shown that auditory information can quantitatively alter tactile and visual perception to create sensory illusions (Bresciani et al., 2005; Shams et al., 2000). Furthermore, it is worth noting that there is also a tradition in philosophy in which vision has been considered unreliable in a way that touch is not, in large part due to the problem of distance and the reduction of the 3-D world onto the 2-D retina.

Finally, Ernst & Banks published in 2002 a seminal work on multimodal cue integration that offered a quantitative model of multisensory integration based on Bayesian principles and an experimental paradigm based on psychophysical methods to validate it. In particular, this model that we shall refer as the optimal integration model allows one to predict the degree to which one sensory modality or the other dominates in the multimodal conditions (Ernst & Banks, 2002). Rather than refer to “modality precision”, the authors showed that the sensory dominance is determined by the reliability of each sensory modality, which can be measured independently. The next section describes the optimal integration model in more detail.

1.1.1 Multisensory Integration and the Maximum Likelihood Estimation Model

When perceiving the world, many different sources of sensory information reach our brain simultaneously. Nevertheless, the Nervous System (NS) is perfectly capable of organizing and process all the information. The sensory cues could be about complementary aspects of the environment. In this case, the brain collects more and more different information that “cooperates” to disambiguate the perceptual event, and different combination rules have been described for these situations (Clark & Yuille, 1990; Howard & Rogers, 2002; Yuille & Bülthoff, 1996). For example, the visual localization of a position in space requires combining visual cues, that provide

information about the target in a retinal frame of reference, with proprioceptive information, that provides information about the direction of the gaze e.g. Snyder et al., 1998). Alternatively, the signals could be redundant or, in other words, they could contain the same information. For example, both visual and proprioceptive cues might provide information about the size of a hand-held object. In the two last decades, it has been shown that the NS can use redundant information extensively to obtain a more robust percept and this process is defined as *sensory integration* (Ernst & Bühlhoff, 2004). The mechanism underlying this integration is described in the seminal work by Ernst & Banks (2002), which demonstrated that by integrating the available visual and haptic cues, the participants obtain a final integrated estimate that is not only lower than that of the single cue but the lowest possible given the noise associated with each cue. This optimal way to humans to integrate visual and haptic information is obtained by performing a weighted average between the cues: visual dominance occurs when the variance associated with visual estimation is lower than that associated with haptic estimation, contrariwise haptic dominance occurs in the opposite case. In other words, Ernst & Banks (2002) demonstrated that the nervous system seems to combine visual and haptic information in a fashion that is similar to a maximum-likelihood integrator.

To empirically demonstrate this theory, the authors investigated cue combination quantitatively. They firstly, determined the variances of the estimates performed within the unimodal conditions. Indeed, noise is inherent in every sensory signal and perception is best thought as a probabilistic process. For example, when asking an individual to estimate the size of an object many times, the exact answers typically vary when measured properly. Accordingly, it is possible to obtain a probability density distribution of the estimated size s based on the responses of the observer (see Figure 1.2). The distribution can be described by the mean $\bar{S}$ and standard deviation σ . The variance (σ^2) represents the variability associated with the estimation of the size. Accordingly, the inverse of the variance σ^2 associated with the distribution define the so-called *reliability* (r) of the sensory cue:

$$r = \frac{1}{\sigma^2}.$$

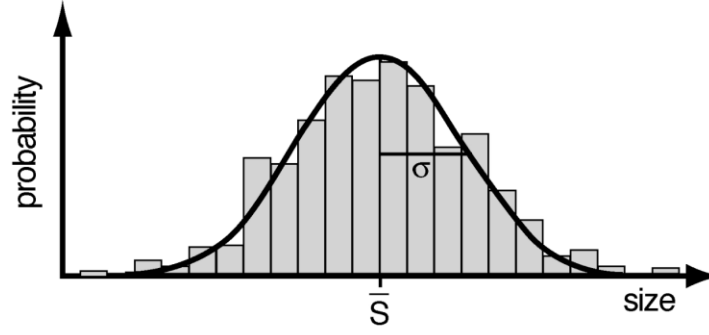


Figure 1.2. Probability Density Distribution of an object's sizes (adapted from Ernst, 2006). On the x-axis the different size estimations, on the y-axis the density of probability with which each of the estimation was chose by the participant. The figure describes the simplest case where the answers are normally distributed and unbiased. The Mean $\bar{S}$ of the distribution and Standard Deviation σ are represented.

Ernst & Banks (2002) estimated the reliability of the sensory cues in unimodal conditions where only the visual s_V or haptic s_H information was available, and in multimodal conditions where the two cues were simultaneously available (i.e. redundant information). In each condition, the authors used a two-alternative-forced choice task (2AFC) to estimate the reliability of the sensory cues in the unimodal and bimodal conditions. At each trial, the participants had to compare a standard stimulus with a comparison stimulus, the size of which varied between trials. Then, they fitted a psychometric function and estimated the discrimination threshold, i.e. the smallest difference between two object sizes that can be reliably estimated. The discrimination threshold, also sometimes referred as the Just Noticeable Difference, is a measure of the reliability of the available sensory cue(s).

The maximum likelihood estimation (MLE) model posits that the integrated signal s_{VH} corresponds to a weighted average between the available sensory cues:

$$s_{VH} = w_V S_V + w_H S_H.$$

where the weight w of each sensory signal is proportional to the reliability of the stimulus:

$$w_V = \frac{r_V}{r_V + r_H} = \frac{\sigma_H^2}{\sigma_V^2 + \sigma_H^2}.$$

$$w_H = \frac{r_H}{r_V + r_H} = \frac{\sigma_V^2}{\sigma_V^2 + \sigma_H^2}.$$

It can be demonstrated that this estimate is optimal in the sense that these weights yield an integrated signal with the lowest possible variance:

$$\sigma_{VH}^2 = \frac{\sigma_V^2 \sigma_H^2}{\sigma_V^2 + \sigma_H^2}.$$

Accordingly, the optimal integration model (MLE) yields *two predictions* that can be computed from the variances of the unimodal estimates and need to be verified experimentally to conclude that the visual and haptic information are optimally integrated. The first prediction is that the JND or discrimination threshold in the bimodal condition should be smaller than the discrimination thresholds in the unimodal conditions and correspond to the variance σ_{VH}^2 predicted by the model. The second prediction relates to the PSE and can be verified when the unimodal sensory cues are incongruent, i.e. when they are slightly different. In this case, the prediction is that the bimodal PSEs should be shifted towards the most reliable sensory modality.

In order to test the model prediction, Ernst & Banks (2002) manipulated the reliability of the visual signal by adding some noise (visual noise levels: 0%, 67%, 133%, and 200%). Further, they included three different bimodal conditions. In the congruent bimodal condition, the sizes of the standard stimulus specified by the visual and haptic cue were the same (i.e., the difference Δ between the visual and haptic cue was 0). Conversely, in the incongruent conditions, a small and not consciously perceivable conflict between the haptic and visual cues specifying the size of the standard stimulus was introduced. In one case, the visual stimulus was slightly larger than the haptic one for all these bimodal conditions ($\Delta = +3$ or $+6$) in the other case, the opposite held true ($\Delta = -3$ or -6). For each experimental condition and level of noise, the responses of the participants were fitted with a cumulative normal probability distribution to obtain a psychometric function representing the probability of judging the comparison stimulus as taller than the standard stimulus. From the psychometric curves two distinct parameters were extracted for each condition: the point of subjective equality (PSE) and the discrimination threshold (Difference Limen, DL) – or Just Noticeable Difference (JND). By definition, the PSE is the stimulus size that is perceived to be taller than the standard in the 50% of the trials. The DL refers to the stimuli, and it corresponds to the amount of changes of a stimulus required to produce a just noticeable difference (JND) in the sensation. It was computed as the difference between the PSE and the stimulus size that was perceived to be taller than the standard in 84% of the trials.

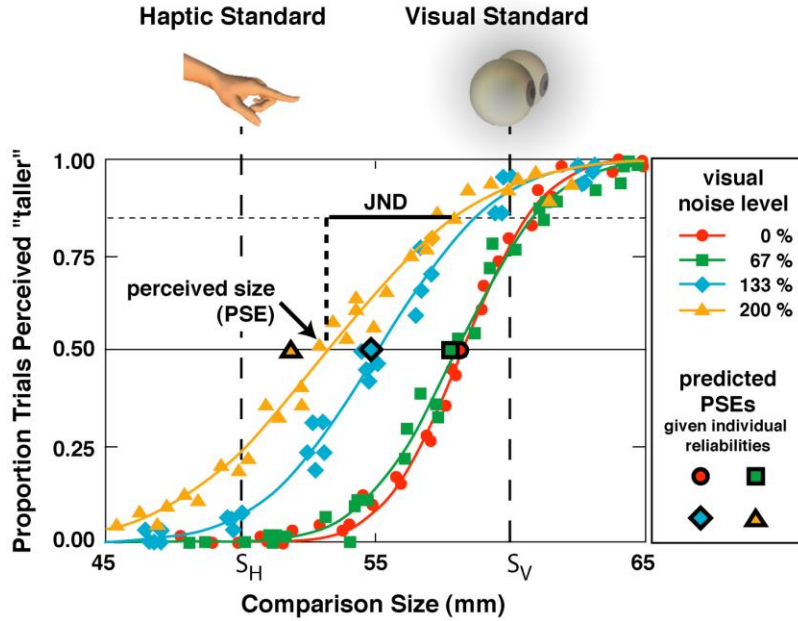


Figure 1.3. Results of Ernst & Banks' (2002) experiment. The picture shows the psychometric curves of the participants for the incongruent bimodal performance of the different blurring levels. The horizontal grey line represents respectively the PSE (solid line) and the JND (dotted line). The colors of the psychometric curves coded the level of visual blurring. The symbols represent the predicted PSEs for each level of blurring following the MLE model. Taken from (Ernst, 2006).

Figure 1.3 represents the average performance in the incongruent condition where the haptic cue specified a smaller size than the visual cue for different levels of visual blurring. In accordance with the MLE prediction, the figure shows that the PSE is shifted towards the haptic size (vertical dotted line on the left) when the visual cues become less reliable. It also shows that the PSEs are close to the values predicted by the optimal integration model.

Overall, the results by Ernst & Banks (2002)'s experiment demonstrated that both the optimal integration predictions were verified, and participants integrated in a statistically optimal fashion visuo-haptic size information.

1.1.2 The Haptic Modality and bimanual Sensory-Motor Integration

The term haptic refers to the greek work *ἅπτω*, to grasp or to touch. The sensor organs of the haptic sense include mechano-receptor in the skin and proprioceptors underlying the sense of position and movement like the muscle spindles and Golgi tendon organs. While sharing much with proprioception and kinesthesia, the haptic sense is more an exteroceptive sense and the perception of properties of objects in the environment.

An essential characteristic of the haptic sense is that is an active sense (JGibson, 1962), meaning that unlike the visual system, where information could also be available with minimal movements, haptic perception requires that one must moves the hands to explore the property of the touched objects. This is obviously necessary when the size of the object exceeds the size of the hand, or the properties of interest, such as the weight or stiffness of an objects, requires an active movement to be perceived (see Klatzky & Lederman, 2003; Lederman & Klatzky, 1993 for reviews).

After Ernst & Banks (2002), many studies have demonstrated that the MLE is an operative strategy widely used by the NS to come up with a coherent and reliable percept to integrate a variety of sensory information (e.g., Alais & Burr, 2004; Bresciani et al., 2005; Gepshtein & Banks, 2003; Knill & Saunders, 2003b).

Of particular interest for this chapter, several studies demonstrated that the principles of multimodal integration apply not only to cues from different sensory modalities but also to different but redundant cues within one sensory modality. For example, Knill & Saunders (2003) investigated whether different visual cues specifying the slant of a plane-stereopsis and texture information are optimally integrated within the visual system. They found that the weight to texture information increased with the surface slant as predicted by the optimal integration model since texture information is very reliable for high slants and unreliable for low slants.

The haptic sense can provide multiple and redundant information about some object's property such as its texture, size, or shape. For example, when exploring haptically the shape of an object, it has been shown not only that both geometrical cue and interaction force provide information about its shape (Robles-De-La-Torre & Hayward, 2001), but also that they are optimally integrated (Drewing & Ernst, 2006). In this case, the geometric cue corresponds simply to the position of the finger on the surface of the object, and the force cue corresponds to the reaction that tend to be perpendicular to the contact surface and also vary with the shape of the object. This research demonstrate not only that the optimal cue integration might occur within a single sensory modality, but also within the haptic modality.

However, there is surprisingly little evidence of optimal integration between the two hands in bimanual action. To some extent, this can be explained by the fact that traditional studies on bimanual behaviors focused on the motor side of intermanual coordination and control (Kelso et al., 1979; Marteniuk et al., 1984) and mainly investigated the limitations of bimanual coordination (Peters, 1985; Spijkers & Heuer, 1995). While a review of this literature is out of scope of this thesis, it is noteworthy that these studies have shown that the control of the two hands tend to be controlled together in bimanual action, though processes might differ depending on the type of bimanual action. Interesting, Ivry et al., (2004) suggested that many of the coordination constraints proposed for bimanual operations might not be linked to the motor system, rather they can be understood by referring to symbolization processes (Ivry et al., 2004)

On the perceptual side, the number of studies that have investigated bimanual perception is limited and did not necessarily focus on bimanual integration. Several studies have explored whether it is easier to compare or discriminate between two stimuli when using one or two hands. Kappers and colleagues hypothesized that using the two hands might make the task easier by allowing a direct comparison of the two stimuli and by avoiding the involvement of memory processes when exploring the two stimuli successively with one hand (review in Kappers, 2011). On the other hand, it is also possible that the performance is lower in the bimanual condition because information might need to be transferred between the two hemispheres and the simultaneous exploration of two stimuli might be more attentionally demanding. In series of studies, Kappers and colleagues did not find support for their initial hypothesis. Participants discriminated the curvature of shapes less well in a bimanual conditions where they explored the two surfaces simultaneously with respect to the unimanual conditions where they explored the two surfaces one after the other (Kappers et al., 1994; Kappers & Koenderink, 1996; Kappers, 2011; van der Horst & Kappers, 2008). Similar results were found by Craig, 1985) in a discrimination task involving Braille-like stimuli. A possible explanation for this result is that the simultaneous stimulation of the two hands might interfere or mask each other. As a matter of fact, Tamè & Holmes (2016) provide an example of such masking by showing that vibrating one part of the body reduces tactile sensitivity on the contro-lateral homologous part. Van der Horst & Kappers (2008) found that a partial after effect in a curvature perception task subsisted when the adaptation and test surface were touched by different hands, which suggests that representation shared by the two fingers might exist in the somatosensory cortex (Iwamura, 2000; Iwamura et al., 1994). Another explanation for this result is that the task might be more attentionally demanding when presenting two different stimuli together. In fact, while not completely excluding possible contribution of masking, Craig (1985) observed that the performance in bimanual condition improved considerably when the subject was told which finger to attend in the bimanual condition. Finally,

there is also some evidence that the transfer of information between two hemispheres might degrade the information and hamper the comparison. For example, Charron et al. (1996) measured the performance in a two-point tactile discrimination in which the examiner touched the palm of the participants with a two-point caliper twice. The task was to report whether the distance between two points was the same or different between the first and second stimulus which were always applied one after the other, either on the same hand or on different hands. They found that for tactile stimuli near the threshold, the performance was better when the touches were applied on the same hand than when they were applied on different hands. This effect can be observed when the two stimuli are difficult to discriminate and a little degradation might have a noticeable impact (Charron et al., 1996). While these studies provide interesting information about the effect that masking, attention or memory can have on performance when comparing to stimuli, they cannot provide information on bimanual integration processes because the task involved the comparison of different stimuli and requires participants to focus on the difference between the stimuli presented to each hand.

To date, as noted previously, only a few studies focusing on bimanual integration processes and they have yielded contrasting results. Squeri et al., (2012) investigated whether information from the two hands was integrated optimally in a curvature perception task, where a bilateral robot moved the observer's hand(s) passively along the arc of a circle. They found no significantly different performance in the bimanual conditions with respect to the unimanual conditions. Panday et al., (2013) asked observers to discriminate the size of large curved panels forming cylindrical shape (Panday, Tiest, et al., 2013). The cylindrical stimuli lay on a table and the side(s) were explored with one or both hands. They found better performance in the bimanual condition. However, in a control condition where the observers had to report the distance between two flat surfaces, they found no difference between the performances in the unimanual and bimanual conditions. To explain these results, the authors proposed that curvature cues (i.e. 2nd-order cues according to Pont et al., 1997) related to the deformation of the hand on the cylinder might be integrated but not positional information (i.e. 0th-order cues; Pont et al., 1997) related to the position of the hand in space. They hypothesized that 2nd-order cues consistent with cylindrical shape would suggest to the observer that the hands were touching the same object, that is the information coming from the two hands are redundant and thus should be integrated ([as reviewed in Section 1.1.1, Chapter 1](#)). On the contrary, 0th-order cues would not be able to elicit the impression that the sensory information from the limbs refer to the same source of information, thus making cues integration unnecessary. Accordingly, they attributed the absence of integration in Squeri et al. (2012) to the fact that participants experienced only 0th-order position cues while the robot moved one or both of their hands along the curved trajectory. This hypothesis could also

explain the results of a more recent study by Wong et al. (2014), in which in a position discrimination task bimanual proprioceptive acuity was not found to be significantly better than the best unimanual performance (Wong et al., 2014). Finally, Plaisier & Ernst (2012) used virtual reality to assess the discrimination performance in a task of virtual boxes stiffness perception. They found that participants were better in discriminating during bimanual perception rather than unimanual ones. Coherently with Panday et al. (2013) the authors suggested that integration might have occurred because the participants could see that they touched a single object, which might have informed them that the bimanual information had a shared source. Noteworthy, they also hypothesized that active exploration, which is necessary to probe the stiffness of the object, might have promoted bimanual integration.

In a recent study, we hypothesized that the reason why positional information was not integrated is that the objects touched by the participants was grounded (Xu et al., submitted, see [Appendix A](#) for the complete manuscript; see Xu & Baud-Bovy, 2017 for a preliminary report).. In absence of vision, the haptic system does not have direct evidence of touching the same object with the two hands when the object is grounded because force is not transmitted between the two hands. In this study, participants had to estimate the size of a large pair of pliers by opening or closing it. The results of this study demonstrated that participants discriminated the pliers' size better when they were free to move the pliers. In particular, we surmise that the boosting effect of movement on optimal integration is caused by the fact that holding the experimental stimuli with the two hands in the dynamic condition could enhance the assumption that both hands are holding the same object. The idea is that the motion coupling and force transmitted between the two hands might be used by the brain as a sign that the information coming from the two hands originates from the same source, are thus redundant and should be integrated ([see Section Paragraph 1.1.1, Chapter 1 for a review on sensory integration mechanism](#)).

Overall, in this [Section 1.1](#), I highlighted the yet-to-be-fully-understood questions emerging from bimanual integration research. In particular, the ongoing questions consists in: 1) under what conditions optimal integration of information coming from the two hands is possible and 2) what is the effect of movement on such bimanual operations. These questions are addressed in [Chapter 3](#), where we report the results of an experiment on bimanual integration of box-like objects.

1.2 Touch and the Body

The term soma derives from Ancient Greek $\sigma\omega\mu\alpha$, which indeed means body. Thus, the immediate relations between the somatosensory system and the body is evident. Indeed, the skin itself is coextensive with body surface, it corresponds to the boundary between the outside world and the inside of ourselves, and it is formed by somatosensory receptors. Contrary to what happens with the other senses, it is impossible to touch without being touched (Merleau-Ponty, 1942), for this reason touch has been recognized as a deeply social sense (Ratcliffe, 2013). This reciprocity is primitive and allows us to explore the environment, even before we born.

In 1927 Martin Heidegger introduced the idea of a circular interaction between body and the mind in his work “Sein und zein” (i.e. “Being and Time”; Heidegger, 1927). From the 1940s, the concept found expression in Merleau-Ponty’s writing, who was the first to propose a double definition of the body: on the one hand as a physical structure, on the other hand as the environment of cognitive processes (Merleau-Ponty, 1942). The dual nature of the body has long been understood, and many later works that had capital importance in the fields of psychological and cognitive sciences underlined and extended the importance of the concept (Maturana & Varela, 1987; Piaget, 1952; Vygotsky, 1967). These studies redefine the central role of the body in human existence, and shows its pervasiveness in our perceptual experience. The importance to clarify the way we refer to the body has a longstanding story (Lhermitte, 1942). At a physical level, the body is the essential instrument allowing the interaction with the external environment, through all the senses and movements. However, like any other item, the body can be the object of our reflections, and we construct and store its representation in our brain.

Clinical phenomena, such as phantom limb perception in amputees or spinally injured individuals, or heautoscopy or other out of body experience are the clear expression of the dissociation between the physical body and the way we mentally represent it. The need for a model of such representation has long been recognized. However, a widespread confusion both terminological and conceptual, has characterized the nature and the properties of the concept of body representation (Frederique de Vignemont, 2010; Gallagher, 1986). Based on the clinical observations, a postural model of the body namely “body schema” was proposed by the neurologists Henry Head and Gordon Holmes. It was defined as “*a postural model of ourselves which constantly changes. Every new posture or movement is recorded on this plastic schema, and the activity of the cortex bring ever fresh group of sensations evoked by altered posture into relation with it*”. In this same work, the authors proposed the existence of another model associated with touch localization. They stated: “*In the same way, recognition of the locality of the stimulated*

spot demands the reference to another “schema.” [...] This faculty of localization is evidently associated with the existence of another schema or model of the surface of our bodies which also can be destroyed by a cortical lesion” (Head & Holmes, 1911). Afterwards, the terms body image and body schema were used interchangeably by (Schilder, 1935) to refer to *“the picture of our own body which we form in our mind, that is to say, the way in which the body appears to ourselves”*. Together with the physiological basis of the body image, such the postural and tactile impressions, also the libidinous and sociological aspects linked to the body image were discussed in his work (Schilder, 1935). Even, a unique term “body image schema” was proposed (Fisher & Abercrombie, 1958; Fisher & Cleveland, 1958), and many alternative definitions were presented by subsequent authors (Gallagher, 1986; Gerstmann, 1942; Gibson, 1966). Despite its serious consequences on the study of body experience, the confusion on the adoption of these terminologies can be understood easily if one considers all the possible modalities that can be used to relate to the body. As previously seen, several authors tried to propose model of body based on clinical evidence. For example, many works based on the principle of double dissociation of body information processing (Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu et al., 1991), or of memories mechanisms (e.g. short vs long term memory; (O’Shaughnessy, 1980), or of the reference body (e.g. own vs other body; (Felician et al., 2003). Another important aspect that has been used to modeling body representation has its roots in the Action-Perception distinction (Dijkerman & de Haan, 2007; Goodale & Milner, 1992), and the body representations are defined based on their different functional role (Gallagher, 2006; Head & Holmes, 1911). Given the focus of this thesis on the sense of *touch*, I will now focus on the body models which highlight the interdependence between the body and somatosensory experience.

1.2.1 Somatosensory models of the body

Longo et al., (2010) proposed a model of somatoperceptual information processing (Figure 1.4). The term “somatoperception” describes higher-level percepts of the body and objects contacting the body, and it was used in contraposition with the well documented investigation of the basic mechanisms of somatosensory processing, defined as somatosensation. Indeed, the idea was not to propose a neural circuit model of somatic information processing, rather the aim was to present a model of the abstract knowledge and attitude about bodies defined as “somatorepresentation”.

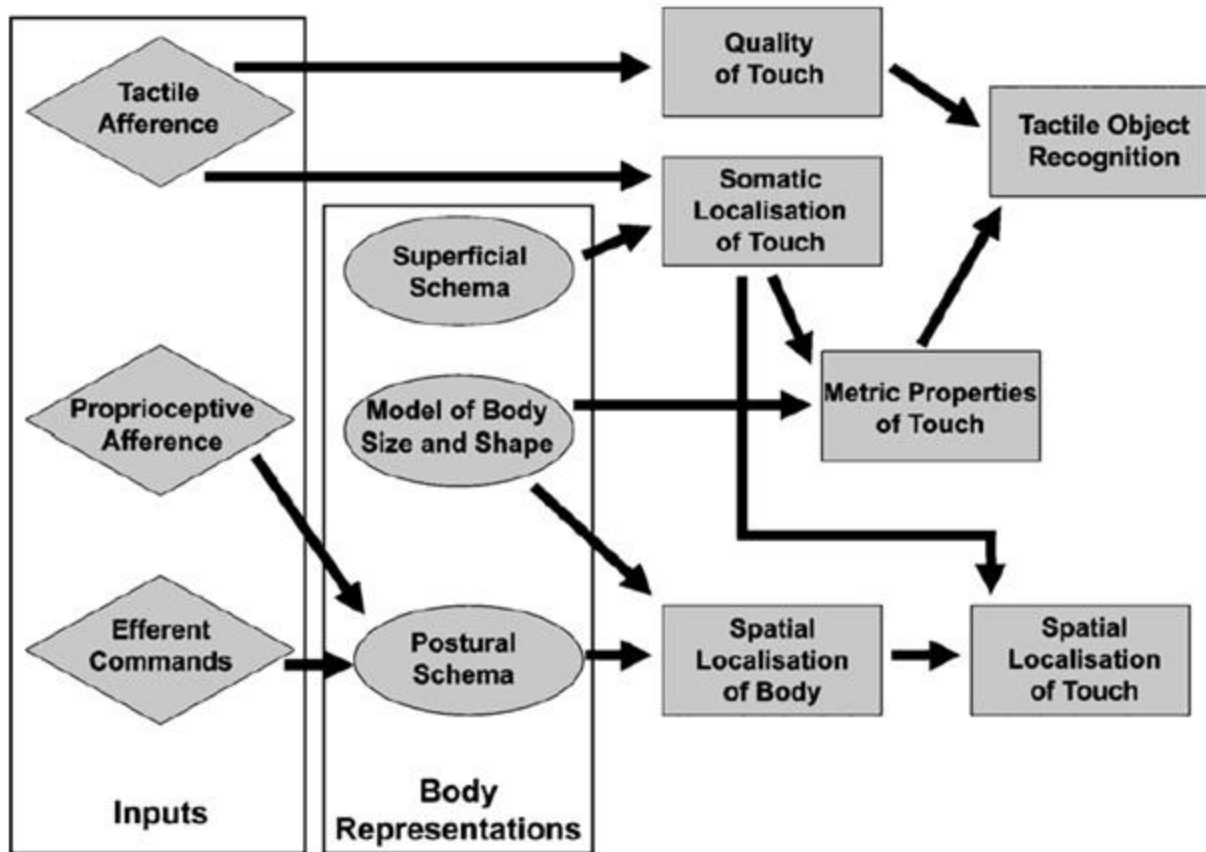


Figure 1.4. Model of somatoperceptual information processing. The diamond represents the inputs, the ovals represents the different representation of the body stored in the mind, while the rectangle represents the perceptual processes (taken from Longo et al., 2010).

When we try to chase a fly that has landed on our left arm, several processes are set in motion. First, we perceive some specific sensation property (e.g., we feel touch and not vibration sensation). Then, thanks to the perceived size of the object touching the skin, we are able to distinguish if it is the fly we want to get rid of, or a cat or another animal. We also know where the fly has landed on our skin, and we can identify its position in external space. Finally, we know precisely the location of the right arm, which we will use to drive away the insect. The model provided by Longo et al. (2010) includes all these basic processes: quality of touch, metric properties of the touching object, somatic localization of the touch on the body or in the external space, spatial localization of the body. The black rows in figure 1.4, show the link between the somatic percepts and the Mental Body Representations (MBRs) proposed as sub-serving each of these.

As visible from figure, the quality of touch is the only somatoperceptual information that is independent from any MBR, and it connects directly with tactile afferent information. Conversely, the ability to localize the touch on the body surface links with both tactile afferent information and the superficial schema MBR. As previously mentioned, the existence of such a MBR, was proposed based on the observation of sensory processing dissociations between the ability of the patients to localize the touch and their ability to report whether they were touched or not (Head & Holmes, 1911). Other clinical studies reported cases of patients performing systematic localization errors in which the representation of the hand was partially preserved but shifted in an altered position (Rapp et al., 2002). Together with the outcomes from TMS research (Porro et al., 2007), the clinical results suggest that the localization of a stimulus within a somatotopic map, is not sufficient to localize the stimulus on the body, thus a cognitive representation of the body is needed in order to accomplish these tasks.

The MBR called postural schema corresponds with the definition of body schema given by (Head & Holmes, 1911) and presented in the previous section. According to their definition, this schema allow one to localize the position of the body in the space (somatic percept depicted as rectangle in Longo's et al. 2010 model, Figure. 1.4). It is continuously updated based on afferent proprioceptive information from muscle, tendons and joint and skin mechanoreceptors and efferent motor commands specifying new movements (inputs represented as diamonds in Longo's et al. 2010 model). This system, however, does not suffice to determine the absolute position of the body in external space. To overcome the gap, the Nervous System must merge the information about the location of the body in the space with information about the dimension of the parts interconnected by the different joints. This metric information cannot derive from the external environment, thus they have to stem from a stored representation called by Longo and colleagues: Model of Body Size and Shape. This metric representation is also needed in order to perceive the size of external objects. For example, in the Tactile Estimation Task (TET) an individual is touched in two different points on his or her arm by an experimenter, and is asked to reproduce the perceived size between the two points (Green, 1982; Keizer et al., 2011, 2012). Mechanoreceptors on the skin allow to localize the position of the two points touched, but do not provide body size information per se. Thus, the localized touch has to be referred to a MBR in which this metric information is included (Longo, 2015; Longo et al., 2010).

Around the same time, (Serino & Haggard, 2010) proposed an analytical model of the relation between the touch and the body (Figure 1.5). The model shows the connection between the mental representations and the afferent information coming from the external world or from the body itself.

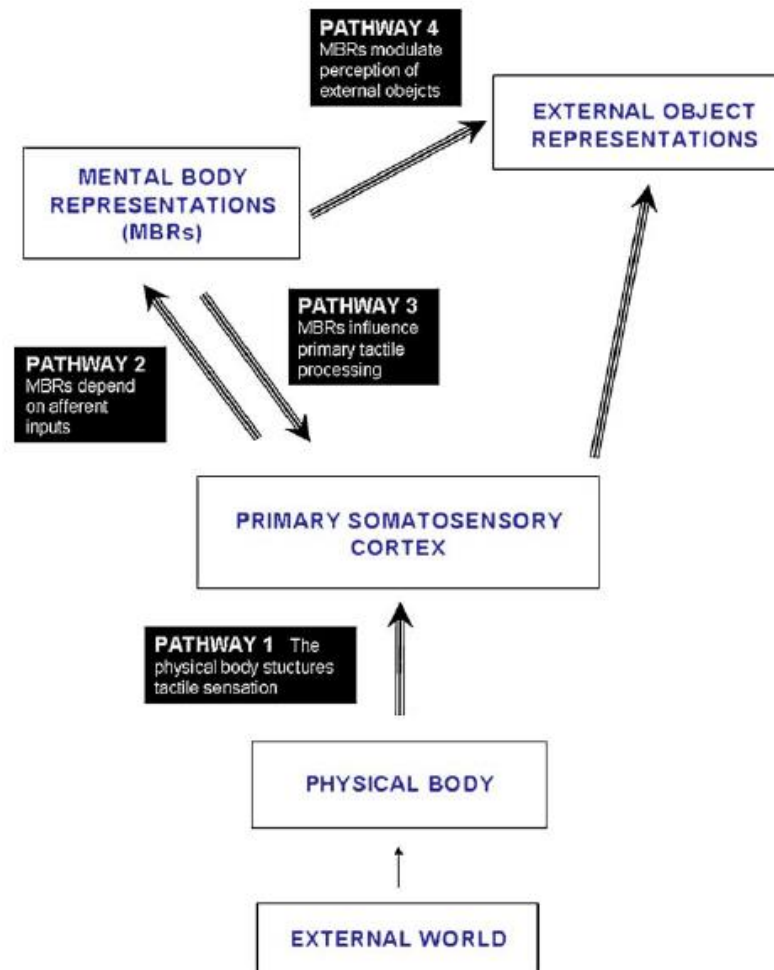


Figure 1.5. Analytical model of the relation between touch and the body proposed by (Serino & Haggard, 2010). The black boxes show the four pathways identified by the authors in order to explain the relation between the body and the stimuli received on it, and the external world and the representations of the body and the external objects that are built upon these. The arrows show the direction of the pathways.

The first Pathway represents the physical structures receiving light touch information coming from the external environment through contact with the body, and conveying it to the primary somatosensory cortex (SI). The information is transmitted through the dorsal column of the spinal cord and the thalamus to the contralateral SI. The well-known “cortical homunculus” represents the topographically organized map of the contralateral side of the body where the SI neurons of each hemisphere encode the properties of the tactile stimuli (Penfield & Boldrey, 1937). As reported in the original work, the homunculus appears as a “*grotesque creature*”; in fact, the body parts are not represented proportionally to their real size. Neurons with small receptive fields and

high density innervate the body parts characterized with the highest tactile acuity, and thus represented as larger in the homunculus (e.g. the lip, or the tip of the fingers). Many clinical conditions, such as deafferentation, amputation, etc., show alterations that can be produced in the sensory experience when such a pathway is disrupted, and the SI is stimulated in absence of peripheral inputs (for a review Serino & Haggard, 2010).

The second pathway links the signals in SI with the MBRs, which are defined as: “*abstract representation of one’s own body, derived from sensory input but capable of being dissociated from it, and playing a functional role in perception and/or action*” (Serino & Haggard, 2010). The model posits the existence of different types of MBR (i.e. body schema and body image), which receive information from SI but are also updated with multisensory information (Costantini & Haggard, 2007). Evidence such as the altered experience of the body after anesthesia (Gandevia & Phegan, 1999) or during the Rubber Hand Illusion (RHI; Ehrsson et al., 2005; Tsakiris & Haggard, 2005) demonstrates the effect of tactile information on the MBRs. However, many researchers found that vision of the body improves individuals’ tactile performance, by reducing reaction times (Tipper et al., 1998) or improving the tactile acuity (Taylor-Clarke et al., 2002). Accordingly, a third Pathway showing the reciprocal influence of the MBRs on the tactile processing has been included in the model. Finally, the fourth pathway identified by (Serino & Haggard, 2010), connects the MBRs to the representation of external objects. As previously mentioned, sensory information does not provide direct information about the size of the touched object. Accordingly, if we are able to report the perceived size of objects touching our skin, and if our judgment of size is affected by body sensory signals coming from different modalities, then the tactile stimuli has to be referred to a stored and multisensory map of it (Frédérique de Vignemont et al., 2005; Taylor-Clarke et al., 2004).

The two models mutually agree on the existence of several cognitive representations of the body. These representations are recognized as more than one, since they appeared to subserve different aspects of the sensory experience. Further, both models provide that the processing of metric features of the external objects is mediated by such mental representations of the body, and thus: “*Being touched by an object does not provide any information about my own body. Rather, my own body provides a reference or context against which the tactile object is perceived.*” (Serino & Haggard, 2010).

1.2.2 How to assess Mental Body Representations

For a long time, the study of body representations focused on the body image, i.e. the conscious perception, experience and attitude towards one's own body size and shape (Cash & Brown, 1987; de Vignemont, 2010; Longo & Haggard, 2012). In order to assess the perceptual and subjective dimensions included in the definition of body image, mainly questionnaires, structured-interviews or visual tasks were exploited (for a review see Gardner & Brown, 2011). However, new techniques to measure other implicit body representations had been developed, and mainly involves the somatosensory modality. A vast number of studies use the “error of localization” as method to assess the dissociation between implicit body representations and the conscious body image. For example, one of the most famous perceptual illusion used to study body perception is the Rubber Hand Illusion (Botvinick & Cohen, 1998). During the illusion, participants see a fake hand in front of them while their real hand is hidden from their view, and the real and fake hands are simultaneously stroked with paintbrushes. Results show not only that the participants have the impression to feel the touch on the viewed (fake) hand, but also that when asked to point to the perceived position of their real hand they misplaced it in the direction of the fake hand (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). The illusion has been extended to other body parts such as foot (Crea et al., 2015; Stone et al., 2018), tongue (Michel et al., 2014), or when including the entire body, it is known as full body illusion (Lenggenhager et al., 2007). Other studies have exploited the differences between the actual and perceived localization of tactile (painful or innocuous) stimuli, and proposed to use the mislocalization between the two to assess the perceptual map of the body (Mancini et al., 2011; Trojan et al., 2006). Alternatively, other researchers have used kinematic recordings to investigate participants' movements in response to obstacle in the environment. For example, the shoulders rotating point to fit through a door during locomotion was investigated in order to check whether body schema was impaired in women with Eating Disorders (Keizer et al., 2013). Also, “possibility judgment” was used to investigate the predicted effects of actions, considered as fundamental to optimize motor decisions (Wolpert et al., 1995). Similarly to the previously mentioned study, Guardia et al., (2010) asked the participants to imagine whether or not they could fit through a given aperture without turning the shoulders (Guardia et al., 2010). With the same aim of assessing body-scaled action a subsequent study: the Hoop Task, was designed. The participants had to step into a hoop whether they think they could fit through it (Engel & Keizer, 2017).

In contrast to previous studies focusing on the difference between the expected and perceived position, Longo & Haggard (2010) proposed a localization task providing a metric representation

of body parts, i.e. the so called body model (Longo et al., 2010). The task requires that the participants use a long baton to point at the perceived position of landmarks placed on the contralateral hidden hand such as the tip of the fingers or the positions of the knuckles. The paradigm allows the experimenter to obtain information about the subject's private representation of the hand parts (landmarks), independently from the actual position of the hand. The results of this initial study showed a distortion in the profile of the hand of healthy individuals as wider and squatter than it actually is, which has been confirmed by several subsequent studies (Galigani et al., 2020; Longo, 2017; Saulton et al., 2016).

Another interest task used to assess the body metric consists in the distance estimation of dual tactile pressures. Seminal studies demonstrated that the perceived distance between tactile stimuli varies as a function of the body frame and stimuli orientation (Green, 1982; Weber, 1996). The classic interpretation of this effect is that the distortion is a reflection of the size of representation in the somatosensory cortex. However, homuncular distortions and the spatial density of mechanoreceptors does not explain Weber's illusion fully (Longo & Haggard, 2011; Taylor-Clarke et al., 2004). Indeed, several studies showed that changes in the perceived size of the body induced through different sensory modalities, alter the magnitude of this perceptual distortion (Frédérique de Vignemont et al., 2005; Taylor-Clarke et al., 2002, 2004). Overall, this evidence suggests that the somatosensory system organization shapes tactile distance perception. Recent studies suggest that also the posture of the body could affect the tactile perception. Hamada & Suzuki (2003, 2005) showed that neural interaction in SI and SII is modulated by the hand dynamic, suggesting that the actual posture of the body is related to receiving somatosensory input (Hamada & Suzuki, 2003, 2005). More recently, behavioral studies showed that changes in the internal posture of the hand from an “*apart posture*” (i.e. fingers spread) to a “*together posture*” (i.e. fingers pressed together), do alter the perception in positional perceptual maps and tactile distances. In particular for tactile objects perception, the alteration relates to the absolute distance in both the proximo-distal and medio-lateral directions, but not the relative perception between the two axes (Longo, 2017). Furthermore, this modulation has not been extended to other body parts in which the size of the stimuli could be more dramatically be influenced by change in posture.

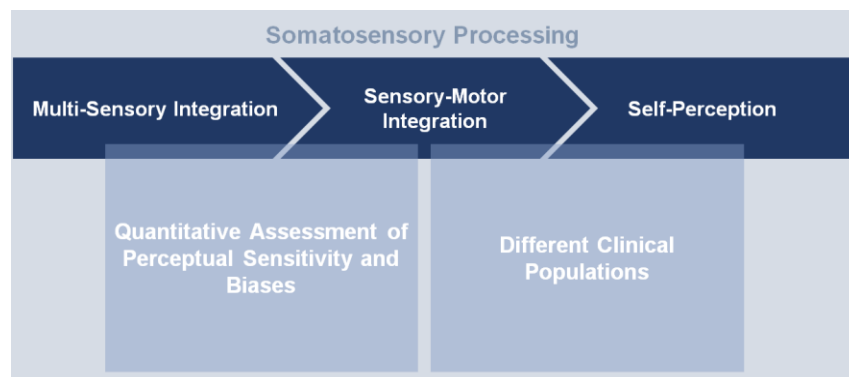
Finally, as reviewed in [Section 1.2.1 \(Chapter 1\)](#), the processing of external objects involves all the body representations presented in Longo et al.'s (2010). To shed lights on what somatosensory processing lead to the modulation between posture and touch, and thus to better understand the interaction between different body representations, further studies should be able to investigate the single contribution of each of these while performing a same task.

1.3 Thesis Outline

In this introduction, I reviewed the theoretical background underlying this work and highlighted the current achievements and limitations in the modelling of the somatosensory integration processing and somatosensory body representations. In particular, I emphasized the general principle that human nervous system combines sensory cues in an optimal manner and the benefits of such phenomenon to come up with an unambiguous percept of the environment (Ernst & Banks, 2002). Then, I have presented two models of the cognitive mechanisms by which humans represent their body and how tactile information interact with such representations (Longo et al., 2010; Serino & Haggard, 2010). As such, **the aim of this thesis is to investigate how these mechanisms apply to different context and modalities, “at the baseline” in healthy, and in clinical populations affected by somatosensory deficits** (Figure 1.6). To quantitatively assess perceptual distortions and alterations in the somatosensory processing we adopt a psychophysical approach adapting standard methods for sensory integration assessment or designing ad-hoc paradigms to assess body representations.

Figure 1.6. A psychophysical approach to Touch. The figure represents the main aspects and n this thesis, which consider the somatosensory processing of information related to: i) Multi-Sensory Integration; ii) Sensory-Motor Integration; iii) Self-Perception.

Chapter 2 investigates whether and how somatosensory feedback is integrated with visual one in two different clinical populations with somatosensory deficits. In the first part of the chapter, the



mechanism is observed in a transradial amputee provided by intraneural stimulation through a bionic hand prosthesis. In the second part, we tackle populations reporting body concerns. In particular we compare the performances of women with Anorexia Nervosa (AN) Restricting Type diagnosis in a severe state of malnutrition, with that of other two groups of gender- and age-

matched participants with a healthy weight and no psychiatric disorder. The participants of this control group are divided into two groups according to their level of body satisfaction score: a group that is as concerned about their bodies as much as patients with AN, and a group with no concerns.

Chapter 3 reports the results of two studies where we assessed the effect of movement on the perception of the size of an object held between the two hands. In the first study, we investigated whether lifting the object might enhance the integration of information coming from the two hands and tested the predictions of the optimal integration model in static and dynamic condition. In the second study, we measured the effect of movement on the ability to perceive a brief change of dimension of the hand held object.

Chapter 4 investigates the perceptual distortions in a task that requires combining information from the different Mental Body Representations underlying touch. The study presents a new paradigm assessing tactile distance estimation and the position sense. By comparing the biases observed in these tasks we aimed to investigate how information about the position of tactile objects on the skin surface was integrated with information about the arm posture.

Chapter 2

Multisensory Integration of Somatosensory Feedback

One's own body is the most multisensory "object" in the world. The multisensory integration of redundant sensory signals coming from different senses is crucial to come up with robust and unambiguous percept of the environment. In this chapter, we assess with a rigorous psychophysical method, the integration of somatosensory information with other senses (i.e. vision) in different clinical populations. In particular, we investigate this phenomenon in people suffering from psychiatric disorder (e.g., Anorexia Nervosa) and from limb loss (e.g., transradial amputation). In both these conditions, disruption of the integration processing have been suggested.

In the first section, we evaluate the integration of artificial information coming from a bidirectional hand prosthesis with residual senses (i.e. vision) in an upper limb amputee. A major goal of limb neuroprosthetics is to restore bodily functions and experiences by designing artificial limbs that act, sense and are perceived ("neurointegrated") like real limbs (Raspopovic, 2020). Current artificial limbs are used only sporadically because they are of limited utility in daily life and are not yet perceived as real limbs. Here, the task of the participant involves the discrimination of objects' size while grasping them with the prosthesis. The amputee individual shows to optimally integrate somatotopic artificial information even not completely natural. The results present in this section are useful not only for neuroprosthetic design optimization, but also to better understand the brain processing of multiple sensations (Risso et al., 2019).

In the second section, we evaluate visual, tactile and visuo-tactile integration of objects in a sample of patients with Anorexia Nervosa (AN) and women with and without body concerns. The few previous studies on Eating Disorders which did not focus on visual and attitudinal aspects, found evidence for the absence of a generalized perceptual deficit. Given the receiving of presumably accurate sensory feedback, the origin of the perceptual body distortion in Anorexia Nervosa, remains mysterious. The task asks the participants to discriminate objects' shape. The results do not support the multimodal integration impairment hypothesis. Rather, we find that patients with AN show a double deficit in 1) objects shape discrimination and 2) objects shape distortion. In particular, the latter bias suggests a possible distortion of the cognitive maps of the body mediating the processing of metric features of the external objects. The transferability of this bias to the sample of healthy women with body concerns suggests that higher level factor, such as body

satisfaction could affect these cognitive body maps. The study provides insights for a better comprehension of the pathology and encouraging results to support the clinical practice (Risso et al., 2020).

2.1 Optimal Integration of Intraneural Somatosensory Feedback with Visual Information: a single case study

The contents of this section are adapted from the following publication: **Risso***, G., Valle*, G., Iberite, F., Strauss, I., Stieglitz, T., Controzzi, M., ... Micera+, S. Baud Bovy +, G. (2019). Optimal integration of intraneural somatosensory feedback with visual information: a single case study. *Scientific reports*, 9(1).

The paper was awarded with the “**Franco Purghé Award 2020**” in psychology of perception or psychophysics.

Collaboration with: Sant’Anna School of Advanced Studies, EPFL and Policlinico A. Gemelli

Personal contributions as co first author: conceived the experiments, participated in the development of the experimental setup and the integration of the bidirectional hand prosthesis with the setup. I acquired the data in all the experiments, performed the data analyses, and wrote and revised the manuscript replying to the reviewers’ comments.

*,+ equally contribution

2.1.1 Abstract

Providing somatosensory feedback to amputees is a long-standing objective in prosthesis research. Recently, implantable neural interfaces have yielded promising results in this direction. There is now considerable evidence that the nervous system integrates redundant signals optimally, weighting each signal according to its reliability. One question of interest is whether artificial sensory feedback is combined with other sensory information in a natural manner. In this single-case study, we show that an amputee with a bidirectional prosthesis integrated artificial somatosensory feedback and blurred visual information in a statistically optimal fashion when estimating the size of a hand-held object. The patient controlled the opening and closing of the

prosthetic hand through surface electromyography and received intraneural stimulation proportional to the object's size in the ulnar nerve when closing the robotic hand on the object. The intraneural stimulation elicited a vibration sensation in the phantom hand that substituted the missing haptic feedback. This result indicates that sensory substitution based on intraneural feedback can be integrated with visual feedback and make way for a promising method to investigate multimodal integration processes.

2.1.2 Introduction

Nowadays there is considerable evidence that the brain integrates redundant information, routinely and unconsciously, in a statistically optimal manner (Ernst, 2012; Ernst & Banks, 2002; Helbig & Ernst, 2007; Hillis et al., 2004; Körding et al., 2007). The optimal integration hypothesis states that the best estimate concerning the attribute of interest corresponds to a weighted average between the cues (Ernst & Banks, 2002)

$$S_{VH} = w_V S_V + w_H S_H \quad (1)$$

where s_V and s_H are the visual and haptic size cues. The weights w_V and w_H ($w_V + w_H = 1$) should be proportional to the reliability of the stimulus:

$$w_V = \frac{R_V}{R_V + R_H} \quad w_H = \frac{R_H}{R_V + R_H} \quad (2)$$

where the reliability $R_i = 1/\sigma_i^2$ is simply the inverse of the noise (variance) of the corresponding cue. Assuming that the visual and haptic cues are independent and normally distributed, it can be shown that the optimal (or Maximum Likelihood) estimate S_{VH} that combines the two cues has a variance:

$$\sigma_{VH}^2 = \frac{\sigma_V^2 \sigma_H^2}{\sigma_V^2 + \sigma_H^2} \quad (3)$$

that is not only lower than that of the single cues but the lowest possible given the noise associated with each cue. It is easy to show that the improvement brought by the integration is maximal when the two sensory modalities are equally reliable (Ernst & Banks, 2002; Körding et al., 2007). The noise associated with each channel can be determined in behavioral experiments by measuring the Just-Noticeable-Difference (JND), i.e. the smallest difference between two stimuli that can be discriminated reliably. Accordingly, the optimal integration model (MLE) yields two predictions

that can be computed from the variances of the unimodal estimates and need to be verified experimentally to conclude that visual and haptic information are optimally integrated.

Recently, implantable neural interfaces have yielded promising results in restoring haptic sensation to the amputee. Both invasive and non-invasive methods have been developed to restore sensory information to prosthesis users in the last decade (Clemente et al., 2016; D’Anna et al., 2017; Graczyk et al., 2016; Marasco et al., 2018; Raspopovic et al., 2014; Tan et al., 2014). In particular, various types of neuroprostheses have been developed to recover lost functionalities at different levels of the nervous system (Angeli et al., 2014; Benabid et al., 2009), including the restoration of peripheral sensory feedback thanks to bidirectional upper limb prostheses (Davis et al., 2016; Graczyk et al., 2016; Oddo et al., 2016; Raspopovic et al., 2014; Tan et al., 2015). Several studies have shown that peripheral nerve stimulation through neural interfaces can restore somatotopic and modality-matched sensations (Graczyk et al., 2016; Tan et al., 2014b) showing improvements in prosthesis control (Tan et al., 2014b; Wendelken et al., 2017) and embodiment (Rognini et al., 2018; Schiefer et al., 2016) even in long term applications (Petrini et al., 2018; Tan et al., 2014b). Sensory feedback delivered by these new neural interfaces can be used to identify the stiffness and shape of objects (Raspopovic et al., 2014), to discriminate the spatial coarseness of texture surfaces (Oddo et al., 2016) and to improve prosthesis control (Petrini et al., 2018; Tan et al., 2014b).

One key challenge for the adoption and commercialization of recent multifunction upper limb prostheses is the integration of the sensory feedback from different sensory modalities (Ning Jiang et al., 2012). Often during everyday life, prosthesis users’ ability to regulate their actions depends on multisensory stimuli such as the audible noise from the motor, pressure information from the socket or visual information about the completion of a movement, which require attention from the user unlike multi-sensory feedback normally used in hand control (Antfolk et al., 2013; Atkins et al., 1996; Biddiss & Chau, 2007).

The objective of this study is to test whether intraneural stimulation substituting natural haptic feedback is integrated optimally with visual feedback. To that end, we adapted the size discrimination task used by Ernst and Banks (Ernst & Banks, 2002) and prepared a set of cylinders that fitted the prosthetic hand well (see Methods). The task consisted in judging which of two hand-held cylinders appeared larger. The participant wore a headset with white noise to suppress audio cues and custom eyeglass to blur vision of the cylinder.

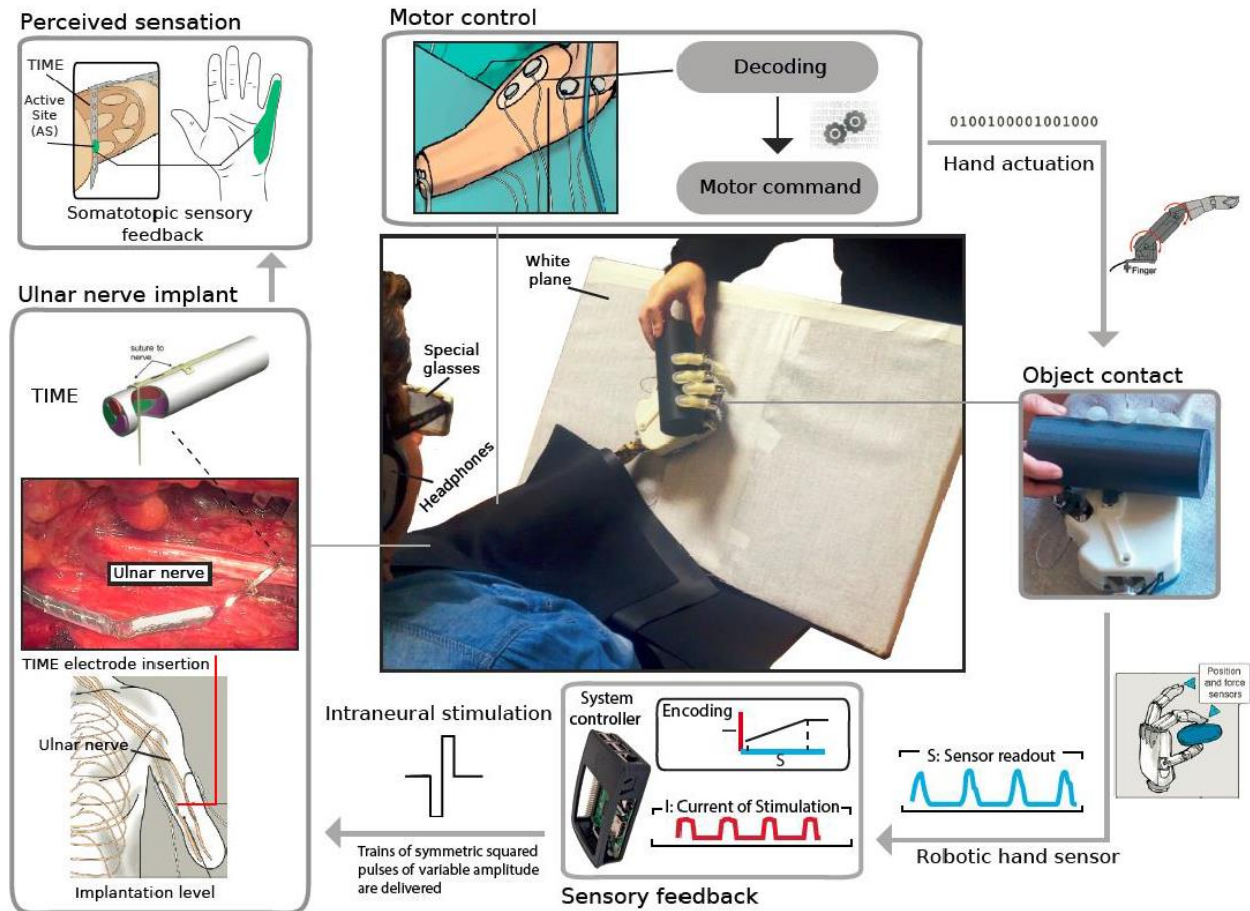


Figure 2. Experimental setup. The figure shows the white plane which the robotic hand leans on. The patient wore special glasses to degrade her vision and headphones to hear white noise during the experiment. The robotic hand is controlled using sEMG activity acquired from the subject's dorsal and ventral forearm muscles, and classified into distinct motor commands (top). As the robotic hand closes its fingers around the object, both force and position are measured in real time (right). Information about force and position is then used to deliver stimulation pulses (somatosensory feedback; bottom). Somatosensory perception is provided by eliciting a sensation that corresponds to the finger and palm that are touched (top left). The sensory stream is delivered by using intraneural stimulation through TIME electrodes implanted in the proximal part of the ulnar nerve (left). The TIME implant is inserted transversally through the exposed nerve fascicles.

Information about the object size was provided visually and/or by stimulating electrically the nerve structures still present in the amputated arm. Specifically, we used a sensory substitution approach based on intraneural stimulation of the ulnar nerve with TIME electrodes (Boretius et al., 2010; Raspopovic et al., 2014) to provide a somatosensory cue about the object size (see Methods). The somatosensory feedback was triggered by the contact of the robotic hand with the object and lasted

until the object was released. The amplitude of the intraneural stimulation was proportional to the object size and thus corresponded to robotic hand aperture for the duration of the grasp.

Before starting the experiment, we characterized the sensations evoked by the neural stimulation (see ‘Somatosensory stimulus physical and perceptual characterization’ section). Perceptually, the stimulus felt like a vibration of the ulnar side of the phantom hand. The patient did not report any delay between the somatosensory and visual feedback when grasping an object. We adjusted the intensity of the neural stimulation to obtain a somatosensory discrimination threshold similar to those obtained by healthy subjects (Gaydos, 1958). We also adjusted the level of blur to obtain a visual discrimination threshold similar to the somatosensory discrimination threshold in order to maximize the margin of improvement predicted by the optimal integration model in the bimodal conditions (Ernst & Banks, 2002; Helbig & Ernst, 2007). The participant underwent a brief learning session (<10 min) to help map the stimulation intensity to the object size. We first instructed the participant to explore the new information by looking at the robotic limb while it was passively opened and closed. Then, we turned the control on and instructed the participant to actively explore the environment, grasping various objects and performing opening and closing movement with the prosthesis. The participant quickly expressed confidence in interpreting the sensation, as well as a readiness to initiate the trials.

In the experiment, each trial consisted in the presentation of two cylinders to the participant by placing them in the robotic hand successively (Figure 2). The diameter of one cylinder, i.e. the comparison stimulus, varied from trial to trial (between 55 and 65 mm) while the diameter of the other cylinder, i.e. the standard stimulus, did not vary across trials (60 mm unless a conflict was introduced between the sensory cues, see below). During each presentation, the participant closed and reopened the hand with the cylinder using a voluntary EMG command. At the end of each trial, the participant was asked to indicate which cylinder felt larger (two-interval forced-choice procedure).

The experiment included two unimodal and three bimodal conditions. In the unimodal somatosensory condition, the participant closed her eyes during the whole trial while the information about the cylinders’ size was conveyed by neural stimulation of the ulnar nerve. In the unimodal visual condition, the participant did the same with eyes open, and the ulnar nerve was not stimulated. In the bimodal conditions, visual and somatosensory information was provided simultaneously and could be congruent or not. The somatosensory and visual cues of the standard stimulus indicated a 60 mm cylinder diameter in the congruent condition or slightly conflicting diameters in the incongruent conditions (60 ± 2 mm). The comparison stimulus always provided congruent visual and somatosensory information.

The responses of the participant in each condition were fitted with a cumulative normal probability distribution using maximum likelihood estimation to obtain a psychometric function representing the probability of judging the comparison stimulus as larger than the standard stimulus. For each psychometric curve, we computed the point of subjective equality (PSE), i.e. the cylinder diameter that was perceived as larger than the standard in 50% of the trials. We also computed the discrimination threshold - or Just Noticeable Difference (JND) – as the difference between the PSE and the cylinder diameter that is perceived to be larger than the standard in 84% of the trials (see methods for more details).

The results in the bimodal conditions were compared to the predictions derived from results in the unimodal conditions and the optimal integration hypothesis. In particular, the JND in the bimodal condition was lower than the visual and somatosensory JNDs as predicted by Eq. 3. We also verified that the PSEs in the bimodal conditions corresponded to the values predicted by Eq. 1.

2.1.3 Methods

Participant. The participant was a 53-year-old female trans-radial (proximal third of the forearm) amputee. The amputation occurred in December 2015, following a traumatic accident at work. In July 2017, the participant underwent implantation of TIME (transverse intrafascicular multichannel electrode) (Boretius et al., 2010; Raspopovic et al., 2011) under general anesthesia through a 15 cm long skin incision to the left arm. Two TIMEs were placed in both the median and ulnar residual nerves (Schady et al., 1994). Stimulation of site 12 (R5) of the TIME implanted in the ulnar nerve (implant TIME 3) induced the sensation of a gradual, charge-dependent vibration on a skin region of the 5th finger. Ethical approval was obtained from the Institutional Ethics Committees of Policlinic Agostino Gemelli at the Catholic University, Rome, Italy, where the surgery was performed. The protocol was also approved by the Italian Ministry of Health. During the entire length of our study, all experiments were conducted in accordance with relevant guidelines and regulations. The participant signed an informed consent for all experiments and for publication of identifying information/images.

Apparatus. *Bidirectional hand setup.* The participant was fitted with a customized bidirectional research prosthesis, allowing her to control the opening and closing of a prosthetic hand by processing surface electromyographic (sEMG) signals, and providing sensory feedback by means

of electrical stimulation of the peripheral nerves. The robotic hand integrated tension force sensors within each digit except the last two fingers (IH2 Azzurra, Prensilia, Italy). The hand was controlled by a custom-build, multithreaded C++ software running on a Raspberry Pi 3, Model B (Raspberry Pi foundation, UK) single board computer. A recording and stimulating device (Neural Interface Processor NIP, Ripple Grapevine, Ripple LLC, US) was also connected to the central single board computer, acquiring sEMG data from four bipolar channels and providing stimulation outputs to the four neural electrodes. A custom molded socket was built with integrated screws to easily fix the robotic hand on the end. Holes were drilled to allow for the placement of sEMG electrodes on the stump. Figure 2 schematically represents the bidirectional hand setup used for the visuo-haptic task.

Prosthesis control. For prosthesis control, a simple three-state K-Nearest Neighbor (k-NN) classifier with three classes (open, close and rest) (Fougner et al., 2012) was used. Four bipolar channels of surface EMG (sEMG) were acquired from residual forearm muscles, two from the dorsal (digit extensor, extrinsic muscle) and two from the ventral (digit flexor, extrinsic muscle) side of the forearm. These signals were recorded over the belly of the muscles. The sEMG data were acquired with a sampling frequency of 2 kHz, and filtered using an IIR filter with 4th order Butterworth characteristics, between 15 and 375 Hz, as well as a notch filter to remove 50 Hz power hum including higher harmonics at 100 and 150 Hz. For the k-NN classifier, the waveform length (WL) was computed over a window of 100 ms for each channel and fed to the classifier every 100 ms. The WL controlled hand actuation speed which was updated every 100 ms and allowed for a gated-ramp control of the robotic hand movements, described by the following relation, already reported in Petrini et al. (2018):

$$V_{hand} = \begin{cases} V_{hand} + Class_{output} & \text{when } Class_{output} = -1 \text{ or } 1 \\ 0 & \text{when } Class_{output} = 0 \end{cases}$$

where $Class_{output}$ is the output of the classifier and V_{hand} is a number in the range between 0 and 511 that controls the velocity of the motors of the robotic hand.

The hand motor velocity increased or decreased by 75.73 deg/sec when the output indicated closing or opening respectively. Otherwise it remained constant. In this way the participant was able to close, open or keep the hand still by modulating the hand speed.

Experimental procedure and conditions. The participant sat in front of a table wearing headphones with white noise and eyeglasses to blur vision. Subsequent other studies (Ernst & Banks, 2002; Helbig & Ernst, 2007), vision was blurred to avoid exclusive reliance on the visual

modality, which is predicted by optimal integration principles when one modality is much more reliable than another. In this study, the participant wore customized eyeglasses that blurred her view of the cylinder (see below). A tilted plane on the table supported the prosthetic hand. The plane was covered with white linen to make the hand and stimuli easily visible. The distance between the hand and the eye was 55 cm. The prosthesis lay in a natural position but was slightly separated from the arm under a cloth to avoid the transmission of possible mechanical cues while grasping the object.

During each trial, two cylinders were successively placed in the robotic hand by the experimenter. The diameter of one cylinder (standard stimulus) was always the same (60 mm) while the diameter of the other cylinder (comparison stimulus) ranged from 55 to 65 mm (55, 57, 58, 59, 60, 61, 62, 63, and 65 mm). Each cylinder was placed in the participant's robotic hand by the experimenter. All cylinders were 3D printed with a variable density to have the same weight (138 g) and length (150 mm). The presentation order of the standard and comparison stimuli was randomized. At the end of each trial, the participant verbally reported which cylinder (first or second) had appeared larger.

The main experiment included two unimodal and three bimodal conditions. In the *unimodal conditions*, the stimuli were presented only in the visual or artificial somatosensory modality. In the *somatosensory condition*, the participant was asked to close her eyes during the trial. In the *visual condition*, no artificial somatosensory feedback was delivered when the participant opened/closed the hand. In the *bimodal conditions*, the two sensory cues associated with the standard stimulus could be congruent or incongruent. In the *congruent condition* V(60)-S(60), the artificial somatosensory stimulation intensity corresponded to the actual size of the standard stimulus (60 mm), which was visually seen. In the two *incongruent conditions*, the standard stimulus' information on cylinder diameter conveyed somatosensory and visually was different. In one incongruent condition V(62)-S(58), the somatosensory stimulation corresponded to a diameter of 58 mm while the visual stimulation (i.e. the actual size of the cylinder placed in the robotic hand) was 62 mm. The opposite was true in the second incongruent condition V(58)-S(62). The information conveyed by the two sensory modalities was always congruent for the comparison stimulus.

For each condition, the value of the comparison stimulus at each trial was controlled by two QUEST procedures. The QUEST is an adaptive psychophysical procedure to compute thresholds efficiently (A. B. Watson & Pelli, 1983). The two QUESTs aimed at stimulus values that were judged larger than the standard in 30% and 70% of the trials, respectively in order to collect data near the inflection points of the psychometric curves and estimate the slope reliably (King-Smith

& Rose, 1997). The experimental condition changed randomly every five trials. At each trial, one of the two QUESTs of the current condition was randomly selected. A condition was completed when 30 trials were collected by each QUEST (i.e., at least 60 trials per condition).

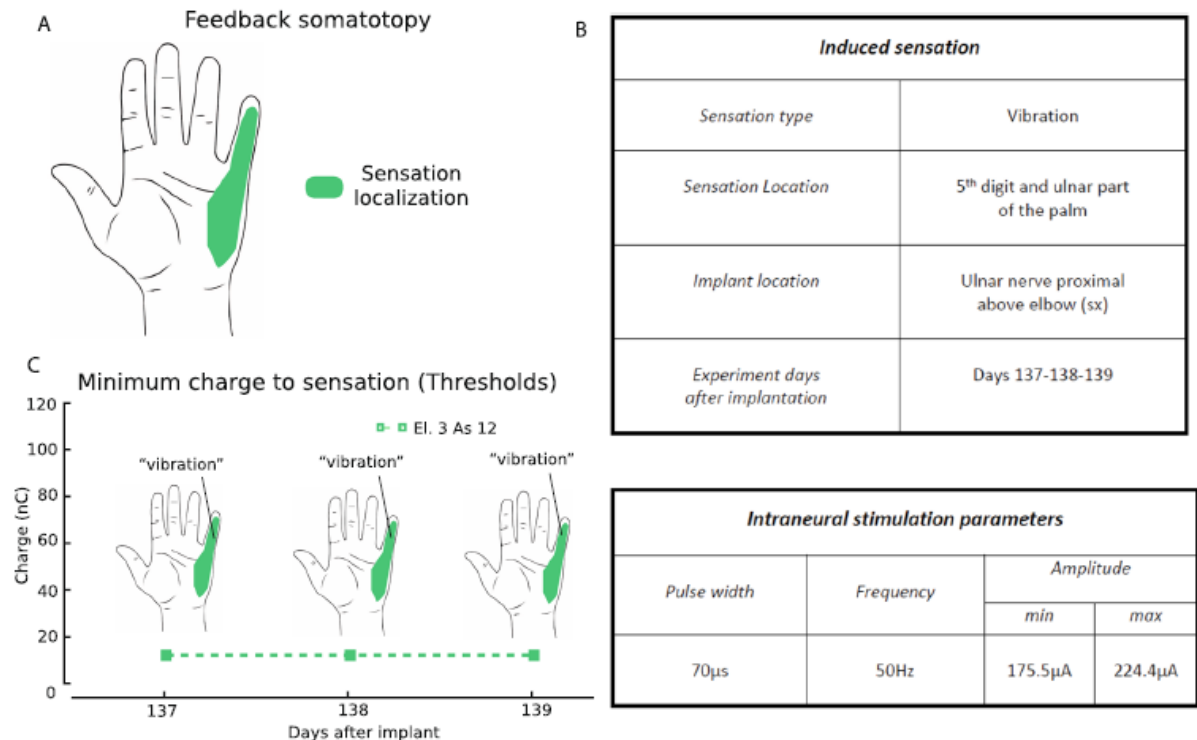


Figure 2.1. Physical and perceptual characteristics of the somatosensory stimulus. (A) Location on the phantom hand of the sensation elicited by the intraneural stimulation of the ulnar nerve by means of TIME electrode (somatosensory feedback somatotopy). (B) General information about the intraneural stimulation-induced sensations. The type of sensation quality is reported, as well as the sensation location and the implant location (top). Set of stimulation parameters used during the experiments referring to the electrode used (bottom). The experiments were performed with the same parameters in all sessions. The minimum charges needed to evoke a sensation, the location and the type perceived on the phantom hand are shown in (C) according to the days of interest.

Somatosensory and visual stimulus characterization and calibration. Before the main experiment, we conducted preliminary experiments to characterize the artificial somatosensory stimulus and to calibrate the artificial somatosensory and visual stimuli to make them equally discriminable in order to be able to demonstrate optimal integration with respect to an alternative hypothesis that the most reliable modality dominates. If one cue is much more reliable than the

other, optimal integration principles give a very large weight to this cue in the bimodal condition and the result cannot be distinguished from the best-modality dominance hypothesis.

Somatosensory stimulus physical and perceptual characterization. The ability of the electrodes to elicit sensations by means of electric current stimulation was investigated before the experiment. To this aim, each of the 14 single contacts of each of the four TIME implants was stimulated with a train of cathodic-first, rectangular biphasic, charge-balanced pulses delivered by Ripple Grapevine LCC (Neural Interface Processor (NIP), Ripple Grapevine US). The frequency of the pulses delivered was 50 Hz for every trial. The injected electric charge varied within the safety limits indicated for the electrodes by the manufacturers and by the ethical committees. Elicited sensations reported by the participant (type, location, and strength on a scale from 1- barely perceivable, to 10 - painful pressure) were recorded (Fig. 2.1). The stimulation led to a vibration sensation on the 5th digit and the ulnar part of the palm of the phantom hand. For the typical time scales involved in our experiments (order of minutes), the participant did not report relevant changes in sensation intensity, which would indicate the presence of adaptation. For all practical purposes, adaptation was insignificant during our experiments. Moreover, the sensation type, location and threshold of the artificial somatosensory sensory feedback were tested before starting the task and they remained stable and reliable over all three days of interest (Fig. 2.1). More information about the sensations elicited by all the active sites is provided in Petrini et al. (2018).

For the experiment, the artificial somatosensory stimuli corresponded to stimulation trains, which were injected when the robotic 5th digit touched the object with a value related to the diameter of the cylinder (from 55 mm to 65 mm with 60 as reference). The intensity was determined in a preliminary phase so that the artificial somatosensory and visual stimuli would be equally discriminable. The safety limit was set to 120 nC (Boretius et al., 2010).

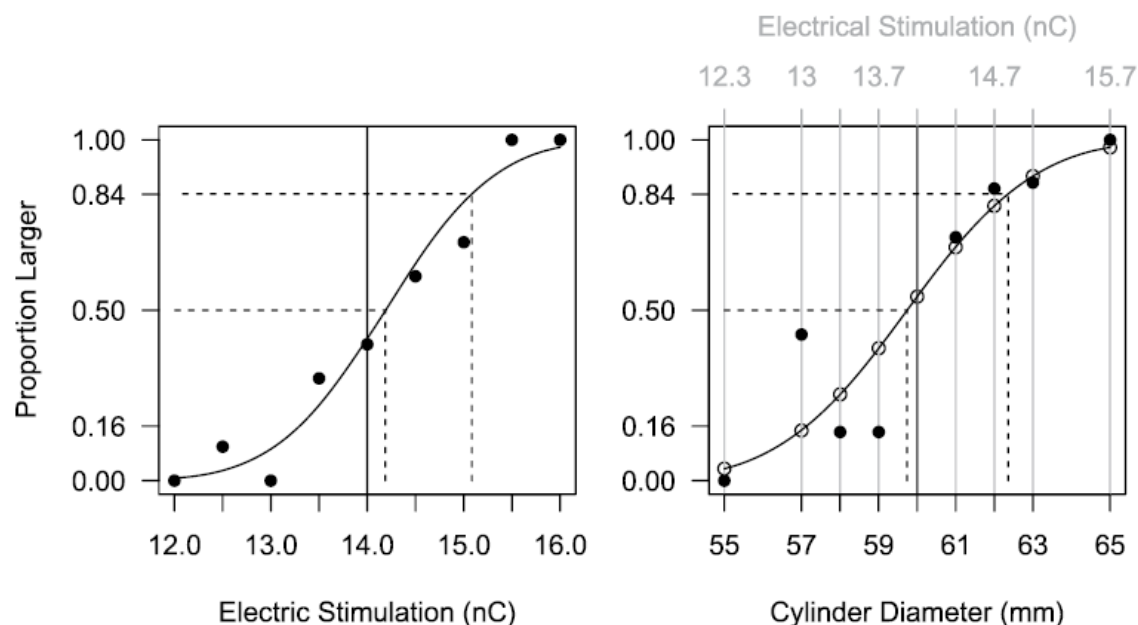


Figure 2.3. From cylinder diameter to neural stimulation. Left: Electrical stimulation discrimination experiment. On the x-axis, the electrical stimulation injected for the comparison stimulus (in nC). On the y-axis, the proportions of trials where the comparison stimulus (horizontal axis) appeared larger than the standard (vertical solid line). Black dots corresponds to the data points. Each stimulus was presented 10 times ($N = 90$). The psychometric function (solid curve) represent the probability of judging the comparison stimulus to be larger than the standard. The horizontal distance between the two dashed lines corresponds to the JND. Right: Mapping between the electrical stimulation and the stimuli size. The grey scale above the top margin indicates the charges used in the main experiment as artificial somatosensory stimuli. Black dots correspond to data points and empty dots indicate the probability of judging the comparison stimulus (horizontal axis) larger than the standard (vertical line) for the different stimulation levels (grey scale).

Somatosensory and visual stimulus calibration. First, we measured the ability of the participant to discriminate artificial somatosensory feedback produced by intraneural stimulation. Two stimuli were presented, and the participant's task was to indicate which of the two was more intense. Each pair consisted of a standard charge (14 nC) and a comparison charge, selected in a comfortable range from 12 nC to 16 nC (step of 0.5 nC). The stimulation pulse-width was fixed at 70 μ s. The experimental test comprised 90 trials. Each stimulus pair was presented 10 times, and both the order of the stimuli within the pair and the order of the pairs were randomized. The two pulse trains lasted 2 s and were separated by a 2 s inter-stimulus interval. The participant was instructed to

focus on the intensity or magnitude of the sensation evoked. The participant was blinded to the particular stimulation conditions of each trial.

Second, we measured the ability of the participant to visually discriminate the cylinders' size. As noted above, the participant wore eyeglasses to blur vision. Two cylinders, the standard stimulus (60 mm diameter) and one of the comparison stimuli, were successively presented by the experimenter at a distance of 55 cm in front a white background. The task was to indicate which of the two cylinders was larger. There were eight comparison stimuli with a diameter ranging from 55 to 65 mm, which were presented 7 times each. The order of presentation of the two cylinders within and among trials was randomized.

The participant's responses were fitted with a cumulative Gaussian probability distribution to obtain a psychometric function representing the probability of judging the comparison stimulus to be larger than the standard stimulus (see Fig. 2.3). Then we computed the JND for the intraneural stimulation (JND_{ST}) and for the visual stimulus (JND_V ; Fig. 2.3, left panel) from the results of these preliminary experiments. Finally, we computed the levels of intraneural stimulation intensity $I(s_H)$ that should be associated with the artificial somatosensory cue s_H to elicit somatosensory sensations that have the same discriminability as the visual stimuli (Fig. 2.3, right panel):

$$I(s_H) = (s_H - 60) \frac{JND_{ST}}{JND_V} + I_{60}$$

where s_H is the cylinder diameter in mm for the somatosensory modality, $JND_{ST} = 0.897$ nC and $JND_V = 2.617$ mm are the 84% discrimination thresholds for the neural stimulation and visual cue obtained in the preliminary experiments, and $I_{60} = 14$ nC is the intermediary level of stimulation that was selected to represent the standard stimulus. The neural stimulation intensities used during the visuo-haptic task were 12.28 nC (55 mm), 12.97 nC (57 mm), 13.31 nC (58 mm), 13.66 nC (59 mm), 14 nC (60 mm reference), 14.34 nC (61 mm), 14.69 nC (62 mm), 15.03 nC (63 mm) and 15.71 nC (65 mm). The stimulation train frequency was fixed at 50 Hz.

Data analysis. The responses of the participant in each condition were fitted with a cumulative normal probability distribution using maximum likelihood estimation, i.e. with a Generalized Linear Model (GLM) with the comparison stimulus as predictor, Bernoulli error distribution and a probit link function to obtain a psychometric function representing the probability of judging the comparison stimulus as larger than the standard stimulus. Goodness of fit was assessed with Pearson's χ^2 normal goodness-of-fit test for generalized linear models. The two unimodal conditions were fitted separately. To obtain a common slope estimate, the three bimodal conditions

were fitted together, with a different intercept for each condition. For each psychometric curve, we computed the point of subjective equality (PSE), i.e. the cylinder diameter that was perceived as larger than the standard in 50% of the trials. We also computed the discrimination threshold - or Just Noticeable Difference (JND) – as the difference between the PSE and the cylinder diameter that is perceived to be larger than the standard in 84% of the trials. 84% JND corresponds to the standard deviation of the normal distribution underlying the psychometric function and is an estimate of the noise associated with the unimodal or bimodal cues. We computed the 95% confidence interval for the PSE and JND from 5000 parametric bootstrap samples with x fixed (Davison & Hinkley, 1997). In the Results, we report the JND and the standard deviation of the bootstrap distribution. The p-values for the pairwise difference in PSEs (or JNDs) between conditions were obtained by inverting the percentile bootstrap confidence intervals. Specifically, for each difference in PSEs (or JNDs), we computed the resampling distribution of the difference and the p value that corresponded to the largest equitailed confidence interval that excluded zero. We then adjusted this p-value for False Discovery Rate to account for the multiple comparisons involved in these pairwise tests. The difference between the optimal (MLE) JND and the bimodal JND was tested in a similar manner. We report the mean and standard deviation of the difference between the two bootstrap distributions.

To examine whether the performance improved during the experiment, we compared early and late trials by adding a predictor in the GLM models to indicate whether the trial belonged to the first or the second half of the condition. As before, the three bimodal conditions were fitted together with a common slope but a different intercept for each condition. We report the p value associated with this predictor.

2.1.4 Results

Figure 2.4a shows the probability of judging the comparison stimulus to be larger than the standard in the two unimodal conditions (top row). The goodness-of-fit tests for all psychometric functions were not statistically significant ($p > 0.91$), indicating a good fit with the data. The Point of Subjective Equality (PSE) indicates the cylinder diameter that was judged equal to the 60 mm standard. As expected, the PSE was close to the standard in the unimodal conditions. The JND corresponds to the difference between the cylinder diameter that was judged larger than the

standard in 84% of the trials and the PSE. Steeper curves corresponded to smaller JNDs. Assuming that the estimates of the cylinder size were normally distributed, this JND definition corresponded to one standard deviation. Figure 2.4b shows the PSEs and JNDs in each condition, together with the Maximum Likelihood Estimate (MLE) predictions.

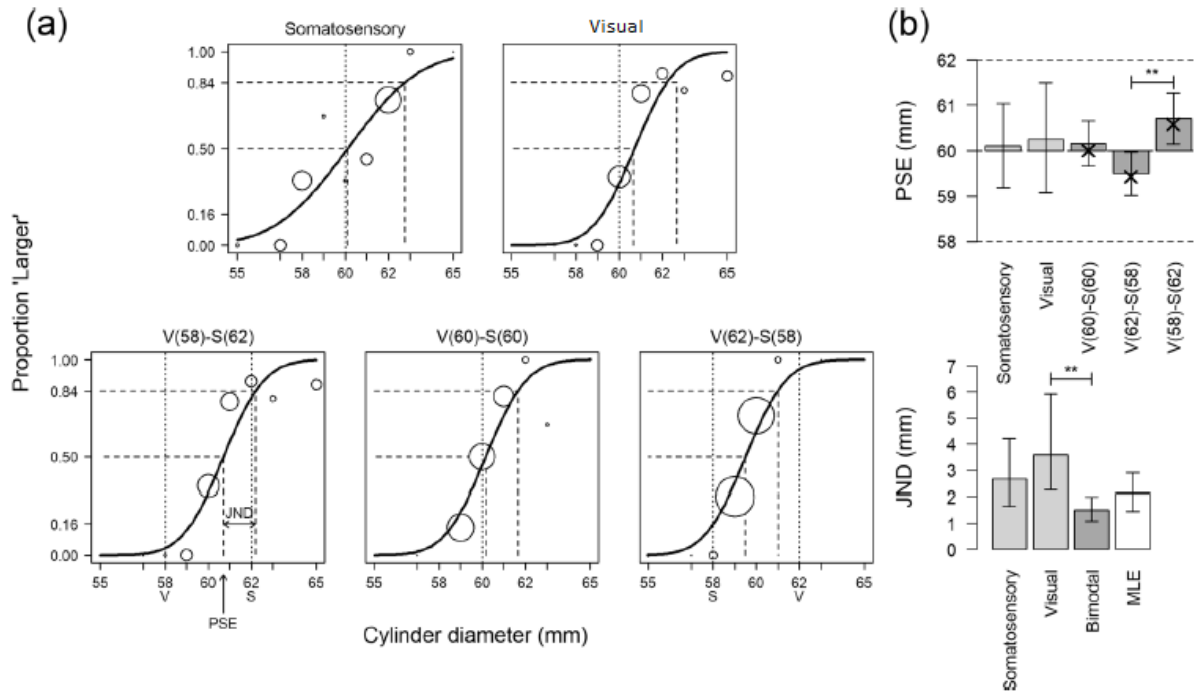


Figure 2.4. Panel (a) Psychometric curves in the unimodal (top row) and bimodal (bottom row) conditions. The x-axis represents the diameter of the comparison stimulus (in mm). The y-axis corresponds to the proportion of responses in which the comparison stimulus was larger than the standard. In the bimodal congruent condition V(60)-S(60), the visual and somatosensory characteristics of the standard corresponded to a 60 mm diameter cylinder (vertical dotted line). In the bimodal incongruent conditions V(58)-S(62) and V(62)-S(58), the visual and somatosensory characteristics of the standard stimulus differed by 4 mm (vertical dotted lines). The somatosensory and visual characteristics of the comparison stimulus were congruent in all bimodal conditions. The vertical dashed line that corresponds to a proportion of 50% of 'Larger' responses indicates the Point of Subjective Equality (PSE) (see, for example, arrow in V(58)-S(62) panel). The distance between the two vertical dashed lines corresponds to the Just Noticeable Difference (JND), which is the difference between the PSE and the cylinder diameter that is perceived to be larger than the standard in 84% of the trials. Panel (b) Representations of PSEs (top) and JNDs (bottom) for unimodal and bimodal conditions. The crosses in the top panel indicate the biases predicted by the optimal integration model. The white bar in the bottom panel represents the JND

predicted by the optimal integration model for the bimodal conditions. The crosses in the PSE plot correspond to the predicted biases. The vertical bars correspond to the 95% bootstrap confidence interval ($N = 5000$ bootstrap samples). Horizontal bars denote statistically significant differences (False Discovery Rate adjusted bootstrap p -value $**p < 0.01$).

The JND was smaller in the somatosensory condition than in the visual condition (2.7 ± 0.6 versus 3.6 ± 0.8 mm), indicating that the artificial somatosensory stimulation gave a more reliable (less variable) estimate of the cylinder diameter than the blurred vision. Therefore, following Eq. 2, the artificial somatosensory cue has an optimal weight of 64% while the visual cue has a weight of only 36%. In the bimodal conditions, the two sensory modalities conveyed simultaneous information about the cylinders' size. In agreement with the optimal integration model, the JND was smaller in the bimodal condition (1.5 ± 0.2 mm) than in the visual (3.6 ± 0.8 mm) or somatosensory (2.7 ± 0.6 mm) condition. However, the difference was statistically significant with the visual JND (bootstrap mean difference: -2.1 ± 0.98 , $p = 0.002$) and only close to significance with the somatosensory JND (-1.8 ± 0.7 , $p = 0.061$). This observation is in agreement with the optimal integration model since the margin of improvement that optimal integration can provide is more limited when one sensory cue is more reliable than the other one. The bimodal JND did not differ from MLE JND (2.13 ± 0.2 mm) statistically (0.6 ± 0.4 , $p = 0.183$). The PSE in the unimodal conditions and in the congruent bimodal condition V(60)-S(60) were near the standard, indicating an absence of bias. When the sensory cues are not congruent, optimal integration principles predict that the PSE should be biased toward the most reliable sensory modality (see Eq. 1). In the incongruent conditions with a 4 mm conflict between the visual and artificial somatosensory information, we found that the difference between the PSEs of the two incongruent conditions V(58)-S(62) and V(62)-S(58) was statistically significant (bootstrap mean difference: 1.2 ± 0.4 , $p = 0.008$). Accordingly, the top panel of Fig. 2.4b shows that the PSE was biased by 0.5–0.6 mm (see crosses) toward the somatosensory modality as predicted by the maximum likelihood estimate (MLE) model. In fact, the PSE predicted by MLE explains 99% of the variance of the PSE observed in the bimodal conditions. The patient never noticed the small conflict between the sensory cues of the standard stimulus in the incongruent bimodal conditions.

In order to find out whether the discrimination threshold varied during the experiment, we verified whether the probability of judging the comparison stimulus to be larger than the standard changed between the first and second half of the trials in each condition (see Data Analysis section). This test revealed no change in the somatosensory ($p = 0.351$), visual ($p = 0.432$) or bimodal ($p = 0.748$) conditions.

2.1.5 Discussion

When grasping an object, visual, proprioceptive and tactile cues provide redundant information about its size (Ernst & Banks, 2002). Previous research has shown that the nervous system continuously reassesses the reliability of each sensory modality and that somatosensory and visual cues are optimally integrated. For example, it has been shown that visual reliability decreases with the amount of blur added to the visual cue (Ernst & Banks, 2002; Helbig & Ernst, 2007) or when the size of the object is difficult to assess visually because it is grasped along the axis of vision (Gepshtein & Banks, 2003).

In this study, we demonstrated that an amputee with a bidirectional prosthesis optimally integrated an artificial somatosensory feedback with vision. To that end, we adapted the object size discrimination task that had been used to demonstrate that adults integrate visual and artificial somatosensory information optimally in a seminal study (Ernst & Banks, 2002). Neural stimulation of the ulnar nerve substituted the haptic cues, which provide crucial information during object manipulation in healthy subjects (Berryman et al., 2006; Johansson & Flanagan, 2009b). The intensity of the stimulation directly encoded the size of the hand-held cylinder. The cylinder set and stimulation intensities were selected to mimic the haptic size discrimination ability of healthy subjects (Ernst & Banks, 2002; Gaydos, 1958). Like in previous studies (Ernst & Banks, 2002; Gepshtein & Banks, 2003; Helbig & Ernst, 2007), vision was blurred so that the visual discrimination threshold would correspond to the somatosensory discrimination threshold. Our results clearly indicate that the participant optimally integrated information about the object's size from the two sensory modalities. Evidence for integration comes from both the lower discrimination threshold and the shift of the PSE in the bimodal conditions.

The stimulation strategy used in this study differed from previous studies with this patient where the amplitude of the stimulation was proportional to the pressure applied on a surface (tactile information) (D'Anna et al., 2017; Petrini et al., 2018; Raspopovic et al., 2014; Valle et al., 2018) and robotic hand closure (D'Anna et al., 2017) (position information). In particular, a notable difference with D'Anna et al., (2017) is that they used two different stimulation channels for tactile and (remapped) proprioceptive feedback. The tactile feedback was referred to most of the ulnar innervation area and encoded the measured force applied by the prosthetic digit. The position feedback encoded robotic hand closure without interruption and was referred to the medial part of the forearm close to phantom wrist. Here, a single-channel encoding strategy substituted the

natural touch sensation with a vibration sensation that was referred to a single site, the ulnar side of the phantom hand. Moreover, the stimulation started only when the robotic hand had completed the grasp and the prosthetic digit touched the object (tactile event). Finally, amplitude of modulation increased proportionally with the cylinder size and, thus, grasp aperture (positional information). Despite a limited training session and the fact that the stimulus did not correspond to a natural touch sensation, the patient discriminated object size stably during the experiment, as shown by the absence of a difference between early and late trials.

A few studies have started to examine multisensory integration with artificial sensory feedback, using both invasive and non-invasive methods. Dadarlat and colleagues (2015) found that non-human primates can combine an artificial multichannel intra-cortical micro-stimulation signal (ICMS) about hand position with vision to form an optimal estimate of hand movement direction. However, this study intentionally created unnatural mappings between the micro-stimulation and the direction of hand movement. In contrast with this study, the primates required a long training process to learn the associations between movement direction and the ICMSs. Another difference with Dadarlat et al. (2015) is that neural stimulation in our study occurred in a peripheral nerve rather than intra-cortically.

Marasco et al., (2018) used vibratory feedback to elicit complex illusory movement sensations and found that tactile and visual information were optimally integrated in a task where the amputee had to detect a temporal delay between the voluntary motor command that triggered the closure of the prosthetic hand and the beginning of the sensory feedback. In such a task, only the timing of the tactile and visual feedback is relevant (Marasco et al., 2018). In contrast, the neural stimulation in our size discrimination task conveyed magnitude information about the cylinder size. It remains to be seen whether vibratory and visual feedback can be used to elicit optimally integrated percepts that refer to the size or shape of hand-held objects.

This study presents several limitations and characteristics that should be investigated further. First, the results are based on a single patient and need to be confirmed with additional subjects.

Second, future research should aim at demonstrating optimal integration in more natural conditions. Since the relationship between the object size and the neural stimulus is essentially arbitrary, it might be possible to demonstrate optimal integration with artificial somatosensory stimulation levels that yield the same discrimination performance as non-blurred vision. Testing the optimal integration hypothesis under these conditions would involve somatosensory and bimodal discrimination thresholds that correspond to super-human performance levels.

In this respect, it should be noted that neural stimulation provided unambiguous and noiseless information about the cylinder's size in our study because it was set directly by the experimenter as a function of object size. While object size might be measured by the sensors in the prosthesis when grasping the object, the estimated object size is likely to be less reliable for various reasons such as trial-to-trial variability in the placement of the fingers on the objects, etc. Obtaining reliable information about object size might become particularly difficult to achieve if there is little size difference between the objects. The somatosensory discrimination threshold might have a lower bound for technical and pragmatic reasons and future research should address this issue.

Third, previous research has shown that redundant information from different sensory modalities must be spatially and temporally correlated for integration to occur (Gepshtein et al., 2005; Gepshtein & Banks, 2003; Pettypiece et al., 2010; R. B. Welch & Warren, 1980). In this study, neural stimulation was triggered by the contact between the cylinder and the robotic hand when the patients voluntarily closed the hand via sEMG. The delay between the contact and the delivered stimulation was 20 ms, well within the integration window shown in previous studies (Di Luca et al., 2009). It would be interesting to explore the extent to which active control of the prosthesis and simultaneity between visual and tactile feedback is important to foster integration in this context.

Finally, the sensations elicited by the neural stimulation were remapped to the phantom hand rather than perceived in-loco, preserving somatotopic information at a gross scale. However, these sensations differed in important ways from the sensations occurring when touching or grasping an object with the healthy hand. In a preliminary sensation characterization test, the participant reported a graduated sensation of vibration in the 5th digit and ulnar part of the palm during the stimulation. Perceptually, object size was encoded by the intensity of the vibration felt on the phantom hand rather than by the perceived position of the fingers. Despite these differences, the artificial somatosensory sensation that substituted the natural haptic cue was integrated with the visual cue in an optimal fashion. Our results suggest that a natural sensation is not a necessary condition for optimal integration, which is an interesting observation in the on-going debate on stimulus features that determine whether sensory cues must be integrated or not (Chen & Spence, 2017). Still, it would obviously be preferable that the artificial stimulus resemble more the natural sensation of touch when grasping an object. In this respect, it should be noted that major strides have been made recently towards the implementation of codes for neuroprosthetic devices to deliver rich, natural and versatile tactile sensations (Bensmaia, 2015; Saal & Bensmaia, 2015; Valle et al., 2018). Compared to non-invasive methods, neural stimulation could in principle provide more specific and qualitatively diverse sensory feedback to the user. This biomimetic approach to sensory restoration, together with our findings and the development of increasingly

sophisticated anthropomorphic robotic limbs opens encouraging scenarios toward the restoration of lost limb functioning.

2.2 Visuo-tactile shape perception in women with Anorexia Nervosa and healthy women with and without body concerns

The contents of this section are adapted from the following publication: **Risso, G.**, Martoni R.M., Erzegovesi S., Bellodi L., Baud-Bovy G. (2020). Visuo-tactile shape perception in women with Anorexia Nervosa and healthy women with and without body concerns. *Neuropsychologia*.

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Personal contributions as first author: experiment conceptualization, and writing of the protocol for the ethics committee (CUBE-2015). Development of the experimental setup. Investigation, data curation and analysis. I wrote the original draft and revised and edited the manuscript replying to the reviewers' comments.

2.2.1 Abstract

A key feature of Anorexia Nervosa is body image disturbances, the study of which has focused mainly on visual and attitudinal aspects, did not always contain homogeneous groups of patients, and/or did not evaluate body shape concerns of the control group. In this study, we used psychophysical methods to investigate the visual, tactile and bimodal perception of elliptical shapes in a group of patients with Anorexia Nervosa (AN) restricting type and two groups of healthy participants, which differed from each other by the presence of concerns about their own bodies. We used an experimental paradigm designed to test the hypothesis that the perceptual deficits in AN reflect an impairment in multisensory integration. The results showed that the

discrimination thresholds of AN patients are larger than those of the two control groups. While all participants overestimated the width of the ellipses, this distortion was more pronounced in AN patients and, to a lesser extent, healthy women concerned about their bodies. All groups integrated visual and tactile information similarly in the bimodal conditions, which does not support the multi-modal integration impairment hypothesis. We interpret these results within an integrated model of perceptual deficits of Anorexia Nervosa based on a model of somatosensation that posits a link between object tactile perception and Mental Body Representations. Finally, we found that the participants' perceptual abilities were correlated with their clinical scores. This result should encourage further studies that aim at evaluating the potential of perceptual indexes as a tool to support clinical practices.

2.2.2 Introduction

Anorexia Nervosa is a multi-faceted psychiatric disorder characterized by disturbed eating behaviors where the patients' attitudes towards their bodies, as well as perceptions of weight and shape are distorted (AN; American Psychiatric Association, 2013). Body parts such as the head, the abdomen or the thighs appear larger to AN patients than what they are in reality (Thomas F. Cash & Deagle, 1997; Smeets et al., 2009). In contrast, patients with AN do not perceive the body shapes of other individuals as distorted. Given the presumed absence of a generalized perceptual deficit, the origin of AN perceptual distortion remains mysterious and the question why patients with AN perceive their body shape as distorted despite receiving, presumably, accurate visual and tactile feedback is still open.

Mental Body Representation in Anorexia Nervosa

Various hypotheses have been advanced to explain perceptual distortions in AN. One explanation is that AN affects Mental Body Representations (MBRs), to use a term proposed by Serino & Haggard, (2010) that refer to various high-level representations of one's own body that play a role in perception or action. MBRs include, body image, body schema and the superficial form, distinctions going back to (Head & Holmes, 1911) seminal work. While derived from sensory

input, MBRs are typically persistent, abstract, and multimodal (Serino & Haggard, 2010). Importantly, there is not yet a general agreement about the neuro-anatomical correlates of MBRs, which are usually defined in functional terms.

Body image is a conscious representation used in the perception of one's own body size, shape or weight (Cash & Brown, 1987; Longo et al., 2010; Longo & Haggard, 2012). It includes a perceptual dimension, which can be assessed with many different techniques like the analogue scale, image marking methods, optical distortion methods such as distorting photography, distorting a mirror, video distortion technique, and figural drawing scales (for a review see Gardner & Brown, 2011). Body image also includes a subjective dimension that consists of the feelings that individuals develop towards their bodies' appearance. Numerous studies have shown that the two dimensions of the body image are dysfunctional in AN (Cash & Brown, 1987; Cash & Deagle, 1997). In particular, these studies have shown that the perceptual distortions correspond specifically to a fattening of the body shape. Importantly, the vertical dimension, the shape of other individuals and the shape of objects are not distorted (Bowden et al., 1989; Slade & Russell, 1973). Moreover, studies that have used the Signal Detection Theory framework suggest that these perceptual distortions do not have a sensory origin because AN patients can detect changes in body shape as well as controls (Gardner & Moncrieff, 1988; Smeets et al., 1999).

Recent studies have shown that AN might also affect the body schema, which is an unconscious sensorimotor representation of the body that is invoked in action (de Vignemont, 2010). For example, it has been shown that patients move as if their bodies were larger than they really are when passing through doors, which suggests that body schema is also distorted in patients with Eating Disorders (Guardia et al., 2010; Keizer et al., 2013; Nico et al., 2010; Urgesi et al., 2011). Finally, AN can also affect the superficial schema, which is also known as the tactile form (Gadsby, 2017) and/or body form representation (Medina & Coslett, 2010). The superficial form provides the information needed to localize the position of the tactile stimulus on the skin and to estimate the physical distance between two tactile stimuli or the size of an object touching the skin. For example, Keizer and colleagues (2011, 2012) have shown that AN patients tend to overestimate the distance between two tactile stimuli relative to controls in the abdomen and the head. In a later study Spitoni et al. (2015) showed that this distortion occurred only along the altered dimension of the body. While these studies show that AN affects patients' own body representations in multiple ways, there is no general agreement on the cause of this disturbed experience. One hypothesis is that affects might cause MBR distortions (Gadsby, 2017). Indeed, some studies have shown that negative mood induction in participants with normal weight (Baker et al., 1995) and who have no indication of Eating Disorders (Plies & Florin, 1992) increases body overestimation. In addition, other studies have shown a relation between body dissatisfaction and

tactile perception of distance (Keizer et al., 2011; Spitoni et al., 2015), but not in a somatosensory time duration task (Spitoni et al., 2015). These results pointed to a significant correlation between body satisfaction and the tendency to overestimate distance on the body. Another hypothesis is that body shape distortions in AN reflect a broader impairment in multisensory integration (see Gaudio et al., 2014 for a review). For example, Case et al. (2012) investigated haptic-visual-proprioceptive integration using the size-weight illusion (SWI). They found that patients with AN were significantly less susceptible to the illusion than healthy controls (HC). Some authors (Eshkevari et al., 2012) have investigated visuo-tactile-proprioceptive integration using the Rubber Hand Illusion (RHI). ED patients reported higher embodiment scores and higher proprioceptive drift than HC showing that they experience a stronger RHI than the control sample. Although these two studies suggest an altered capacity of AN patients to process and integrate multisensory bodily perceptions, their conclusions differ with respect to the weight given to each sensory modality. On the one hand, SWI results suggest that patients gave more weight to visual signals than to somatosensory ones. On the other hand, RHI results support the view that patients with AN showed a reduction in somatosensory processing, or an excessive reliance on visual information, or both the previous hypotheses. While interesting, SWI and RHI do not and cannot measure the weight of each sensory modality independently. As suggested by Gaudio et al. (2014), this issue needs to be addressed with paradigms and tasks that can more precisely assess the role of each sensory modality and more directly test the hypothesis of aberrant multisensory integration in AN patients.

Eating Disorder Heterogeneity

A challenge in Eating Disorder studies is the wide heterogeneity of symptoms and eating habits, which can complicate comparisons between studies. At the neurophysiological level, there is evidence that severe malnutrition can affect sensory nerves anatomically and functionally both in the visual (Caire-Estévez et al., 2012; Moschos et al., 2011) and somatosensory system (Alloway et al., 1989; Renthall et al., 2014; Teixeira et al., 2016). However, not all studies have found a corresponding visual or somatosensory acuity deficit. For example, Caire-Estévez et al. (2012) found that visual acuity was impaired while Moschos et al. (2011) did not. A possible reason for this discrepancy is that the Caire-Estévez et al. (2012) study included only AN Restricting type patients while the Moschos et al. (2011) study included AN Binge/Purging patients as well. In the tactile modality, two studies found low-level sensory deficits in AN restricting type patients who are severely underweight (Epstein et al., 2001; Spitoni et al., 2015). In particular, Epstein et al. (2001) found that AN patients had difficulties in

recognizing which fingers were being touched when closing their eyes and Spitoni et al. (2015) found that the threshold of AN patients was larger in a two point discrimination (2PD) task. However, they did not find alteration in the elementary tactile detection of patients as assessed with the Von Frey task (VF). When the sample of ED is open to more than AN restricting type and the BMI is not severely underweight, neither elementary tactile detection assessed with the VF nor the thresholds in the 2PD task appear to be compromised (Keizer et al., 2012). Altogether, these studies show that low-level sensory deficits might depend on the AN type and degree of malnutrition.

The second issue in ED studies is that the control groups are not always well defined with respect to body satisfaction. As a result, it is difficult to pinpoint the origin of perceptual deficits, which might be linked to body dissatisfaction in general and/or to more specific ailments present only in AN.

To address these issues, this study includes three groups of participants. The AN group included only female patients with a restricting type diagnosis in a state of malnutrition shown by their low BMIs (see Table 1). In contrast, all participants in the healthy control groups were gender- and age-matched, with a healthy weight and no psychiatric disorder diagnosis. After completing body satisfaction tests, the participants in the control group were divided into two groups according to their score: a group that was as concerned about their bodies as patients with AN and a group with lesser concerns.

Table 1 Demographics and clinical assessment of the Healthy Controls (HC), Healthy Controls with Body Concerns (BCHC) and Anorexia Nervosa patients (AN).

	HC (N = 19)	BCHC (N=9)	AN (N = 17)
Age, M (SD) years	24.47 (1.26)	25.67 (2.18)	26.12 (9.34)
BMI, M (SD)	19.86 (1.94)	20.49 (1.43)	15.15 (2.64)
Right-Handedness N (%)	17 (94.74 %)	8 (88.89 %)	15 (88.24 %)
BSQ global score, M (SD)	54.26 (8.53)	117.44 (35.36)	116.12 (42.86)
EDI-2 global score, M (SD)	14.95 (9.58)	68.56 (45.93)	90.59 (39.72)

Objectives

The main objective of this study is to test the multisensory integration impairment hypothesis. To that end, we used an experimental paradigm that has been extensively used to show that people integrate redundant sensory information optimally (Ernst, 2012; Helbig & Ernst, 2007; Hillis et al., 2004; Körding et al., 2007; Risso et al., 2019). The idea behind this paradigm is to assess the reliability of each sensory modality independently and then compare the performance measured in the bimodal conditions with the prediction derived from the performance in unimodal conditions to test the optimal integration hypothesis (Ernst & Banks, 2002; see Methods). While different stimuli have been used to demonstrate optimal multisensory integration, we adapted a task used by Helbig & Ernst (2007) where participants must judge the shape of a small ellipse in the tactile and/or visual modalities. It is noteworthy that this task makes it possible to assess independently the perceptual biases, the weights and reliabilities of each sensory modality in addition to the multisensory integration hypothesis. Therefore, this paradigm also allows us to address several questions, which might shed light on the nature the perceptual deficits in AN. The first question is whether AN patients will perceive the shape of the ellipse in a more distorted way than controls and whether the distortions, if any, will be larger in the tactile or visual modality. The fact that the same stimuli are used in all conditions allows for a direct comparison of the results across sensory modalities. A second question of interest is whether AN affects the reliability of sensory cues in the tactile and visual modalities. Since the weight of a sensory modality is proportional to its reliability in the optimal integration framework (see Methods), this paradigm might allow us to test the hypothesis that somatosensation has more weight than visual information (Eshkevari et al., 2012; Longo et al., 2015) or viceversa (Case et al., 2012). The third question is whether tactile and visual information are integrated optimally (Gaudio et al., 2014), which can be addressed by comparing prediction derived from unimodal conditions and the results in the bimodal conditions (see Optimal Integration Model in the Methods Section).

A secondary objective is to find out whether body concerns can be linked to perceptual deficits or whether these deficits are specific to AN. To do so we compared the performance of the patients to that of the controls with and without body concerns. Evidence in this direction would support the hypothesis that affects might be linked with the corresponding deficits. A final objective is to find out whether perceptual biases and clinical scales characterizing eating disorders and body shape concerns are correlated.

2.2.3 Materials and Methods

Participants

This study adhered to the principles of the Declaration of Helsinki (2013) and was approved by the ethics committee of the San Raffaele Hospital of Milan (Prot. CUBE-2015). Each participant received oral and written information on the purpose and procedure and signed an informed consent form before taking part in the study. The study included three groups of adult women: 17 Anorexia Nervosa (AN) patients, 19 Healthy Controls (HC) and 9 healthy controls with body shape concerns (BCHC). Patients with AN were recruited from the Center for Eating Disorders at San Raffaele Hospital in Milan. Patients were tested during their rehabilitation program. All the patients were diagnosed with Anorexia Nervosa disease by a senior psychiatrist and were characterized by a Restricting subtype and no psychiatric comorbidities (excluding personality disorders). We included both hospitalized patients and patients involved in non-residential treatment. One AN patient was removed from all the analyses because she could not perform the task (see Data Analysis below) and subsequent investigation revealed an IQ slightly below average. The mean duration of illness was 6.75 ± 6.92 . All the patients followed Cognitive Behavioral Therapy and Nutritional Therapy and fourteen of them were under pharmacological treatment. The women in the HC and BCHC groups differ from the AN group in that they have never exhibited Eating Disorder (ED) symptoms. In addition, women in the HC group did not report body shape concerns as assessed by the Body Shape Questionnaire (BSQ; Cooper et al., 1987) nor did they report psychological or behavioral traits common in ED as assessed by Eating Disorder Inventory 2 (EDI-2; Garner, 1991). In contrast, women in the BCHC group had a BSQ global score ≥ 80 . Importantly, no member of the HC and BCHC groups was diagnosed with ED. All had a BMI of above 17 kg/m², which corresponds to the upper limit for the first level of AN severity according to the DSM-5 (American Psychiatric Association, 2013). Demographics and clinical assessment of the three groups are given in Table 1. The BMI was significantly different between groups (one-way ANOVA: $F(2, 42) = 27.65$, $p < .001$). As expected, post-hoc analysis using the Tukey HSD test showed that BMI in AN patients was significantly lower than in HC ($p < .001$) and BCHC individuals ($p < .001$) and that the BMI of the HC and BCHC groups did not differ ($p = .758$). The global EDI-2 ($F(2, 42) = 25.75$, $p < .001$) and BSQ ($F(2, 42) = 22$, $p < .001$) scores were different across groups. The Tukey HSD showed higher EDI-2 and BSQ scores for the AN patients and BCHC groups in both the clinical tests related to the HC ($p < .001$ for all tests) and no statistically significant differences between the AN and BCHC groups for the EDI-2 ($p = .234$) and BSQ ($p = .994$) scores. The age of the participants was matched in the three groups ($F(2, 42) = 0.37$, $p = .696$).

Clinical Questionnaires

The participants filled out clinical self-report questionnaires regarding body shape concerns, common traits in ED, depression and anxiety symptoms. The questionnaires are described below:

Body Shape Questionnaire (BSQ): The Body Shape Questionnaire is a self-report measure of general concerns about body shape, specifically the subjective experience of “feeling fat” (Cooper et al., 1987). It includes 34 items scored on a 6 point Likert scale (where 1 = never and 6 = always) with a possible total score ranging from 34 to 204. A score below 80 represents the absence of concerns related to body shape, while higher scores represent a more negative attitude towards body shape (Melanie Jane Taylor, 1987). The BSQ is easy to fill out and can be rapidly completed by participants. Significant correlations between the BSQ and the total score on the Eating Attitude Test and the Body Dissatisfaction subscale of the EDI-2 establish its concurrent validity. A Cronbach’s alpha between 0.82 and 0.88, with a test-retest correlation of 0.97 was shown (Franko et al., 2012). Its discriminant validity has also been shown to be satisfactory. The BSQ has demonstrated high concurrent and discriminant validity (Cooper et al., 1987).

Eating Disorder Inventory 2 (EDI-2): We used the Italian version of the Eating Disorder Inventory (EDI-2) (Garner et al., 1995). The EDI-2 is a self-report questionnaire developed by Garner and widely used both in research and clinical settings to assess the symptoms and psychological features commonly associated with EA (Garner et al., 1983). It includes 91 items on a 6 point Likert scale (from “always” to “never”), divided into 11 subscales: Drive for Thinness, Bulimia, Body Dissatisfaction, Ineffectiveness, Perfectionism, Interpersonal Distrust, Interoceptive Awareness, Maturity Fears, Asceticism, Impulse Regulation, Social Insecurity. Internal consistency (Cronbach’s alpha values between .82 and 0.93; Thiel & Paul, 2006), convergent and discriminant validity for the EDI-2 were established. Higher scores on the EDI-2 represent greater presence of attitudinal and behavioral features associated with the ED.

Sensory and Multisensory Processing Assessment task

In this study, we assessed the sensory biases and integration of patients and control participants with the Multisensory Processing Assessment (MPA) task, which can be used in a clinical setting easily, as it does not require complicated material. In this task, participants had to distinguish the shape of small ellipses using only visual, only tactile or both visual and tactile information. In a previous study, Helbig & Ernst (2007) demonstrated that healthy participants integrate the tactile and visual information in this task. Participants sat in front of the experimental setup that comprised a chin rest and a metallic structure to present the stimuli. The stimuli consisted of a high

relief ellipse (1.25 mm relief) that protruded on one or both sides of a flat 3D printed black plate (60 mm × 80 mm). The stimuli were inserted vertically between two rails of the metal structure behind a front panel with a 50 mm circular hole at the center (Fig. 2.5). The lighting was controlled by dimming the lights in the room and by illuminating the shape with LED lights placed on the back side of the front panel around the hole. In front of the hole, a semi-transparent screen blurred vision in order to equalize the reliability of visual and tactile information (see below). The height of the chin rest was adjusted so that the stimulus would be at eye level. The distance between the eye and the stimulus was about 35 cm.



Figure 2.5. Experimental setup. The left panel shows a participant reaching for the stimuli in the bimodal condition. The right panel shows a detail from the back side. Note that LED lights surrounded the aperture behind the black panel to control lightning conditions.

At each trial, the experimenter inserted a stimulus plate in the structure and brought it behind the hole. In the visual condition, the stimulus had a high relief ellipse on the front side, which the participants could see through the hole of the panel. In the tactile condition, the participants extended their arm and reached behind the panel to touch the high relief ellipse printed only on the back side of the stimulus plate. Participants touched the stimulus without moving their finger for about 3 s (unlike Helbig & Ernst, 2007, who allowed the participant to move the finger). In the bimodal conditions, the participants looked at a double-sided printed ellipse. Participants could

see the ellipse on the front side of the stimulus while touching the ellipse on the back side. The presentation of the stimulus lasted about 3 s in all conditions and the task of the subjects was to report verbally whether the stimulus was elongated vertically or horizontally.

In order to avoid visual dominance, we degraded the visual information by placing plastic film on a transparent screen in front of the hole (Fig. 2.5). We adjusted the distance of the screen in preliminary experiments with other (healthy) participants so that the discrimination threshold of the visual information would approximatively match the threshold in the tactile modality (see preliminary studies in [Appendix 1B](#)).

In each condition, we used the method of constant stimuli to find out the eccentricity of the ellipse that participants perceived as circular, and the minimal eccentricity difference that participants could be perceived as elliptical. Following Helbig & Ernst (2007), the ellipse eccentricity, $EA_{diff} = y - x$, corresponds to the difference between the lengths of the vertical (y) and horizontal (x) axes.

The experiment included two unimodal conditions and three bimodal conditions. In the unimodal conditions (V or T), the eccentricity EA_{diff} of the ellipses ranged from - 3.0 to 3.0 mm (ellipses in Series A, see. Table 2). In the bimodal conditions (B), the visually and tactilely presented ellipses could be consistent or inconsistent. In the bimodal consistent condition (B0), we used ellipses from Series A printed on both sides of the stimulus plate. In the bimodal inconsistent conditions, there was a conflict between the eccentricities of the visual and tactile ellipses. The conflict, $\Delta = EA_{diff,V} - EA_{diff,T}$, is defined by the difference between the eccentricities of the visual and tactile ellipses. A positive conflict corresponds to a visual ellipse that is more elongated along the vertical direction than the tactile ellipse while a negative conflict corresponds to the opposite case. In the first bimodal inconsistent condition (BM1) with conflict $\Delta = -1$, we used ellipses from Series A on the front (visual) side and the corresponding ellipses from Series B on the back (tactile) side. In the other bimodal inconsistent condition (BP1) with conflict $\Delta = +1$, we used ellipses from Series B in the front (visual) side and ellipses from Series A on the back (tactile) side.

The experiment was divided into four blocks of 80 trials. Each block included two series of eight trials in the five experimental conditions. The eight possible ellipse eccentricities for each condition were randomized within each single series and the experimental condition changed every two series. The order of the conditions within each block was the same for all blocks (V, T, BM1, B0 and BP1). In total, the eight ellipses were presented 8 times in each condition, yielding a total of $5 \times 64 = 320$ trials. The whole experiment lasted about one and half hours and was administered in a single day. Breaks were included as often as needed to avoid fatigue and insure maximum attention during the experiments.

Table 2 Visual, tactile and bimodal stimuli used in the unimodal and bimodal conditions.

	1	2	3	4	5	6	7	8
Ellipse Series A								
Vert. (y, mm)	7	8	8.8	9.4	10	10	10	10
Horiz (x, mm)	10	10	10	10	9.4	8.8	8	7
EA_{diff}	-3.0	-2.0	-1.2	-0.6	0.6	1.2	2.0	3.0
Ellipse Series B								
Vert. (y, mm)	8	9	9.8	10	10	10	10	10
Horiz (x, mm)	10	10	10	9.6	0.4	7.8	7	6
EA_{diff}	-2.0	-1.0	-0.2	0.4	1.6	2.2	3.0	4.0

The eccentricity of the stimuli EA_{diff} corresponds to the differences between the length of the x and y axes. See text for information on how stimuli in series A and B were used in the unimodal and bimodal conditions.

Optimal Integration Model

The optimal integration model (see Introduction) prescribes that the best estimate concerning the attribute of interest corresponds to a weighted average between the cues (Ernst & Banks, 2002):

$$s_b = w_V w_S + w_T w_{ST} \quad (1)$$

Where s_V and s_T are the visual and tactile size cues. For this study, the two sensory cues correspond to the eccentricity EA_{diff} of the ellipse that is seen and/or touched. The weights given to each sensory signal: w_V and w_T , should be proportional to the reliability of the stimulus:

$$w_V = \frac{R_V}{R_V + R_T} = \frac{\sigma_T^2}{\sigma_V^2 + \sigma_T^2} \quad w_T = \frac{R_T}{R_V + R_T} = \frac{\sigma_V^2}{\sigma_V^2 + \sigma_T^2} \quad (2)$$

where the reliability $R_i = 1/\sigma_i^2$ is simply the inverse of the noise (variance) of the corresponding cue. Assuming that the visual and tactile cues are independent and normally distributed, it can be

shown that the optimal (or Maximum Likelihood) estimate s_B that combines the two cues has a variance:

$$\sigma_B^2 = \frac{\sigma_V^2 \sigma_T^2}{\sigma_V^2 + \sigma_T^2} \quad (3)$$

that is not only lower than that of the single cues but the lowest possible given the noise associated with each cue.

Predicted Bias in the bimodal conditions

In the following, we assume that the tactile and visual cues s_i ($i = T$ or V) can be biased:

$$s_i = s_i + b_i$$

where s_i is the perceived eccentricity of the ellipse, s_i the actual eccentricity of the ellipse (EA_{diff}) and b_i the bias reflecting the distortion of the ellipse shape. From the definition of EA_{diff} , a negative bias indicates a widening of the ellipse or elongation of the horizontal axis relative to the vertical axis. By definition, the PSE denotes the eccentricity of the ellipse s that is perceived as circular

$$s_i = s_i + b_i = PSE + b_i = 0$$

which implies that $PSE_i = -b_i$. Therefore, a positive PSE corresponds to a widening of the ellipse.

If the sensory cues are biased and averaged as in equation (1), one can derive a prediction for the bias in the bimodal conditions:

$$\begin{aligned} s'_{B,\Delta} &= w_V s'_V + w_T s'_T \\ &= w_V (s_V + b_V) + w_T (s_T + b_T) \\ &= w_V (s_V + b_V) + w_T (s_V - \Delta + b_T) \\ &= s_V + w_V b_V + w_T b_T - w_T \Delta \\ &= s_V - (w_V PSE_V + w_T PSE_T - w_T \Delta) \end{aligned}$$

where $\Delta = s_V - s_T$ is the conflict between the visual and tactile cues. The PSE in the bimodal conditions predicted the MLE is therefore

$$PSE_{B,\Delta} = w_V PSE_V + w_T PSE_T + w_T \Delta \quad (4)$$

If the two cues are inconsistent ($\Delta \neq 0$), the above equation shows that the PSE is shifted by an amount that is proportional to the tactile weight $w_T \Delta$. This equation also predicts the PSE for the visual dominance hypothesis ($w_V = 1$ and $w_T = 0$) and tactile dominance hypothesis ($w_V = 0$ and $w_T = 1$). In particular, the bimodal PSE_B under the visual dominance hypothesis should correspond to the unimodal PSE_V and not be affected by the conflict Δ since $w_T = 0$. In contrast, the bimodal PSE_B under the tactile dominance hypothesis should correspond to the unimodal tactile $PSE_T \pm \Delta$. Finally, the best modality hypothesis corresponds to the visual or tactile dominance hypothesis depending on which modality has the lowest discrimination threshold.

In summary, the optimal integration hypothesis yields two predictions that can be tested experimentally in the bimodal conditions. First, the bimodal discrimination thresholds should be lower than the unimodal thresholds. Second, the PSEs should be shifted toward the most reliable cue in proportion to the relative reliability (or weight) of that cue, which can be demonstrated experimentally when there is a conflict between the two cues.

Data Analysis

The responses of each participant in each condition were fitted with a cumulative normal probability distribution using maximum likelihood estimation to obtain a psychometric function representing the probability of judging the stimulus as vertically oriented (see Fig. 2.6). The three bimodal conditions were fitted together, with a common slope but a different intercept for each condition. The psychometric functions in the bimodal conditions were computed as a function of the eccentricity of the visual cue and the shift between them reflects the influence of the tactile cue. For each psychometric curve, we computed the PSE, i.e. the ellipse that was perceived as vertically oriented in 50% of the trials and was thus perceived as a circle. The discrimination threshold (DL) – or Just Noticeable Difference (JND) – was defined as the difference between the PSE and the ellipse that was perceived as vertically oriented in 84% of the trials. The DL corresponds to the standard deviation of the normal distribution underlying the psychometric function and is an estimate of noise σ associated with the unimodal or bimodal cues (see equations (2) and (3)).

For each participant, we computed the weight of each cue (eq. (2)) and the optimal DL predicted by MLE from the unimodal DLs (eq. (3)). The data of one AN patient was not included in the analyses because she could not perceive the eccentricity of the ellipses in the tactile modality at all ($DL_H = 64.19$) and also had a large threshold in the visual and bimodal conditions ($DL_V = 3.11$; $DL_B = 3.00$).

We used a two-way mixed ANOVA with the group as a between subject factor and the experimental condition (visual, tactile and bimodal) as a within-subject factor to analyze the PSEs and DLs in the unimodal and bimodal conditions. The ANOVA was followed by Tukey post-hoc tests to test the difference between groups pairwise. Then, we used paired t-tests to compare the observed PSEs or DL with the corresponding predicted values. Finally, we performed a Canonical Correlation Analysis (CCA) between the psychophysical and clinical variables in order to find the two linear combinations (or canonical variables) that are maximally correlated with each other.

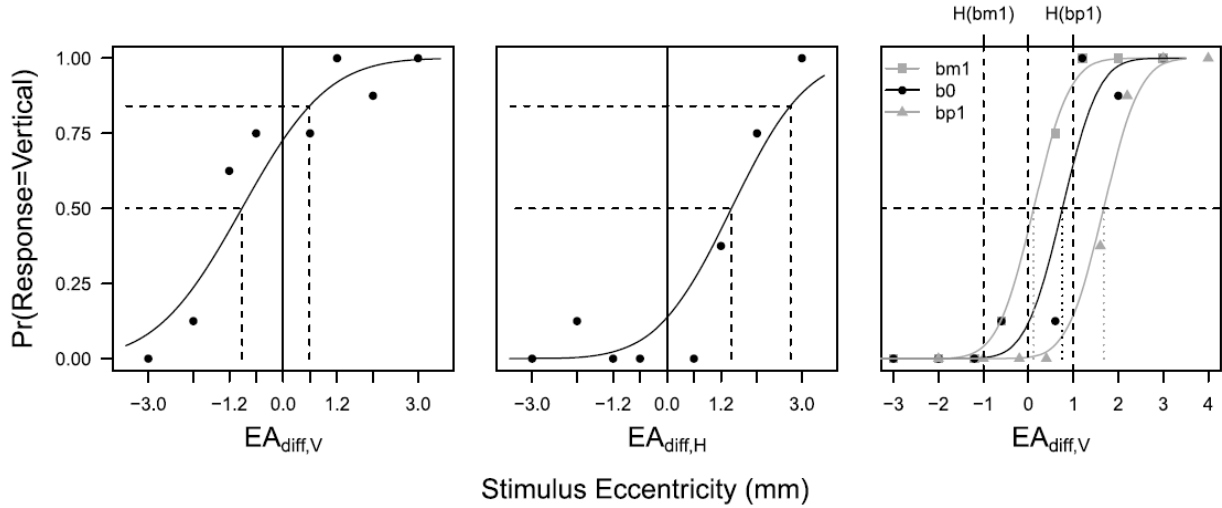


Figure 2.6. Psychometric functions from a control participant. The cumulative normal psychometric curves represent the probability of perceiving the ellipse as vertically oriented as a function of the actual ellipse eccentricity (EA_{diff}). In the unimodal conditions (left and middle panels), the vertical solid line indicates the circular shape. The dotted line corresponding to 50% indicates the Point of Subjective Equality (PSE) and the horizontal distance between the two vertical dotted lines corresponds to the 84% discrimination threshold (DL). In the bimodal conditions (right panel), data from the three conditions were fitted together using a common slope but a different intercept model. The vertical lines represent the prediction of the Maximum Likelihood Estimation (MLE) model (in absence of biases) if the participant relied only on the tactile modality to judge the shape of the ellipses. In contrast, the psychometric curves should overlap if the participant relied only on the visual modality.

To give some indication of the power of the study, we report the power of various t-tests and two-way mixed ANOVAs to detect meaningful differences between groups or experimental conditions. With respect to the PSE, we computed the power of one-sample t-tests to detect a 5% distortion of the ellipse ($EA_{diff} \approx 0.5$ mm, Cohen's effect size $d = EA_{diff}/s_{PSE} = 0.5/0.42 = 1.19$), the power of independent-sample t-tests to detect a 5% distortion between groups ($d = 1.19$), and the power of

paired t-tests to detect the effect of the conflict predicted by the optimal integration hypothesis in the bimodal conditions ($d = w_T \cdot \Delta / s_{PSEdiff} = 0.5 \cdot 1 / 0.52 = 0.96$, see eq. (4)). The power of these tests ranged 72% – 99% depending on the size of the group (in general t test involving the BCHC group were less powerful). With respect to the DLs, we computed the power of paired t test to detect the increase of sensitivity in the bimodal prediction predicted by the optimal integration hypothesis, which corresponds approximatively to a 30% decrease of the bimodal threshold assuming equal unimodal thresholds (see eq. (3)). The corresponding effect size is $d_z = 0.3 \cdot DL_u / s_{DLdiff} = 0.3 \cdot 1.55 / 0.49 = 0.94$, where DL_u is the average DL in the unimodal conditions of the pilot experiment. The power ranged from 68% for the BCHC group to 96% for the HC group. We also computed the power of a two-sample test to detect a 30% change in the DLs between two groups. The effect size was smaller ($d = 0.3 \cdot DL_u / s_{DL} = 0.3 \cdot 1.55 / 0.60 = 0.775$) because the standard deviations in the pilot experiment were larger. The power ranged from 43% for a difference between AN and BCHC group to 60% for a difference between the AN and HC group. Finally, we used simulations to compute the power of two-way mixed ANOVA contrasting the three groups and three conditions with the same assumptions as for the t-tests (Kerns, 2020). For the DLs, the power for the group, condition and interaction effects was 81%, 98% and 76% respectively. For the PSEs, the power of the two-way mixed ANOVA was above 99% for all effects. Power analyses are sensitive to changes in the parameter values and should be taken only indicatively. Estimates of the variability of the discrimination thresholds and PSE_s , s_{DL} and s_{PSE} were obtained by pooling together the results of the pilot studies. We used the results of the main study to compute the standard deviations $s_{PSEdiff}$ and s_{DLdiff} of the difference for each subject between the PSE_s or DL_s in each sensory modality because different subjects participated to the tactile and visual conditions in the pilot experiments. All analyses were conducted with R version 3.6.1 (R Core Team, 2010).

2.2.4. Results

Table 3 reports the Point of Subjective Equalities (PSEs) and Discrimination Thresholds (DLs) in the unimodal conditions for each group and the standard deviation of the individual differences between the PSEs or DLs in the two unimodal conditions. The table includes also the common slope of the psychometric functions fitted to the three bimodal conditions together (see Fig. 2.7.). Note that while we used and reported ANOVAs to analyze our results, we also used robust methods

based on the 20% trimmed mean to check the validity of the main tests (see [Appendix 2B](#) for robust analyses and outlier analysis).

Unimodal Conditions

Fig. 2.7 (left panel) shows the PSEs for the three groups in the unimodal visual and tactile conditions. In the unimodal conditions, the tactile PSE increased on average from 0.5 mm (5%) for the HC to 1.07 mm (11%) for the AN group while the visual threshold increased from - 0.1 mm to 0.1 mm for the same two groups (see Table 3). This positive bias of the PSE in the tactile modality, which increased for the AN group, indicates that vertically elongated ellipses were perceived as circular, and corresponds to a widening or fattening of the ellipse. One-sample t-tests confirmed the PSEs were significantly different from 0 in the tactile modality (HC: $t(18) = 4.45$, $p < .001$, $d = 1.02$; BCHC: $t(8) = 6.13$, $p < .001$, $d = 2.04$; AN: $t(15) = 7.25$, $p < .001$, $d = 1.81$), but not in the visual modality (HC: $t(18) = -1.03$, $p = .32$, $d = 0.24$; BCHC: $t(8) = -0.34$, $p = .74$, $d = 0.11$; AN: $t(15) = 0.84$, $p = .41$, $d = 0.21$). A two-way mixed ANOVA on unimodal PSEs showed an effect of sensory modality ($F(1, 41) = 37.89$, $p < .001$, $\eta_p^2 = 0.48$) and group ($F(2, 41) = 7.06$, $p < .01$, $\eta_p^2 = 0.11$). The interaction between the group and condition was not statistically significant ($F(2, 41) = 0.79$, $p = .46$, $\eta_p^2 = 0.02$). Pairwise t-tests confirmed a statistically significant difference between the tactile and visual modality for all groups (HC: $t(18) = -3.44$, $p < .01$, $d_{rm} = 1.29$; BCHC: $t(8) = -3.66$, $p < .01$, $d_{rm} = 2.05$; AN: $t(15) = -4.65$, $p < .001$, $d_{rm} = 1.80$). The Tukey pairwise comparison within sensory modalities showed a statistically significant difference only between the HC and AN groups in the tactile modality ($t(75.9) = -3.20$, $p < .01$). The discrimination thresholds in the visual condition were larger than in the tactile condition for all groups (HC: $t(18) = 2.39$, $p = .03$, $d_{rm} = 0.69$; BCHC: $t(8) = 2.12$, $p = .07$, $d_{rm} = 0.83$; AN: $t(15) = 2.34$, $p = .03$, $d_{rm} = 0.71$). The unimodal discrimination thresholds increased for the AN group with respect to the two other groups. These two effects were confirmed by a mixed ANOVA that showed a main effect of group ($F(2, 41) = 9.94$, $p < .001$, $\eta_p^2 = 0.33$) and condition ($F(1, 41) = 10.85$, $p < .01$, $\eta_p^2 = 0.21$). The interaction between groups and conditions was not significant ($F(2, 41) = 1.18$, $p = .32$, $\eta_p^2 = 0.05$).

Table 3 DLs and PSEs in unimodal and bimodal conditions for each experimental group. Mean $\pm$ Median Absolute Deviation (MAD) adjusted to give a robust estimate of the standard deviation.

	PSE		DL		
	Visual	Tactile	Visual	Tactile	Bimodal
HC	-0.11 ± 0.53	0.54 ± 0.45	1.18 ± 0.28	0.90 ± 0.34	0.68 ± 0.18
BCHC	0.03 ± 0.35	0.71 ± 0.24	1.24 ± 0.52	0.96 ± 0.33	0.87 ± 0.18
AN	0.10 ± 0.31	1.07 ± 0.55	2.05 ± 0.65	1.40 ± 0.28	1.18 ± 0.37

Finally, we computed the weight for each sensory condition (see eq. (2)). The average weight of the somatosensory cue increased slightly from the HC control group (0.62 ± 0.20) to the AN group (0.65 ± 0.17 ; see right panel of Fig. 2.7.). A one-way ANOVA revealed that the difference across groups was not statistically significant ($F(2, 41) = 0.10$, $p = .90$). Only the tactile weight was included in this analysis because the sum of two weights is equal to one by definition.

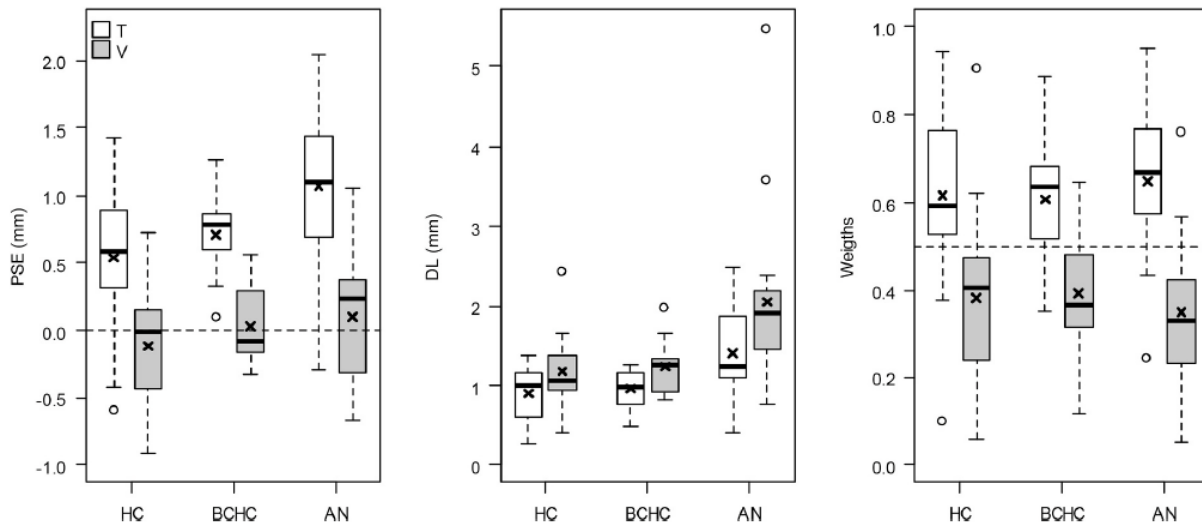


Figure 2.7. Points of Subjective Equality (left), discrimination thresholds (middle) and weights (right) in the unimodal conditions (T: tactile, V: visual). The boxplots show the means (crosses), the median (horizontal bars) and inter-quartile range (boxes). The whiskers extend to the most extreme data point, which is no more than 1.5 times the IQR.

Bimodal Conditions and Optimal Integration

Optimal integration makes two predictions in the bimodal conditions: i) the PSEs should be shifted toward the most reliable cue in proportion to its relative reliability (or weight) when there is a conflict (see eqs. (1) and (2)), ii) the bimodal discrimination thresholds should be smaller than the unimodal thresholds. Fig. 2.8. (left panel) shows the PSEs in three bimodal conditions for each group (black solid symbols) and the predictions according to the visual dominance hypothesis (grey empty symbols), tactile dominance hypothesis (grey solid symbols) and optimal integration hypothesis (black empty symbols). A two-way mixed ANOVA of the bimodal PSEs revealed a statistically significant effect of the conflict Δ ($F(2, 82) = 163.14$, $\varepsilon = 0.86$, $p < .001$, $\eta_p^2 = 0.80$), which indicates that the PSEs, which are expressed relatively to the eccentricity of the visual ellipse (see Methods), are influenced by the tactile cue. The small increase in the PSEs of the BCHC and AN groups relative to the HC group was not statistically significant ($F(2, 41) = 2.08$; $p = .14$, $\eta_p^2 = 0.09$). The interaction was also not statistically significant ($F(4, 82) = 0.58$, $\varepsilon = 0.86$, $p = .66$, $\eta_p^2 = 0.03$).

Fig. 2.8. also shows that the average PSEs in the bimodal conditions (black solid symbols) were close to the value predicted by the optimal integration hypothesis (black empty symbols) for all groups and conditions. Paired t-tests confirmed that the differences were not statistically significant ($p > .05$). Moreover, the actual PSEs differed markedly from the PSE predicted by the visual and tactile dominance hypotheses in bm0 ($\Delta = 0$) and bp1 ($\Delta = +1$) bimodal conditions where these predictions differed from the optimal integration prediction.

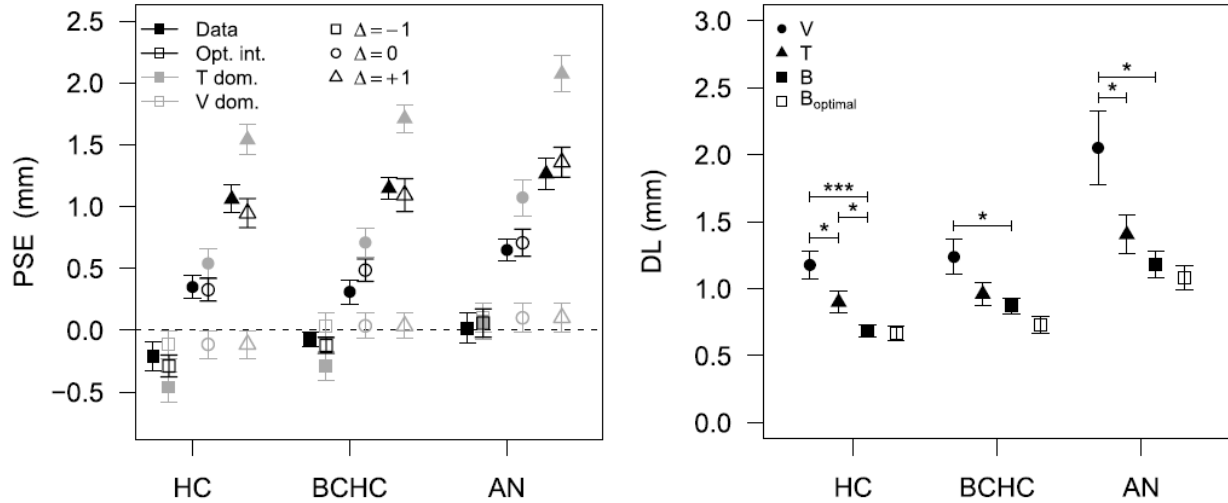


Figure 2.8.0-1 Points of Subjective Equality and Discrimination thresholds in bimodal conditions. Left: Average point of Subjective Equality ($\pm$ SE) in bimodal conditions. Observed (black solid symbols) and predicted (grey or empty symbols) in the bimodal conditions (black empty: optimal integration hypothesis, grey solid: tactile dominance hypothesis, grey empty: visual dominance hypothesis). In the consistent bimodal condition (circles), the PSEs for the visual and tactile dominance hypotheses correspond to the PSEs in the unimodal conditions. In the inconsistent bimodal conditions (squares or triangles), the PSE for the visual dominance hypothesis corresponds to the unimodal condition and is not affected by the conflict since $w_h = 0$ in equation (4). In contrast, the PSE for the tactile dominance hypothesis corresponds to the unimodal PSEH $\pm \Delta$ (see eq. (4)). Right: Discrimination thresholds. Average discrimination thresholds ($\pm$ SE) in the unimodal (circles and triangles) and bimodal (squares) conditions. The empty squares (B_{optimal}) corresponds to the average discrimination threshold predicted by the optimal cue combination model, which was computed for each subject (see eq. (3)). The stars indicate the p value of the corresponding paired t-tests (*: $p < .05$; **: $p < .01$; ***: $p < .001$; see also text).

Fig. 2.8. (right panel) shows the discrimination thresholds in the unimodal and bimodal conditions. A one-way ANOVA on the bimodal thresholds showed a significant effect of group ($F(2,41) = 13.3$, $p < .001$, $\eta^2 = 0.39$), which reflects the worse performance by the AN group relative to the BCHC group and HC group as in the unimodal conditions. In order to test whether the visual and tactile cues are integrated optimally, we compared the observed (B) and predicted (B_{optimal}) bimodal thresholds. For the three groups, the difference was not statistically significant (HC: $t(18) = 0.26$, $p = .79$, $d_{\text{rm}} = 0.09$; BCHC: $t(8) = 1.38$, $p = .20$, $d_{\text{rm}} = 0.77$; AN: $t(15) = 0.81$, $p = .43$, $d_{\text{rm}} = 0.25$). As predicted by the optimal integration hypothesis, the bimodal thresholds were lower than the visual threshold for the three groups (HC: $t(18) = -4.27$, $p < .001$, $d_{\text{rm}} = 1.44$; BCHC: $t(8) = -2.56$, $d_{\text{rm}} = 1.21$, $p = .03$; AN: $t(15) = -2.83$, $p = .01$, $d_{\text{rm}} = 1.06$) and lower than the tactile

threshold but only for the HC group ($t(18) = -2.26$, $p = .04$, $d_{rm} = 0.80$). In fact, the bimodal thresholds are also compatible with the tactile dominance hypothesis for the BCHC and AN groups because the difference between the tactile and bimodal thresholds was not statistically significant (BCHC: $t(8) = -0.65$, $p = .53$, $d_{rm} = 0.40$; AN: $t(15) = -1.61$, $p = .13$, $d_{rm} = 0.45$).

Canonical Correlation and Classification Analysis

In this section, we examine the relation between the psychophysical and clinical variables, and whether it is possible to use psychophysical scores to classify controls and patients.

The objective of the Canonical Correlation Analysis is to find the linear combination of clinical variables (BMI, BSQ and EDI) that is best correlated with a linear combination of psychophysical variables, which included the two PSEs and DLs in the unimodal conditions and the DL in the bimodal condition.

As shown in Fig. 2.9, the two first canonical variates were highly correlated ($r = 0.704$; Wilk's lambda test: $F(15, 99.782) = 2.076$, $p = .017$), indicating that psychophysical and clinical variables share a lot of information. The first canonical variable for the clinical scores gave higher weights to EDI-2 and BMI scores (standardized canonical coefficients: EDI-2 = 0.073, BMI = -0.074, BSQ = 0.037). For the psychophysical scores, the weight was largest for the unimodal PSEs and the tactile and bimodal DLs ($PSE_V = 0.067$; $PSE_T = 0.089$; $DL_V = 0.001$; $DL_T = 0.051$; $DL_B = 0.055$). The correlation within each group ranged from 0.19 for the AN group to 0.51 for the HC group, indicating that the global correlation was primarily driven by the difference between groups.

Canonical variates can also be used to classify patients by identifying thresholds that break the continuous values into two or three regions. The first canonical variate based on clinical variables separated the HC (white dots) and AN (black dots) groups almost completely (34/35 or 97% these women were classified correctly), which might be expected since BSQ was used as a criterion to define the BCHC group and the BMI of AN patients differed markedly from both control groups. Interestingly, 91% (32/35) of women belonging to the HC and AN groups were classified correctly by the psychophysical variables in this analysis. The BCHC women formed an intermediate group between the HC and AN groups (grey dots). If one puts together both control groups, the clinical and psychophysical variates correctly classified 91% (40/44) and 89% (39/44) of the women in these two groups respectively.

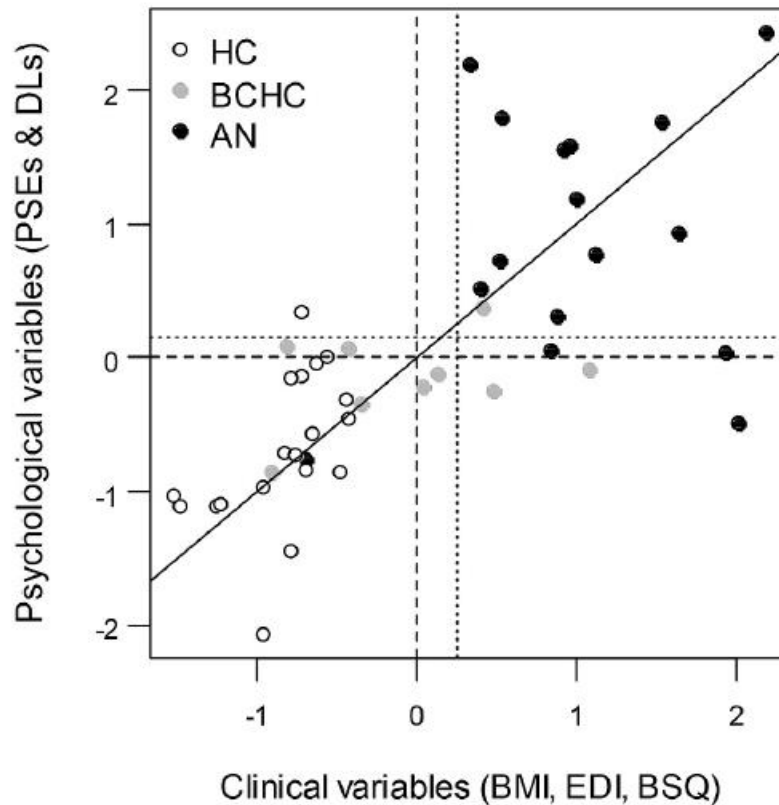


Figure 2.9.0-2 Canonical Correlation Analysis. The solid line corresponds to the regression line. The dashed lines separate the HC group from the AN group while the dotted lines separate the HC and BCHC groups from the AN group.

To assess the significance of these results, we compared the percentage of correct classifications between healthy controls (combining HC and BCHC groups) and AN patients obtained with different methods using leave-one-out cross-validation. The percentage of correct classifications based on psychophysical variables was 80% for the canonical correlation, 89% for logistic regression and 93% for linear discriminant analysis. In comparison, the percentage of correct classifications based on clinical variables was 87% for canonical correlation, 91% for logistic regression and 89% for linear discriminant analysis. These results show that methods like the logistic regression and the linear discriminant analysis are better at classifying participants. The classifiers based on clinical variables included only three variables and usually performed better. On the other hand, we did not attempt to optimize the set of psychophysical variables.

2.2.5 Discussion

The perceptual deficits in Anorexia Nervosa form a disparate set. Psychophysical tasks such as the one used in this study allows one to measure precisely two different but complementary aspects of perception. The points of subjective equality (PSEs) measure the accuracy, veridicality or bias of the perception (e.g. the strength of an illusion), while the discrimination thresholds measure the precision of the perception (e.g. the sensory acuity or noise in a sensory channel). The task used in this study allowed us to measure and compare the visual and tactile biases and performance in the perception of the shape of small ellipses. Finally, in the bimodal condition, this task also allows one to investigate multi-sensory integration processes, assess the weights given to each sensory modality and test the optimal integration hypothesis.

The first section of this discussion is focused on the large tactile biases observed in controls and patients with AN. Then, we compare the discrimination performance and multisensory processes of these two populations. The next sections are focused on the results of the control group with body concerns and how psychophysical variables correlate with clinical ones. Then, we identify the pathways that might be at the origin of the perceptual distortions observed in this study in a model that integrates tactile and visual input with body and object representations. Finally, we discuss the limitations of the study before summarizing the main findings in the conclusions.

Distortions of ellipses' shape

A first motivation for the study was to investigate the perceptual biases in the different sensory modalities and populations. While the ellipses' eccentricity was perceived veridically in the visual modality, all groups notably overestimated the width of the ellipse relative to its height in the tactile modality. The shape distortion was about 5% for the healthy control group, 7% for the healthy control group with body concerns and 11% for the AN group. In contrast, the ellipse shape was perceived almost veridically in the visual modality, with a difference of less than 2% between the three groups.

The observation that healthy individuals perceived the ellipses as wider in the tactile modality differs from the results of the original study by Helbig & Ernst (2007). A possible explanation for this discrepancy is that hand orientation can affect the perceived shape of our stimulus. Participants in our study touched the ellipse with the fingertip aligned or close to the vertical direction without moving. In contrast, the participants in Helbig & Ernst (2007) study appeared to touch the ellipses with an angle close to 45° (see Fig. 2 in Helbig & Ernst (2007)). Our results are in agreement with

studies showing that the perceived size of objects is larger when the objects are oriented medio-laterally across the hand rather than proximo-distally (Longo, 2017; Longo & Haggard, 2011).

Importantly, we also found that AN patients overestimated the ellipses' width more than the control group. This observation is in agreement with various reports that AN patients overestimate the distance between two points on the skin in a distorted way (Keizer et al., 2011, 2012; Spitoni et al., 2015; see also Introduction). The classical explanation for size or shape distortions in the tactile modality is that the density of tactile receptors affects the cortical representation of tactile stimuli in the primary somatosensory cortical area. The presence of biases in the haptic perception of the size of objects across different body parts is a classic observation known as Weber's illusion. Typically, the perceived size of an object touching the skin (or the perceived distance between two points) decreases in body parts with lower tactile acuity and mechanoreceptor innervation. However, the spatial density of mechanoreceptors does not explain Weber's illusion fully. First, the distortion is attenuated with respect to the actual variations in receptor density and tactile acuity. The magnitude of Weber's Illusion is only 10% of what would be predicted considering the variation in tactile acuity or mechanoreceptor density across skin regions (Taylor-Clarke et al., 2004). Second, the magnitude of the distortion can be further reduced by manipulating the size of the body visually (Taylor-Clarke et al., 2002). These findings show that perceptual distortions also involve higher level, possibly multimodal mechanisms that partly compensate for low-level distortions (Longo & Haggard, 2011).

The results of our study, however, cannot be explained in this manner. As a matter of fact, there is little evidence that receptor density changes within a body part and, in particular, that the density of mechanoreceptors is higher in the medio-lateral direction with respect to the proximo-distal direction. To explain this type of distortion, Longo & Haggard (2011) have suggested that it might be caused by the shape of tactile receptive fields (RFs), which are typically more elongated along the proximo-distal axis with the long axis being about twice the length of the short axis (RFs; (Brooks et al., 1961; Brown et al., 1975; Powell & Mountcastle, 1959). While this is a possibility, Longo & Haggard (2011) also note that the magnitude of the distortions is typically smaller. In fact, the magnitude of the tactile distortions observed in our study amounted to only 10% of the ellipse size, much less than the 50% that might be predicted from the RF eccentricity. If the shape of the RF field played a role in the distortion, this observation suggests that higher level compensatory processes would attenuate the distortion (Taylor-Clarke et al., 2004). Alternatively, if the shape of the RF did not play a role, then this distortion would necessarily originate at a higher level of somatosensory information processing.

That the AN patients perceived the shape of the ellipses as more distorted than did the controls reinforces the idea that higher-level processes play an important role in any explanation of the observed spatial distortions. As a matter of fact, there is no evidence that mechanoreceptor density and/or the shape of their RFs change in AN with respect to healthy controls. In fact, the results of our study, like those of (Spitoni et al., 2015), suggest that higher-level processes involved in the tactile perception of distances or shapes function abnormally in AN. While it is not possible to exclude a priori that different mechanisms underlie the observed perceptual distortions in healthy controls and AN patients, the simplest explanation is that the same processes are involved in both cases.

Discrimination Thresholds

The second motivation for the study was to find out whether AN would affect the reliability of the visual and tactile cues. We found that the tactile and visual discrimination thresholds increased for the AN group relative to the control group, which indicates that patients with AN were worse at discriminating the ellipses shapes than the control group in both sensory modalities. Interestingly, we did not find a statistically significant difference between the two control groups, which suggests that the decrease in reliability of the sensory cues has an origin that is specific to AN.

As reviewed in the Introduction, there is some discrepancy in the literature about the presence of low-level sensory deficits. However, most studies including patients with AN restricting type and a severe degree of malnutrition like our group found that visual or somatosensory acuity decreased in these patients (Caire-Estévez et al., 2012; Epstein et al., 2001; Spitoni et al., 2015). Accordingly, the increase of tactile and sensory threshold in our study might reflect a reduced capacity to reliably estimate the dimension of the ellipses, due to a decrease in the tactile and visual acuity of our patients (sensory thresholds are classically interpreted as a measure of noise of the corresponding sensory cues in Psychophysics, see Gescheider, 1997).

A possible problem with our interpretation is that our task is not a direct measure of sensory acuity since judging the shape of an ellipse requires comparing the extension of the ellipse along two orthogonal axes. Thus, it is not possible to exclude that the higher thresholds observed in our study might reflect a limit in the precision of the comparison process rather than the precision with which each dimension is estimated. It would be useful to add such a measures in future studies.

Another possible problem with our interpretation of the observed increase DL in AN is that some studies that used a Signal Detection Theory framework found that AN patients were not worse at discriminating body shapes than controls in the visual modality (Gardner & Moncrieff, 1988;

Smeets et al., 1999). However, the mean BMI (15.15 ± 2.64) and weights (39.8 ± 6.9 kg) of AN patients in our study was markedly lower than in those studies (BMI in Smeets et al., 2009: 17.74 ± 2.95 ; mean weight in Gardner & Moncrieff, 1988: 44.6 kg). This difference between the patients might explain why these studies did not find an effect on the sensitivity.

Another question related to the discrimination thresholds is whether patients with AN give more weight to somatosensory inputs than to the visual ones (Eshkevari et al., 2012; Longo et al., 2015) or viceversa (Case et al., 2012). To address this question we computed the weight of each of the sensory cues for each group. In the optimal integration theoretical framework, the weight of a cue is proportional to its reliability and normalized with respect to the other sensory cues (see eq. (2)). The weight of the tactile cue slightly increased by about 4% in the AN group with respect to the HC or BCHC group. However, there was considerable overlap between the groups and the difference was not statistically significant. Our study does not bring strong evidence supporting the idea that the reliability of the tactile cues changed relative to the reliability of the visual cues. Further research with a larger sample and/or different stimuli is needed to find out whether AN affects the weight of the tactile and visual cues.

Multisensory Integration

The third motivation and main objective of this study was to test the hypothesis presented in the Introduction that body shape distortion in AN might be linked with an aberrant multisensory integration process (Case et al., 2012; Eshkevari et al., 2012). More specifically, the aim was to directly test whether AN patients integrate multi-modal sensory information optimally (see Methods). Our results show that the PSEs in the bimodal conditions corresponded to the values predicted by the optimal integration hypothesis. They also differed clearly from the values predicted by the tactile or visual dominance hypotheses for all three groups. In summary, the analyses of the PSEs in the bimodal conditions with and without conflict indicate that AN patients integrated tactile and visual processes optimally like the two other control groups. In contrast, the analysis of the bimodal discrimination thresholds provided less clear-cut results. For the HC group, we found that the bimodal thresholds were on average lower than the two unimodal thresholds and did not differ from the predicted optimal threshold in agreement with previous findings (Helbig & Ernst, 2007). For the BCHC and AN groups however, the evidence was less conclusive because the magnitude of the bimodal DLs was close to the tactile threshold or in between the tactile thresholds and the optimal threshold. For both groups, the difference between the bimodal threshold and either the tactile or the optimal threshold was not statistically significant. As noted in the Results, the bimodal thresholds for these two groups are compatible with both the tactile

dominance hypothesis and the optimal integration hypothesis. Indeed, the tactile threshold did not differ either from the bimodal threshold or from the optimal threshold.

Body Concerned Healthy Control Group

A secondary objective of the study was to investigate whether body concerns can be linked to perceptual deficits or whether these deficits are specific to AN. Initial evaluation revealed that some healthy controls had body satisfaction scores in the range of the AN patients even though these participants had no history or diagnosis of Eating Disorders and a healthy BMI. To assess whether some perceptual deficits might be linked to body concerns and not specific to AN, we decided to split these participants in two control groups and analyze the BCHC group separately from the HC group who did not have the same body concerns.

With respect to the perceptual biases, we found the PSE of the BCHC participants were somewhere in the middle between the HC and AN groups in all conditions (see Fig. 2.7 for unimodal conditions and Fig. 2.8 for bimodal conditions). These results suggest that body concerns might be associated with a perceptual bias, independently of the AN diagnosis. Interestingly, previous studies investigating the relationship between perception and body satisfaction found a positive correlation between body satisfaction and tactile perception performances in patients with AN (Keizer et al., 2011; Spitoni et al., 2015). Moreover, Taylor & Cooper (1992) showed that the induction of low mood in a sample of female students led to greater disturbances in body size perception in the form of a more severe tendency to overestimate their body size, and significantly greater dissatisfaction with their body size. Furthermore, among the women who received the negative mood condition, the induction of low mood led to greater disturbances in body size perception (i.e. overestimating their body size significantly more and feeling greater dissatisfaction with their body size) in those who had body shape concerns compared to those with little or no concern with their body shape. Together, these results reinforce the hypothesis of a link between a distorted Body Representation and body dissatisfaction.

In contrast to the PSE, the discrimination thresholds of the BCHC participants did not differ from the HC. In particular, the DLs of the BCHC group did not increase in the unimodal conditions. This result suggests that body dissatisfaction affects the more abstract cognitive model of the body, but not the elementary sensory processing of the participants.

With respect to multisensory integration processing, the results on the discrimination thresholds are not fully conclusive. Overall, we believe that the PSEs provide strong evidence that this group integrated tactile and visual information in the bimodal condition like the two other groups and

that this study does not support the idea that multisensory integration processes involved in the visuo-tactile perception of 2D shapes are specifically affected by AN and/or body dissatisfaction.

Canonical Correlation Analysis

The last objective of this study was to find out whether perceptual biases are correlated with clinical scales characterizing eating disorders and body shape concerns. The main result of the canonical correlation analysis was that the first pair of canonical variates was highly correlated, indicating that psychophysical and clinical variables could categorize patients and controls in their respective group. While the correlation was driven more by group differences than by individual differences, the results of this analysis still suggest that evaluating the perceptual abilities of the patients could provide information that might be relevant clinically. Psychophysical variables classified AN patients and the control group without body concerns almost as well as clinical variables. In both cases, the women with body concerns were distributed in the middle with scores that partially overlapped the two other groups. We believe that this preliminary result should encourage further studies to investigate perceptual processes that might potentially help the clinician in the diagnosis.

An integrated Model of Perceptual Deficits in Anorexia Nervosa

In a review of somatosensation, Serino & Haggard (2010) developed a model of the interactions between tactile information and body representations in the brain (see Fig. 2.10). According to this model, the influence of MBRs might partially compensate for spatial distortions that originate from primary somatosensory contexts that are related to variations in mechanoreceptor density across body parts (Longo & Haggard, 2011; Taylor-Clarke et al., 2004). Importantly for the interpretation of our results, this model posits the existence of a pathway (Pathway 4) that mediates the formation of object representation from primary tactile sensations. This pathway would not provide direct information about the tactile object (Pathway 6) but a reference that modulates the perception in a top-down manner. For example, this pathway would explain how manipulating the size of a body part visual (via Pathway 5) can affect the tactile size of the object being touched (Taylor-Clarke et al., 2004).

Although AN is not discussed in Serino & Haggard (2010), their model is useful to interpret the results of our study. First, as noted in the introduction, there is considerable evidence that all MBRs are distorted in this disease. For our study, the most relevant MBR is probably the superficial schema, which mediates the formation of object representations from primary tactile sensations by

providing a reference frame and metrical information about the position and size of the tactile stimulus on the skin (Pathway 4). In this framework, the widening of the ellipses' shape observed in AN suggests that the superficial form, like body image and body schema, is distorted in AN. Moreover, the fact that healthy controls with body concerns perceived the shape of the ellipse as wider than healthy controls without body concerns suggests this distortion of the superficial form is not specific to AN but more generally related to body satisfaction and even, possibly, mood (Taylor & Cooper, 1992). In our opinion, it would also make sense to hypothesize that similar but relatively smaller distortions of the superficial form might be at the origin of the perceptual errors of the healthy group without body concerns. This explanation would be in line with the observation that healthy controls perceive body parts as larger than they really are (Longo & Haggard, 2011).

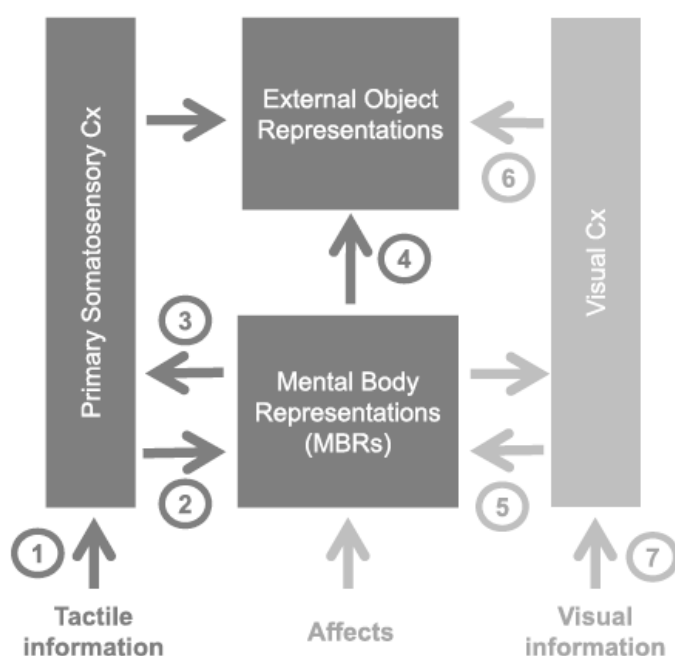


Figure 2.9.0-3 Relation between Mental Body Representations (MBRs) and External Object Representations (adapted and extended from Serino and Haggard, 2010). Dark grey circles 1 to 4 identify the pathways discussed in Serino and Haggard (2010). Light grey elements extend the original figure and are discussed in the text. Pathway 1 connects the body to “the somatosensory homunculus”, which is topographically organized and reflects the density of mechanoreceptors in the skin. Pathway 2 connects this area to higher-level representations of the body, such as body image, body schema or the superficial schema, which are involved in perception and/or action (Head and Holmes, 1911; Lloyd et al., 2003; Taylor-Clarke et al., 2002). Pathway 3 represents a top-down influence that might enhance or inhibit low-level tactile processing (Tipper et al., 1998; Taylor-Clarke et al., 2002). Finally, Pathway 4 mediates the formation of object representation from primary tactile sensations (see text).

In contrast, the increase of the discrimination thresholds, which is specific to the AN group in the visual, tactile and bimodal conditions might be attributed to a less precise processing of tactile (Pathway 1) and visual (Pathway 7) information. As discussed previously, this interpretation would be in line with previous results on elementary visual and somatosensory perception in patients with AN.

Limitations of the Study

The first limitation of the study is the small sample size, in particular for the BCHC group, which primarily affects the power of the comparison among groups. A larger sample size would be needed to perform a reliable within-group correlation analysis since it is known that sample correlations are inaccurate in small sample sizes (Schönbrodt & Perugini, 2013) and sensitive to outliers (Wilcox & Rousselet, 2018). The small size of the BCHC group is due to the difficulty to recruit this population in a targeted manner since it is not known in advance whether the healthy controls will have body concerns comparable to AN patients.

The second limitation of the study is the precision with which discrimination thresholds were measured. In our study, each condition included 64 trials, which is less than the 192 trials per condition used in the (Helbig & Ernst, 2007) study. The number of trials was limited by the duration of the experiment and availability of AN patients to participate in more sessions. Since a larger number of trials is necessary to estimate the discrimination thresholds with the same precision as the PSEs (King-Smith & Rose, 1997), it is possible that the weak correlations between observed and predicted thresholds in the bimodal conditions within groups might simply reflect the lack of precision in the estimation of the individual discrimination thresholds. A limited number of trials, however, does not invalidate comparison between conditions and/or groups since increasing the number of participants increases the precision of average value. In this respect, it might be noted that the sample size of the HC and AN groups in our study was larger than the number of participants in the original study by (Helbig & Ernst, 2007) (10 participants).

The third limitation of the study is the difference between the visual and tactile discrimination thresholds in the control group. To test the optimal integration hypothesis, it would be desirable to equalize the two thresholds because this hypothesis predicts that the gain in the bimodal condition is largest when the two sensory cues are equally reliable. When this is not the case, it becomes more difficult to distinguish between the best modality hypothesis and the optimal integration hypothesis because the predictions of the two hypotheses in the bimodal conditions become more similar. In our study, the two unimodal thresholds differed in all groups despite having been adjusted following a pilot study with a different group of healthy participants. The difference was

larger for the BCHC and AN groups, which rendered the results more difficult to interpret. In fact, the thresholds in the bimodal conditions did not differ in a statistically significant manner from the threshold observed in the tactile modality and/or from the threshold predicted by the optimal integration hypothesis.

2.2.6 Conclusion

The experimental paradigm in this study allowed us to measure the bias and the reliability of tactile and visual stimuli, separately and together. In this study, we related these two measures of sensory processing to different parts of Serino & Haggard's (2010) model of somatosensation and we proposed that the observed perceptual deficits might be caused by different dimensions of Anorexia Nervosa. First, we suggest that the perceptual biases observed in our study could be caused by distorted mental representations of the body and that body dissatisfaction might contribute to this perceptual distortion in AN patients and healthy women who are particularly concerned about their bodies. Second, we hypothesized that the increase in the discrimination thresholds in the tactile and visual modality that was specific to the AN group might be related to a loss of tactile and/or visual acuity linked with the malnutrition status of the patients. Third, the paradigm used in this study allows us to make quantitative predictions about the performance in bimodal conditions to test different hypotheses about sensory integration. In this respect, our results suggest that AN patients, like the two control groups, integrated tactile and visual information optimally. This result, based on the analysis of the PSEs, should be confirmed with more precise measurements of the discrimination thresholds in the future. Finally, we believe that the study of perceptual deficits in AN might also bring benefits in the future to the clinical evaluation and understanding of Anorexia Nervosa and related eating disorders.

Chapter 3

Bimanual Information Processing

After presenting results regarding the integration of somatosensations with other senses in [Chapter 2](#), here we evaluate information processing within the somatosensory modality. Indeed, bimanual operations to generate voluntary actions and interact with the surrounding environment is a cardinal feature of human behavior. In this chapter, we investigate the cognitive limitations and benefits involved in these coordinated movements.

In the first section, we study the sensory integration of proprioceptive information from the two hands when apprehending the size of objects, and we evaluate the influence of lifting the object on bimanual integration. To that end, we measure the unimanual and bimanual discrimination thresholds of the participants evaluating wooden boxes or an actuated apparatus with two movable flat surfaces. Contrariwise to the surprising lack of evidence on bimanual cue integration, the results indicate optimally integration of the information coming from the two hands. We then discuss our results referring to the cognitive factors that influence multisensory integration, and we suggest that many of the constraints to optimal bimanual integration could reflect limitations associated to the symbolization processes rather than the sensory system per se.

In the second section, we compare the minimum transient change of length of a bimanually hand-held virtual bar that could be detected in a dynamic or static condition. The bimanual coordination network is not rigid and static but rather a dynamic entity that changes as a function of task complexity (Swinnen & Wenderoth, 2004a). However, relatively few studies have investigated proprioceptive precision in dynamic tasks. Here, we use a bimanual haptic interface to compare proprioceptive discrimination thresholds in static and dynamic conditions. We found markedly worse performances during movements, suggesting that the human sensory system accomplishes the best bimanual operations during static performances.

In this chapter, the intent is to highlight the relevance of cognitive sources of constraints, that often have been neglected in the literature on bimanual operations (Ivry et al., 2004).

3.1 Bimanual Integration in the Haptic Discrimination of Size

The contents of this paragraph are adapted from the following under manuscript: **Risso, G.**, Xu, Q., Baud-Bovy, G. (in submission). Bimanual Integration in the Haptic Discrimination of Size.

Personal contributions as first author: participated to the experiments conceptualization, developed the experimental setup, acquired the data in all the experiments, performed the data analyses, wrote and revised the manuscript.

3.1.1 Introduction

Multiple sensory systems reveal information about the environment and the information provided by each sensory system is often redundant. For example, both the visual system and the haptic system can provide information about the size or shape of an object. While there is a long history of research on multi-sensory integration (Ernst & Bühlhoff, 2004a), the emergence of a new theoretical framework – Bayesian Integration - has renewed the interest in this topic (Bresciani et al., 2005; Ernst & Banks, 2002; Helbig & Ernst, 2007). A specific prediction of Bayesian framework which has received considerable experimental validation, is that to minimize the variability of the integrated signal the brain weights redundant information according to its reliability. While much of the original research has focused on the integration of cues across sensory modalities, multiple sensory cues might also provide redundant information within a sensory modality. For example, in the visual modality, the distance or the slant of a plane can be estimated from a variety of cues such as binocular disparity, perspective, occlusion, etc. (Hillis et al., 2004b; Knill & Saunders, 2003a; Landy & Kojima, 2001; Young et al., 1993). In the haptic modality, positional information and the contact force might influence the perceived shape of the object (Drewing & Ernst, 2006b; G. Robles-De-La-Torre & Hayward, 2001).

The main objective of this study is to find out whether positional information used to assess the size of a box-like object held with both hands are optimally integrated. A prediction of Bayesian integration is that the estimate of the size of the hand-held box (or of the distance between the two limbs) should be more precise when using the two hands than when using one hand. To date, only

a few studies have investigated whether redundant information from the two hands are optimally integrated. Moreover, these studies have yielded contrasting results. Squeri et al., 2012 tested the optimal integration hypothesis in experiments where the curvature of a large shape was haptically explored by following its contour with one or two hands. Wong et al., (2014) tested the bimanual integration hypothesis in a position discrimination task in absence of vision, where the position could be reached with one or two hands. Notably, the experimental setup in both studies consisted of robotic arms with handles. The participants grasped the handles that moved their hand(s) along the desired trajectory or to the desired position, and they made two-alternative forced-choice judgments about stimuli curvatures or positions. Neither study found evidence that participant discriminated curvature or position better when using both hands.

In another study, Panday et al. (2013) conducted two experiments on the haptic perception of the size of large objects. Their setup consisted in two surfaces that the participants could explore with one or both hands. The two surfaces were mounted on a rail that allowed one to vary the distance between them by moving them symmetrically with respect to the body midline. The task was to indicate which of two stimuli appeared bigger. In the first experiment, participants touched two curved surfaces that could represent the two sides of a large cylinder. In the second experiment participants touched two flat surfaces. Interestingly, Panday et al. (2013) found that the performance was markedly better in the bimanual condition only in the first experiment with curved surfaces. To explain the discrepancy between the results of the two experiments, they proposed that curved surfaces might better elicit a representation of the object shape in higher-order brain processes, than flat surfaces.

Another experiment by Plaisier & Ernst (2012) also provides evidence that optimal bimanual integration in the haptic modality is possible. In their study, participants had to judge the stiffness of a virtual box with one or two hands. The results showed that the discrimination thresholds were lower in the bimanual condition, as predicted by optimal integration principles. They hypothesized that integration might have occurred in their study for two reasons. First, the movements were active unlike in the previous studies. Second, the participants could see that they touched a single object, which might have informed them that the bimanual information had a shared source. A common characteristics of the experiments where bimanual integration did not occur is that the hands touched unseen grounded surfaces. A possible explanation to explain the lack of bimanual integration in these experiments is that the stimuli or experimental situation did not trigger bimanual integration because there was no indication that the two hands touched the same object and provided redundant information about the size of the object or the distance between the two hands. This hypothesis was tested in a recent experiment where participants were asked to estimate the length of two ~50 cm long wooden stick(s) connected by a hinge joint at the top by simply

moving them. In the unimanual condition, the hinge joint was fixed to a rigid structure while the joint could be fixed or free to move in the bimanual condition. The results of this study showed that performance in the bimanual condition was better than the performance in the unimanual condition only when the plier was free to move (Xu et al., n.d.; see Xu & Baud-Bovy, 2017, for a preliminary report). Because considerable care was taken to avoid giving additional cues in the free condition, this results suggests that being able to move the bimanually held object promoted the integration of information from the two hands.

The goal of Experiment 1 is to investigate bimanual integration in a size discrimination task similar to Panday et al (2013) with box-like stimuli with flat surfaces. The experiment included two unimanual conditions: left and right hand, and two bimanual conditions: static where the box was held onto the table and dynamic, where the participants could lift the box with the two hands. Based on previous evidence, we hypothesized that bimanual integration would occur only in the dynamic conditions, when lifting the object would promote the idea that they are touching a unique object.

3.1.2 Experiment 1: box size discrimination

3.1.2.1 Methods

Participants. Nineteen participants, nine women and ten men (mean age 26.47 ± 3.89 years), participated in the experiment. All participants were right-handed except for one. None of the participants reported any known hand or neuromuscular disorder. All participants were naïve as to the goal of the experiment and had no previous experience with the task. One participant was excluded from the data analysis because he did not perform the task well enough to estimate the sensory threshold. The Ethics Committee of the Region of Liguria approved the experiment that was conducted according to the ethical principles defined by the Helsinki Declaration. All participants gave their informed consent before the experiment.

Apparatus and stimuli. Stimuli consisted of nine equally weighted wooden boxes with a width ranging from 32 to 48 cm in 2-cm steps (30 cm height x 30 cm depth). The 40 cm wide box was used as the standard stimulus, while other boxes were used as comparison stimuli. All boxes were built to have the same weight (1413 ± 30 gr) and centre of mass (Figure 3).



Figure 3. Experimental setup. The figure represents a blindfolded participant haptically interacting with a wooden box in the four experimental conditions. The top panels show the bimanual grounded (left) and free (right) conditions. In the bimanual free condition, the participant lifted the box a few centimeters above the table. The bottom panels represent the unimanual condition.

Experimental procedure and task. Participants were blindfolded before entering the experimental room so that they would not see the stimuli at any time. In the experimental room, the participants sat on a fixed chair with their bodies at 20 cm from the edge of a table. Before each experimental session participants were asked to point exactly in front of their body mid-line at least three times with arms extended and hands joined. The average position was marked on the table and used to centre the boxes during their presentation.

The task was a size-discrimination two-alternative-forced-choice task. During each trial, participants felt the size of two boxes in succession and at the end of the trial reported verbally which one was the largest.

The experiments included four conditions. In the unimanual conditions, each participant had to touch the side surface of the box with the left or right hand. In these conditions, he/she was asked to focus on the distance between the touched side of the box and the body mid-line. In the bimanual grounded condition, the experimenter maintained the box throughout the presentation to avoid movement while the participant touched the two lateral surfaces of the boxes with both hands for up to 5 seconds. In the bimanual free condition, the participant lifted the box a few centimetres, and then put it back to its initial position. In both bimanual conditions, participants were asked to

focus on the size of the box. Before the beginning of the experiment, the participants practiced the task in each condition until they felt comfortable.

Each trial included the presentation of the standard stimulus (40 cm) and one of the 8 comparison stimuli. The order of presentation of the comparison and standard stimuli was randomized. Each comparison stimulus was presented seven times in each condition (method of the constant stimuli; Fechner, 1860), yielding a total of 224 trials. The experiment included seven blocks of 32 trials, which were subdivided into four sub-blocks of eight trials. Each sub-block corresponded to a condition and included all comparison stimuli in a random order. The order of presentation of the different conditions inside each block was randomized as well. The total duration of the experiment was 90-120 minutes per participant, divided into two sessions.

At the end of the experiment, we asked all the participants to report what they thought they were touching.

Optimal integration model.

Integration of two redundant signals is optimal when the integrated signal s_{12} cues s_1 and s_2

$$s_{12} = w_1 s_1 + w_2 s_2$$

when each signal is weighted according to its reliability (Ernst & Banks, 2002, see Sabes, 2011 for example of how such a signal could be computed at the neuronal level). Mathematically, the variance of the integrated signal is minimized when the weights are

$$w_1 = \frac{R_1}{R_1 + R_2} \quad w_2 = \frac{R_2}{R_1 + R_2}$$

where the reliability $R_i = 1/\sigma_{i2}$ is defined as the inverse of the noise (variance) of the corresponding signal. Accordingly, the variance of the optimally integrated signal is

$$\sigma_{12}^2 = \frac{\sigma_1^2 \sigma_2^2}{\sigma_1^2 + \sigma_2^2}$$

which is not only lower than that of the single cues but the lowest possible given the noise associated with each cue. This noise can be determined in behavioural experiments measuring the discrimination thresholds. A consequence of this framework is that, in the presence of a conflict between the single signals, the bimodal estimate should be biased toward the most reliable sense. (Ernst & Bühlhoff, 2004).

Data Analysis

For each participant and condition, a logistic psychometric function was fitted to the responses using maximum likelihood estimation. For each psychometric curve, we computed the point of equality (PSE), i.e. the box size perceived as larger than the standard distance in 50% of the trials, and the discrimination threshold (or discrimination limen, DL), which corresponded to the difference between the PSE and the box size perceived to be larger than the standard in 75% of the trials.

We used a non-parametric Friedman test for repeated measures on the discrimination thresholds DLs and PSEs to test the differences between the unimanual and bimanual conditions. Non-parametric statistics were used to check with robust methods that there was no influence of subjects giving extreme responses. Whenever a statistically significant effect was found, we tested the difference between conditions pairwise with a two-tailed Wilcoxon signed-rank tests. To test whether integration took place, we computed the bimanual threshold predicted by optimal integration principles (Maximum Likelihood Estimation) for each participant and we tested whether the observed bimanual discrimination thresholds were smaller than or equal to the predicted MLE thresholds with a one-tailed Wilcoxon signed-rank tests. Finally, we also examined if individual bimanual thresholds were well associated with the predicted MLE thresholds. In particular, we used Pearson-product-moment correlation to test the relationship between the observed values and the MLE predictions. For all tests, the level of statistical significance was set at 5% (Error Type I $\alpha = 0.05$).

Power analysis was conducted for effect sizes that corresponded to the difference between the discrimination thresholds in the unimanual and bimanual conditions predicted by the optimal integration hypothesis. The power of Friedman's test corresponds to the power of a one-way repeated-measure ANOVA after adjusting sample size with its asymptotic relative efficiency (A.R.E), which is $k/(k+1) \cdot 3/\pi \approx 0.716$ for $k = 3$ levels if one assumes normal distributions and has $k/(k+1) \cdot 0.864 = 0.648$ for $k = 3$ as lower bound (Hora & Iman, 1986). First, we computed Cohen's effect size $f = \sigma_{DL}/\sigma$ where σ_{DL} is the standard deviation of the effects of interest and σ is an estimate of the within-group residual error (excluding across-subject variability). We estimated σ_{DL} by assuming that the expected mean values for two unimanual conditions would correspond to the average discrimination threshold value ($m_{DLu} = 2.95$ cm) and that the value for the bimanual condition would correspond what optimal integration predicts if one assumes that the two hands have the same threshold, i.e. $\sqrt{2}/2 = 70\%$ of the unimodal threshold. The standard deviation of these three values yielded $s_{DL} = 0.499$ and using the residual standard deviation $s = 0.674$ of a one-way repeated-measure ANOVA, which excludes the variability across subjects, to estimate the residual error σ , yielded the effect size $f \approx s_{DL}/s = 0.739$. Given this effect size, the power of

Friedman test with $n = 18$ participants at a significance level $\alpha = 5\%$ is 98% if one assumes normal distributions ($n_{ARE} = 12.89$) and 96% for the lower bound ($n_{ARE} = 11.66$).

For Wilcoxon signed-rank tests, we computed the power of a paired t test after adjusting sample size according to Wilcoxon signed-rank tests A.R.E (0.955). For this analysis, we computed Cohen's effect size $d_z = |\mu_d|/\sigma_d$, where μ_d is the expected difference between unimanual and bimanual conditions, which corresponds to 30% the value of the unimodal threshold (see above), and $\sigma_d = \sqrt{2} \sigma$ is the expected standard of deviation of the difference. Under these assumptions, Cohen's d_z was 0.91 and Wilcoxon signed-rank test had a power 94% ($n_{ARE} = 17.19$). In summary, we obtained effect sizes for both tests by combining *a priori* information about the *difference(s)* between the conditions of interest with a scaling factor ($m_{DLu/s}$) that was derived from the experiment¹.

3.1.2.1 Results and Discussion

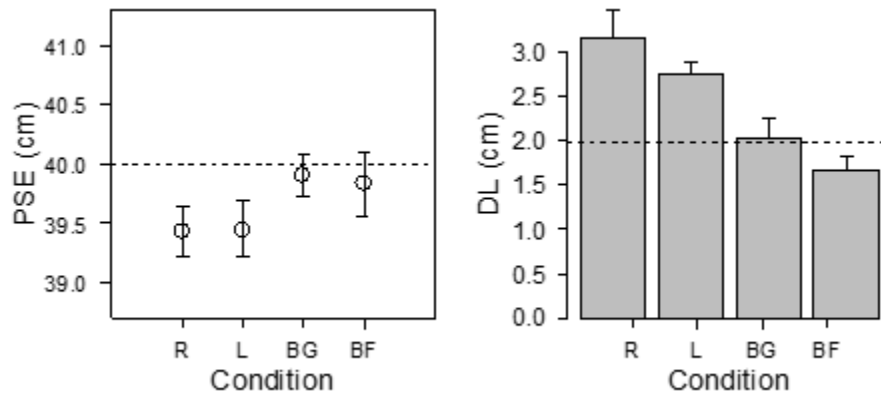


Figure 3.1. Results of the box size discrimination experiment. The left panel represents the mean PSE (on the y-axis) for each condition (x-axis): Right (R), left (L), bimanual grounded (BG), and bimanual free (BF) condition. Vertical bars represent the standard error. The dotted line represents the standard box size (40 cm). The right panel represents the mean discrimination thresholds (on the y-axis) for the four conditions (x-axis); the dotted line represents the predicted MLE threshold.

Figure 3.1 shows the mean haptic PSE (top left panel) and thresholds (top right panel) of the participants for the four experimental conditions. The PSEs were close to the standard and did not

differ statistically across conditions (Friedman test: $\chi^2(3) = 6.8$; $p=0.08$). In contrast, the differences between the discrimination thresholds across conditions were statistically significant (Friedman test: $\chi^2(3) = 29.13$ $p<0.001$). In the unimanual conditions, the mean threshold was lower for the left hand (Mean $\pm$ SD: 2.75 ± 0.58 cm) than for the right hand (3.15 ± 1.30 cm) even though the difference was not statistically significant (Wilcoxon test adjusted for multiple comparison: $z = 1.18$, $p = 0.30$). As predicted by the optimal integration principles, the box size was estimated more precisely in the bimanual conditions than in the unimanual ones. Specifically, the unimanual DLs were higher than the bimanual grounded (2.03 ± 0.99) and free (1.67 ± 0.61) DLs. The Wilcoxon tests confirmed the statistical significance of the difference between unimanual and bimanual conditions (right hand vs grounded: $z = 3.35$, $p < 0.01$; right-hand versus free: $z = 3.66$, $p<0.01$; left hand versus grounded: $z = 2.70$, $p < 0.05$; left hand vs free: $z = 3.66$, $p<0.01$). The bimanual DLs did not differ from the MLE prediction (1.98 ± 0.47 cm) as confirmed by unilateral Wilcoxon tests (grounded vs MLE: $z = -0.65$, $p = 0.83$; free vs MLE: $z = -2.66$, $p = 0.99$).

Table 1. Summary of experimental conditions for the three groups

Experiment	Comparison stimuli length (cm)	conditions order	Stimuli Subjective Experience
1 st Boxes	{32, 34, 36, 38, 40, 42, 44, 46, 48}	Mixed within subjects	• 17/18 participants perceived boxes • 1/18 participant perceived a stool
2 nd Boxes	{32, 34, 36, 38, 40, 42, 44, 46, 48}	Blocked, Grounded condition as first	• 3/16 participants perceived boxes • 3/16 participants perceived separated panels • 1/16 participant perceived a stool • 9/16 participants perceived panels linked (at their center, base or top)
3 rd Sliding Panels	{22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32}	Only grounded	Participants could see the setup before starting the experiment

All the participants reported they were touching a single object. 17 out of 18 were reported that they were touching and/or holding boxes (see Table 1). The participant who reported that the object was a stool had in a mind a cubic stool with vertical panels and a top that allowed seating.

The results of the first experiment confirmed only partially our initial hypotheses. As expected, we observed optimal bimanual integration in the lifting condition. However, evidence in favour of an optimal integration emerged also in the grounded condition. Previous literature reviewed in the

Introduction suggests that the advantage to lift the object consists in the cognitive conceptualization of the perceived object, which in turn would promote the integration. Accordingly, we hypothesized that the knowledge they were touching a single object acquired during the dynamic condition, might have promoted bimanual integration also in the static condition. Indeed, as a matter of fact the participants, had no reasons to think that we changed the experimental stimuli between one condition and the other. To address the issue, we repeated the experiment with another group of participants who always performed the static condition first, followed by the right or left unimanual conditions (in a randomized order), and then by the free dynamic condition as the last one.

3.1.3 Experiment 2: box size discrimination, fixed randomization

3.1.3.1 Methods

Participants. Sixteen participants, eight women and seven men (mean age 30.31 ± 12.67 years), participated in the experiment. All participants were right-handed. None of the participants reported any known hand or neuromuscular disorder. All participants were naïve as to the goal of the experiment and had no previous experience with the task. The Ethics Committee of the Region of Liguria approved the Experiment that was conducted according to the ethical principles defined by the Helsinki Declaration. All participants gave their informed consent before the experiment.

Experimental procedure. The apparatus, experimental procedure and data analysis were the same of the Experiment 1. The only difference between the two experiments consisted in the randomization order. Indeed, in this experiment we decided to maintain a fixed randomization order along all the participants. In particular, all the participants performed the bimanual grounded condition as first condition. Following the right and left unimanual conditions (randomized one with the other) were performed. All the participants performed the bimanual lifting condition as last. During the two unimanual and the bimanual grounded conditions no interaction between the two hands were allowed. The participants were never informed that they are touching boxes, and they did not have any cue to understand they were touching a unique object until the last condition begun. Before starting the bimanual lifting condition, all the participants were asked to report what they believed they were touching.

Data were analysed in the same way as in Experiment 1. The power analysis in this experiment also followed the same tracks as in Experiment 1. The average discrimination threshold in the unimanual condition was $m_{DL} = 3.11$ cm and the residual error was $s = 1.10$ cm. For Friedman

test, Cohen's effect size was $f = s_{DL}/s = 0.53/1.10 = 0.48$, which yielded a power of 59% or 64% for the test depending whether sample size was adjusted for a lower-bound ($n_{ARE} = 24.09$) or normal distributions ($n_{ARE} = 21.80$). For Wilcoxon signed-rank test, Cohen's effect size was $d_z = |m_d|/s_d = 0.91/1.55 = 0.59$, which yielded a power of 82% for the test. Note that for an 80% power the sample should be increase to 26 participants.

3.1.3.2 Results and Discussion

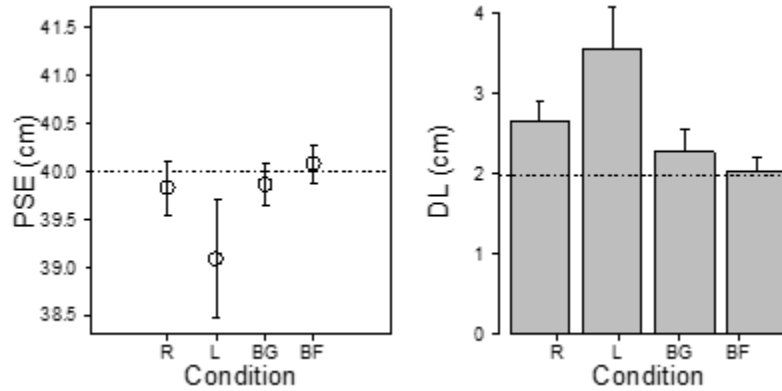


Figure 3.2. Results of the box size discrimination experiment. The top left panel represents the mean PSE (on the y-axis) for each condition (x-axis): Right (R), left (L), bimanual grounded (BG), and bimanual free (BF) condition. Vertical bars represent the standard error. The dotted line represents the standard box size (40 cm). The top right panel represents the mean discrimination thresholds (on the y-axis) for the four conditions (x-axis); the dotted line represents the predicted MLE threshold.

The results are very similar to these obtained in the first experiment. Figure 3.2 shows the mean haptic PSE (top left panel) and thresholds (top right panel) of the participants for the four experimental conditions. The PSEs were close to the standard and did not differ statistically across conditions (Friedman test: $\chi^2(3) = 1.06$; $p=0.78$), indicating little bias and no effect of condition on the biases. The differences between the discrimination thresholds across conditions were statistically significant (Friedman test: $\chi^2(3) = 11.24$; $p=0.01$). In the unimanual conditions, the mean threshold between the left hand (Mean $\pm$ SD: 3.56 ± 2.00 cm) and the right hand (2.66 ± 0.99 cm) was not statistically significant (Wilcoxon test adjusted for multiple comparison: $z = -1.79$, $p = 0.12$). As predicted by the optimal integration principles, the box size was estimated more precisely in the bimanual conditions than in the unimanual ones. Specifically, the unimanual DLs were higher than the bimanual grounded (2.26 ± 1.12) and free (2.03 ± 0.67) DLs. The Wilcoxon tests showed statistical significance difference between left-hand and bimanual conditions (left

hand versus grounded: Wilcoxon: $z = 2.87$, $p = 0.01$; left hand vs free: t Wilcoxon: $z = 2.47$, $p = 0.034$). The right-hand condition was not significantly different from neither of the bimanual conditions (right hand vs grounded: Wilcoxon: $z = 1.96$, $p = 0.10$; right-hand versus free: Wilcoxon: $z = 1.96$, $p = 0.20$). However, the right hand condition significantly differ from the MLE prediction (1.98 ± 0.72 cm; Wilcoxon: $z = 3.38$, $p < 0.01$).

Finally, 13 out of 16 participants were able to say that they were touching a single object (see Table 1).

The results of the second experiment confirmed the findings of Experiment 1. Despite the experimental manipulation to prevent that additional cue from the dynamic condition could affect the participants behaviour in the static performance, we found optimal integration in both the lifting and grounded conditions. Surprisingly, the majority of the participants had the subjective experience of touching connected objects, and only three of them reported the sensation of experiencing different objects with the two hands. These results contrasts with Panday et al (2013), who did not find bimanual integration when participants touched two flat panels. Our wooden boxes were lightly build, and not as solidly fixed to the table as the experimental setup used by Panday et al (2013). Further, since the surfaces were in fact connected we supposed that some vibrations or micro-movement might cue the subject that the two panel are connected thus promoting integration. Accordingly, we designed the third experiment, in which we tried to reproduce the results of Panday et al. (213). This latter setup consisted into vertical metallic plane mounted an actuated linear guide that allowed to adjust the distance between them. To ensure that the touched surface are not connected we allowed the participants to see the setup at the beginning of the experiment.

3.1.4 Experiment 3: distance discrimination of flat surfaces

3.1.4.1 Methods

Participants. Eighteen participants (mean age 26.67 ± 2.52 years; 8 females and 10 males) participated in the experiment, including ten right-handed, one left-handed and one ambidextrous person. None of the participants had participated in the first experiment; nor did they have or report any known hand or neuromuscular disorders. All participants gave their informed consent prior to testing.

Experimental procedure. The experimental setup was a linear guide (see Figure 3.4) with two actuated blocks that could move along a 51 cm long workspace. Two vertical flat surfaces (20

by 30 cm) were affixed onto the actuated blocks. A custom program adjusted the distance between the two plates during the experiment. The device was placed 10 cm from the edge of a table.

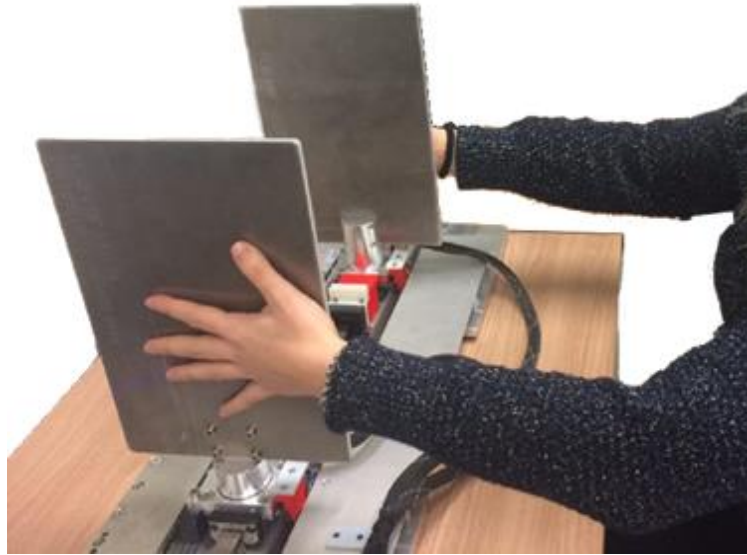


Figure 0-1 Discrimination of distance between flat surface experimental setup. Representation of a participant interacting with the setup in the bimanual condition. The experimental setup is a force feedback device with a long rectangular workspace (10.5 x 51.0 cm). The mechanical structure consisted of two vertical flat surfaces powered by two motors. During the haptic exploration of the stimulus, the participant was blindfolded and wore a headset playing white noise in order to suppress any additional auditory cue given by the sliding of the panels.

The task and experimental procedure was the same as in Experiment 1. Each participant sat 20 cm from the table on a fixed chair with their body 20 cm from the edge of the table. Participants were blindfolded and wore a headset playing white noise to suppress audio cues. The experiment included two unimanual conditions (right and left hand) and one bimanual condition. In the unimanual conditions, participants were instructed to focus on the distance between the flat panel and the mid-line of their body. In the bimanual condition, participants were instructed to focus on the distance between their two hands.

Each trial involved the successive presentation of the standard stimulus (27 cm distance) and a comparison stimulus (one of ten possible distances ranging from 22 to 32 cm by 1-cm steps, excluding the 27 cm distance). Both stimuli were centred on the body midline, which was identified with the same procedure as in the first experiment. The administration order of the standard and comparison stimuli was randomized. The whole experiment included seven blocks of 30 trials, yielding a total of 210 trials. Each block was divided into three sub-blocks of 10 trials, where all comparison stimuli were presented in the same condition. The order of presentation of

the different stimuli inside each sub-block, and conditions inside each block were randomized. The total duration of the experiment was 50-60 minutes per participant, divided into two sessions.

Data were analysed in the same way as in Experiment 1. The power analysis in this experiment also followed the same tracks as in Experiment 1. The average discrimination threshold in the unimanual condition was $m_{DL} = 2.36$ cm and the residual error was $s = 0.66$ cm. For Friedman test, Cohen's effect size was $f = s_{DL}/s = 0.40/0.66 = 0.60$, which yielded a power of 85% or 98% for the test depending whether sample size was adjusted for a lower-bound ($n_{ARE} = 16.03$) or normal distributions ($n_{ARE} = 14.50$). For Wilcoxon signed-rank test, Cohen's effect size was $d_z = |m_d|/s_d = 0.69/0.93 = 0.74$, which yielded a power of 82% for the test.

Results and discussions

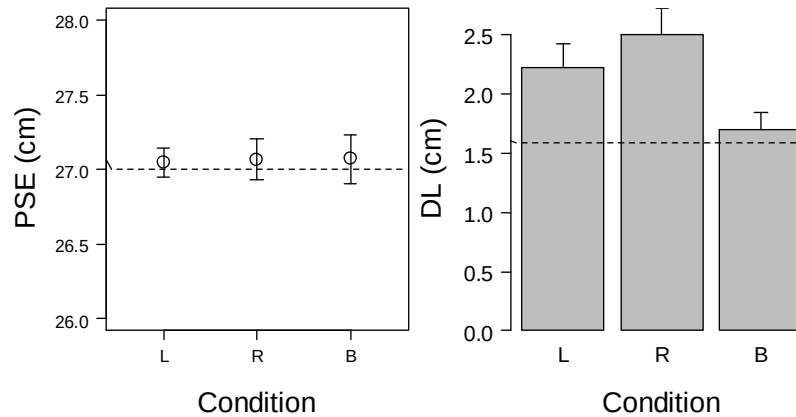


Figure 3.5 Results of the distance discrimination experiment with flat surfaces. Left panel: Mean PSEs (y-axis) for each condition (x-axis): right (R), left (L) and bimanual (B) conditions. The dotted line represents the distance of the standard (27 cm). Right panel: Representation of the mean discrimination thresholds (on the y-axis) for the four conditions (x-axis). The dotted line represents the predicted MLE threshold. Vertical bars represent the standard error.

Figure 3.5 shows the PSE (left panel) and DLs (middle panel) for the three experimental conditions. The PSEs differed little from the standard and the condition had no statistically significant effect (Friedman test: $\chi^2(2) = 0.08$; $p=0.96$). The differences between discrimination thresholds across experimental conditions were statistically significant (Friedman test: $\chi^2(2) = 8.11$; $p=0.02$). The discrimination performance between the left hand (mean $\pm$ SD: 2.22 ± 0.85 cm) and the right hand did not significantly differ (2.50 ± 0.96 cm; Wilcoxon test adjusted for multiple comparison: $z = 1.00$, $p = 0.32$). The discrimination performance with both hands (1.70 ± 0.60 cm) was better than the unimanual right and left hand. The difference was statistically significant for

the right (Wilcoxon test adjusted for multiple comparison: $z = 2.96$, $p = 0.01$) and for the left hand (Wilcoxon test adjusted for multiple comparison: $z = 2.18$, $p = 0.04$). The threshold in the bimanual condition did not differ from that predicted by optimal integration (MLE DL = 1.58 ± 0.52 cm; Wilcoxon test adjusted for multiple comparison: $z = 0.87$, $p = 0.01$). The predicted and observed bimanual thresholds were just moderately correlated at the individual level ($r = 0.43$, $n = 16$, $p = 0.07$).

We found evidence of optimal integration also in this third experiment in which we allowed participant to see that they are perceiving haptic information of position from separate panels, clearly grounded to an actuated linear guide.

3.1.5 General Discussion

The goal of the study was to investigate whether information from the two hands is integrated when subjects estimate the size of a box. In the introduction, we hypothesized that participants would not integrate proprioceptive positional information used to assess the size of the box in the grounded condition but would do so in the lifted condition. Contrary to our expectation, the results of the three experiments reported in this study indicated that individuals can integrate optimally bimanual information not only in the dynamic, but also in the grounded condition. To discuss these results, it might be useful to recall some general principles of multi-sensory integration. The goal of multi-sensory integration is to obtain a more reliable percept by fusing together noisy signals. However, a major problem that the brain must solve is to determine when information should be integrated or not. As a matter of facts, integration is beneficial when the information contained in sensory cues is redundant, as very clearly explained in a review by Ernst & Bühlhoff (2004): “[...] *to be integrated, the sensory estimates must be in the same units, the same coordinates and about the same aspect of the environmental property*”.

This issue was also a central in the early research on inter-sensory bias (reviews in Welch & Warren, 1980; Welch 1999). In a review, Welch (1999) proposed to divide factors that affect inter-sensory bias into: 1) non-cognitive (i.e. the number of amodal stimulus properties that are shared by the two sensory modalities (see also Welch & Warren, 1980) such as spatial location, shape, etc), and 2) cognitive factors (i.e. familiar association, cross-modal correspondence, semantic

processes, etc.). According to this model, both cognitive and non-cognitive factor would affect the magnitude of intersensory bias *by supporting the assumption that the sensory cues refer to a single distal object or event* (unity assumption). In Welch's (1999) words: "the stronger the observers' assumption that they are in the presence of a single distal object, the greater will be the magnitude of inter-sensory bias. As noted by Chen & Spence (2017) in a recent review, the unity assumption still plays an important role in research on multi-sensory integration although they propose to replace this assumption by the concept of "prior of common cause" or "coupling prior", which is formalized in some recent Bayesian models (e.g. Berniker & Kording, 2011; Ernst, 2007). However, this still leaves open the question of understanding which experimental factors affect these priors.

Previous studies on bimanual integration suggest that the unity assumption plays an important role for understanding when bimanual integration occurs and when it does not. For example, to explain the difference between bimanual integration occurring with curved surfaces but not with flat surface, Panday et al. (2013) hypothesized that "curvature gives information about the shape of the object, whereas position does not". According to Panday et al. (2013), shapes would be represented at a higher-level in the brain, where cues from both hands would be represented and integrated. In contrast, in absence of this cognitive representation of shape, positional information would not improve in the bimanual condition with respect to the unimanual condition, as also demonstrated by Wong et al.(2014) and Squeri et al. (2012) . Accordingly, Plaisier & Ernst, (2012) found strong evidence for bimanual integration in a stiffness discrimination task where participants pushed actively against virtual deformable objects. To explain this finding, they hypothesized that active touch might be important and that a common cause could be inferred because the visual scene showed a single object in the bimanual trials. Finally, the result of Xu et al, pliers' study (in submission, see [Appendix A](#)) described in the introduction, provide further evidence that the unity assumption might matters. In this study, bimanual integration occurred only in the free manipulation condition, where it was obvious that two hands were holding the same object. We proposed that the coordination pattern required to manipulate a single object with the two hands and/or the transmission of force between the two hands were strong cues of holding a single object.

At a first sight, the results of the experiments in this study appear inconsistent with previous evidence but there are several important differences that should be highlighted.

The first difference consists in the type of haptic cues that provides information about the size of the object. In this study, the hand position is directly related to box size in unimanual and bimanual conditions. Because the box is aligned with the body midline, the two hands provide redundant information about the size of the objects and/or the difference between the standard and comparison stimuli. In contrast, estimating the size of a pair of pliers based on hand movement requires estimating the radius of curvature, which depends on the change of orientation of the hand occurring during the opening and closing movements. Estimating the pliers' size might require a more sophisticated processing of proprioceptive signals than the simple comparison of hand positions in box size estimation.

Another difference is that the manipulation of box-like objects is probably a much more familiar experience than the bimanual manipulation of pair of pliers. As described by Welch's (1999), familiar association reflecting the associations between sensory cues occurring during lifetime experience should promote the idea that the information come from a common source. Accordingly, bimanual integration might occur more easily when exploring or manipulating familiar objects such as boxes. For a familiar object, the available cues together with the participants' knowledge that they were holding a box might have sufficed to trigger bimanual integration in the grounded condition. This explanation is strengthened by the reports of the participants who consistently reported holding a unique object, even in the second experiment where they had seen the boxes and not yet experience lifting them. Conversely, lack of familiarity with pliers might explain why bimanual integration occurred only in conditions in which there is a signal that both hands were holding the same object (i.e. free condition for pliers and/or familiar shape conceptualization for unknown objects).

Parenthetically, it can be noted that we found slightly better discrimination performance in the lifting conditions than in the grounded ones (see Figs. 3.1 & 3.2). Therefore, our results do not contradict the idea that lifting the objects might facilitate the integration (Xu et al., submitted). However, the potential benefit of lifting the object is limited and hard to see in this study due to the fact that integration occurred already in the grounded conditions (ceiling effect).

Admittedly, we lack a simple explanation to explain why we found bimanual integration in the third experiment. The experimental setup and procedure in this experiment were almost the same as Panday et al. (2013), who did not find bimanual integration. The only difference in the procedure

is that they hid the setup throughout the entire experiment, while we allowed the participants to see the setup before starting the experiment. Our intention was to avoid the inference observed in the second experiment, according to which the participants assumed they were holding a single distal object, although they could not see the experimental setup. Thus, we reasoned that seeing the setup with two panels might prevented such a prior. It is possible that seeing the two separate panels resting on a common base might have been sufficient to provide “prior common cause” with respect to the origin of the bimanual signals contrarily to our expectation. Further research might be needed to clarify the effect of visual feedback in this task.

Another yet-to-be-fully-understood question emerging from this study is whether the level of processing of sensory of proprioceptive integration depends on explicit knowledge of holding a single object. In fact, there are several reasons to consider that the belief of holding a single object, and the level of processing of the sensory information might be two independent factors for bimanual integration. First, it should be mentioned that it might not be necessary to be conscious that sensory cues have a common cause to integrate them (see note 2 in Chen & Spence, 2017; Deroy, 2014; Welch & Warren, 1980). Similarly, in the intersensory bias literature, it has been acknowledged that a bias might occur without awareness of the presence and nature of the intersensory conflict (Welch, 1999). Second, in Xu et al (under review) experiment, the mere knowledge of holding a single object did not suffice to trigger bimanual integration in the pliers' experiment. As a matter of facts, the participant did not integrate in the grounded conditions despite having seen the pair of pliers at the beginning of the experiment, and despite the fact that grounded and free conditions were alternated. For this reason, we hypothesized that the crucial factor to explain bimanual integration was not the explicit knowledge of holding an object but rather the unique pattern of movement and force that is present when the two hands manipulate an ungrounded object.

3.1.6 Conclusion

In conclusion, the results of this study demonstrate that positional information coming from the two hands about the size of a box-like object can be integrated both in the grounded and free conditions. In all experiments, we observed smaller discrimination thresholds in the free condition than in the grounded one. While this study does not provide strong independent evidence that the free manipulation of a bimanually-held object enhance bimanual integration at the perceptual level, it does not contradict it. As a matter of fact, given that the performance observed in the grounded condition is close to the extent predicted by optimal integration principles, it is not possible to see an additional benefit in the free manipulation condition.

3.2 Size-Change Detection Thresholds of a Hand-Held Virtual Bar at Rest and during Continuous Movement

The contents of this section are adapted from the following manuscript: Baud Bovy, G., **Risso, G.**, Zenzeri, J. (in submission). Size-Change Detection Thresholds of a Hand-Held Virtual Bar at Rest and during Continuous Movement.

Personal contributions as second author: I acquired the data of the experiment and participated to the setup of the experiment, the data processing and pre-processing, and to the manuscript drafting and revision.

3.2.1 Introduction

One does not have the impression to lose track of the position of our hand when moving it even without seeing it. We have a keen sense of the position of our limb in space, both at rest and during movement that is grounded in the proprioceptive system. Thanks to decades of research the

physiological basis of this system is well known although the amount of processing required to yield accurate information about our movement is not always well appreciated.

Kinesthesia is classically divided into position sense and a movement sense (Uwe Proske & Gandevia, 2012). Studies involving tendon vibrations and ultra-slow movements have shown that it is possible to dissociate these two senses to some extent (Cordo et al., 2000). In addition, it is necessary to further distinguish between a static position sense, the perception of joint angle in absence of movement, and a dynamic position sense, the perception of joint angle during movement (Cordo et al., 1994). In fact, it has been proposed that different neurophysiological mechanisms might underlie slow position percepts during movement at very low velocities and fast position percepts for moderate-to-fast velocities because the detection thresholds for passive movements increase markedly at low speeds (Cordo et al., 2000).

Classical paradigms to study proprioception include the reproduction with the same limb of a location, posture, or distance and the detection of passive movement of the other limb (Hillier et al., 2015). Relatively few studies have investigated the precision with which one knows the position of his limb during voluntary movement. The question is difficult since there is no obvious way of reporting the perceived position of a limb during movement. Some have measured the precision with which humans indicate when the unseen hand passes through a target angle (Cordo et al., 1994). Others have measured passive movement detection thresholds with actively contracted muscles (Proske et al., 2000).

In this study, we compare the precision of the position sense at rest and during movement by asking participants to indicate whether the length of a virtual bar that they held by its extremities with both hands increased or decreased in static and moving conditions.

3.2.2 Materials and Methods

Participants

The study included 18 participants (5 left-handed, 13 females) aged between 23 and 52 years (mean $\pm$ SD: 28 ± 7.2 years) with no known neuromuscular disorders. The group included graduate and doctoral students. The study adhered to the principles of the Declaration of Helsinki (2013) and was approved by the ethics committee of Regione Liguria. Each participant received oral and

written information on the purpose and procedure and signed an informed consent form before taking part in the study.

Experimental Setup and Procedure

The experimental setup was a bimanual manipulandum with a large elliptical workspace (80 x 40 cm) made of two mechanical structures, each powered by two direct-drive brushless motors. The manipulandum had low intrinsic mechanical impedance at the end-effector (inertia <1 kg; negligible viscosity and friction). It provided a high level of back-drivability and a good isotropy (manipulability index = 0.23 ± 0.02 ; force/torque ratio = 2.21 ± 0.19 N/Nm) with a large available force level at the handle (continuous force: 50 N; peak force: 200 N) allowing for experiencing a wide range of haptic stimuli (Casadio et al., 2006). The controller consisted of three nested loops with a 16-kHz sampling rate (current loop) and 1-kHz rate (impedance control loop), plus a 100-Hz virtual reality loop. The software environment was based on Python, RT-Lab[®] and Simulink[®]. The participants stood in front of the manipulandum and grasped its handles with the arms flexed. The height of the handles was adjusted so that the joint elbows angle of each participants was flexed of about 90 degrees. The handle position was recorded at 100Hz for off-line analysis.

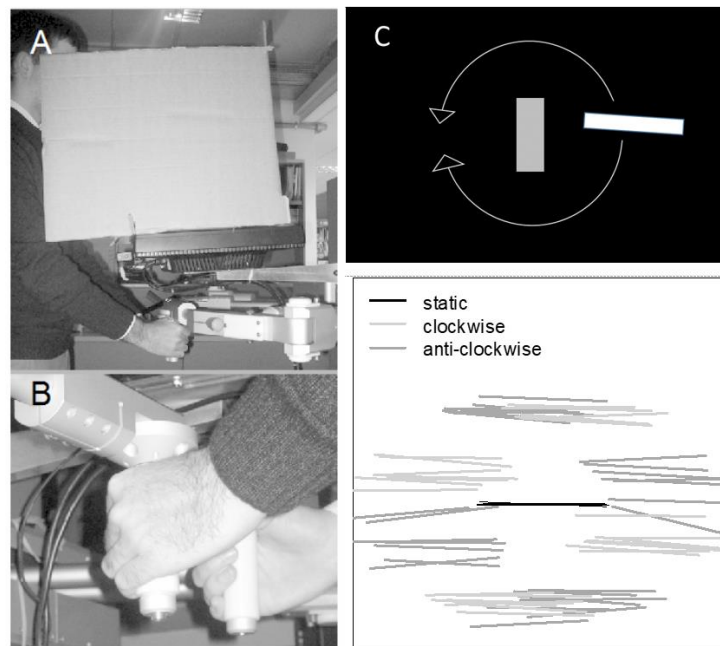


Figure 3.6. A: Experimental setup. B: Handle below the monitor. C: Visual scene in the moving condition. D: Average position of the virtual bar for in participant in each condition.

A virtual bar (0.15 m) linked the two handles. The virtual bar was modeled as a linear spring, connecting the two handles of the manipulandum (stiffness = 2500 N/m and damping = 30 N/m/s). The participants controlled the movements of the bar, which could move freely in the horizontal plane throughout the experiment. Depending on the trial, the length of the virtual bar was linearly increased or decreased over the course of 0.5 s and then linearly brought back to its initial length over the course of the following 0.5 s. The screen was positioned horizontally above the manipulandum and hid the hands. The virtual bar was represented by a white rectangle with fixed dimensions (0.15 x 0.04 m) and was aligned with the position of the manipulandum handles.

All subjects were tested under two different experimental conditions, the order of which was counterbalanced across subjects. In the static condition (ST), the participants kept the virtual bar above the reference position, which was displayed at the center of the screen throughout the trial (see Fig. 3.6). When the bar was well centered and aligned, the bar color changed from white to green. One second later, the bar color changed to yellow during the presentation of the stimulus before returning to the white color. The intensity of the stimulus (i.e. the size and direction of change of the virtual bar length) was controlled by two interlaced QUESTs targeting 17% and 83% percent of positive responses (i.e., "bar lengthened") respectively. This procedure ensures that the subject is tested with stimuli near the "corners" of the psychometric function, which is crucial to obtain a reliable estimate of its slope (King-Smith & Rose, 1997). At each trial, the bar length was determined by one of the two Quests selected randomly. At the end of the trial, the subjects indicated verbally whether the temporary change in bar length had corresponded to a lengthening or shortening (forced choice response). The static condition finished when at least 40 trials were completed with each QUEST.

In the dynamic condition, the participants were asked to move the virtual bar in such a way to "draw" circles around a central bar. Ten of the participants moved the bar in the clockwise and the other eight moved the bar anticlockwise. The color of the rectangle at the center of the screen was white when the participant moved at the desired velocity of $16 \text{ cm/s} \pm 0.3 \text{ ms}$), red when they moved too fast and blue when they moved too slowly. The trial started once the participant had completed at least 1 complete circle around the central bar at the desired velocity. The bar changed color from white to green for 1 s before the stimulus (to signal the impending stimulus) and then to yellow during the presentation of the stimulus before returning to the white color. The color changes were timed as a function of the bar position so that the stimulus would approximatively coincide with one of four possible positions (top, left, right and bottom) along the circular trajectories. At each position, the size and direction of the stimulus was controlled by two interlaced QUESTs that targeted 17% and 83% percent of positive responses. The position and

Quest within each position was randomly selected at each trial. The dynamic condition finished when at least 20 trials had been completed for each quest.

Data analysis

First, we checked the position and velocity of the bar in all trials. In particular, we computed the position of the bar in the middle of the stimulus period for each trial (see Fig. 3.6).

The distance between the two hands defines the *actual bar length*:

$$l(t) = \{ (x_L(t) - x_R(t))^2 + (y_L(t) - y_R(t))^2 \}^{1/2}$$

where $(x_L(t), y_L(t))$ and $(x_R(t), y_R(t))$ correspond to recorded hand position trajectories. The *grasp force* is the force applied by the subject along the direction of the bar when squeezing or extending it. The grasp force is measured indirectly from the difference between the actual and desired (or reference) length of the bar:

$$f_{\text{grasp}}(t) = -k (l(t) - l_{\text{ref}}(t))$$

where $k=2500$ N/m is the stiffness of the simulated bar. The reference length $l_{\text{ref}}(t)$ is normally 15 cm except during the stimulus period where it temporarily increased or decreased (see above).

Third, we extracted from the trajectories for each trial

- i) the *actual bar length change*, $\Delta_L = l(t_1) - l(t_0)$, where t_0 is the time of the beginning of the stimulus and $t_1 = t_0 + 0.5$ s is the time in the middle of the stimulus period where the lengthening or shortening of the bar is maximum,
- ii) the *average grasp force* (f_0) and the *grasp force variability* ($SD(f_0)$) during the second that preceded the stimulus,
- iii) the average grasp force during the first and second halves of the stimulus period (f_1 and f_2 respectively), and the *grasp force change* between the first and second halve of the stimulus period, $\Delta_F = f_1 - f_2$.
- iv) the *grasp stiffness* k_G where $\Delta_F = k_G \Delta_L$

The data about the hand position was missing for one subject in the static condition for a technical problem during the experiment, which prevented computing grasp force for this subject in this condition.

Fourth, we used maximum likelihood estimation to fit a logistic function to the responses of the subject and compute the probability of judging that the bar had lengthened as a function of the

actual (transient) change in the bar length. For each psychometric curve, we computed the Point of Subjective equality (PSE) and the Discrimination Threshold (DT). The PSE corresponds to the stimulus that was perceived as lengthening in the 50% of the trials. The discrimination threshold (DL) - or Just Noticeable Difference (JND) – corresponds the difference between the PSE and the bar length that was perceived as lengthening in 75% of the trials.

For each subject, we computed the PSEs and DLs separately for the static condition and the four position in the dynamic conditions. We used one-way repeated-measure ANOVAs to analyze the effect of the bar position or of the movement direction on the grasp force and psychophysical variables in the dynamic condition. The relation between bar position and movement direction change depending on the direction of rotation, which was counter-balanced across subjects (Clockwise: Top = rightward, Right = toward body, Bottom = leftward, Left = away from body; Counter-clockwise: Top = leftward, Right = away from body, Bottom = rightward, Left=away from body). Since we did not find any difference across bar position and/or movement direction (see Results), we computed an average PSE and DL in the dynamic condition from a single psychometric function that was fitted after pooling together the four positions together for each subject.

The p values of the repeated-measured ANOVA values were adjusted for lack of sphericity using Greenhouse-Geisser epsilon and the effect size was estimated with partial eta squared. In general, average value are reported together with the corresponding standard deviations. All analyses were conducted in R (R Core Team).

3.2.3 Results

In the dynamic condition, participants generally performed the desired movements at the desired velocity. The average movement speed was 16.1 ± 3.4 cm/s along a circular trajectory (radius 13.2 ± 1.6 cm), which corresponds to a frequency of 0.19 ± 0.04 Hz and period of 5.4 ± 2.0 s. Figure 3.6 shows the average bar position for each subject at the middle of the stimulus period, when the change of the bar length reached its maximum or minimum extension.

Perceived bar length change

Figure 3.7 shows the two QUESTs in the static condition for one subject. A logistic psychometric function was fitted to the responses in the static and dynamic conditions separately (thick lines in Fig. 3.7B). In the dynamic conditions, we also fitted a separate psychometric functions to the four possible bar positions at the moment of the stimulus to investigated whether the position of the bar or the direction of movement relative to the body influenced the PSE or the DL.

Because participants were divided into two groups, with one group moving the bar in the clockwise direction and the other group moving the bar in the anticlockwise direction, the bar moved in opposite directions at each position depending on the group. For example, the bar at the "far" and "close" positions moved rightward for one group and leftward for group. Similarly, the bar at the "left" and "right" positions moved "toward" the body for one group and "away" from the body for the other group.

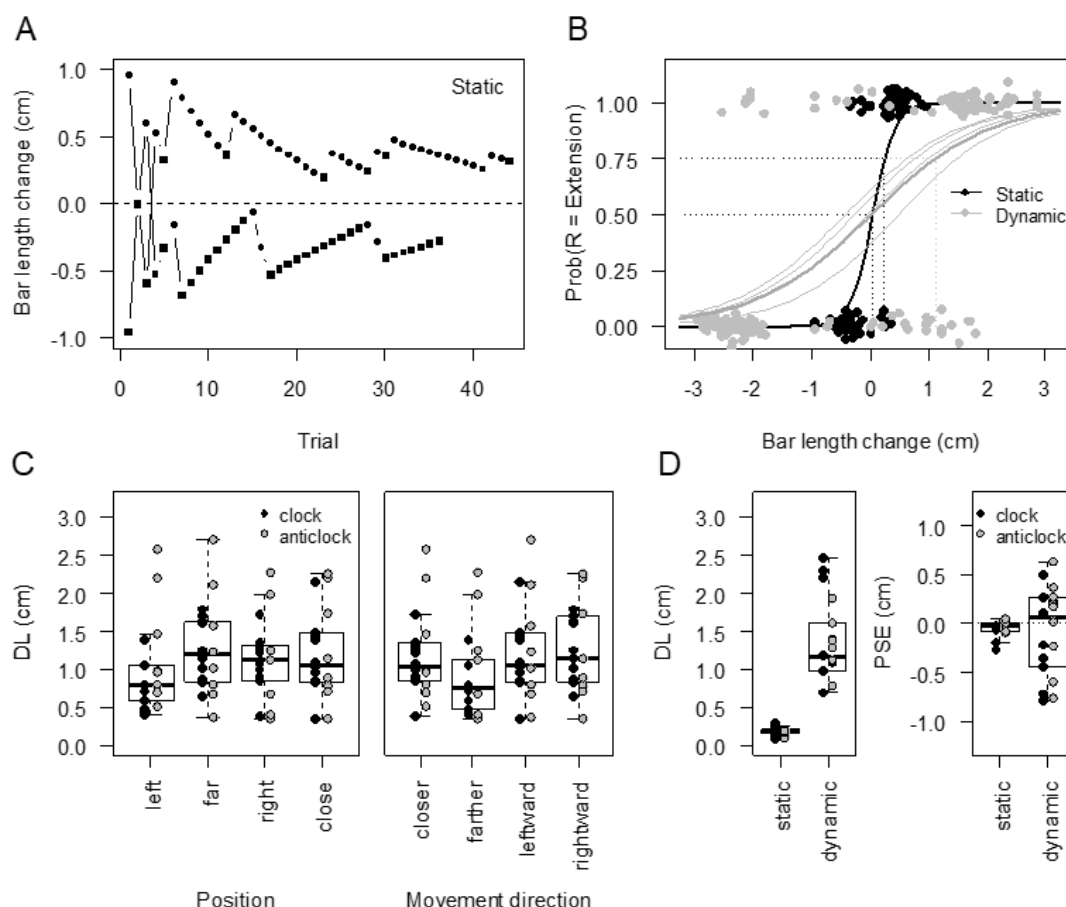


Figure 3.7. Results on perceived length. A: Example of double QUEST in the static condition for a typical subject. The symbol codes the responses "bar shortened" (squares) and "bar lengthened" (circles). B: Psychometric function in the static (black) and dynamic conditions (grey) for the same

subject as in Fig. 3.6A. The psychometric functions represent the probability of perceiving a bar lengthening as a function of the actual bar length change. In the moving conditions, a psychometric function was fitted for each position separately (thin grey lines) as well as for all positions together (thick grey line). C: DLs in moving conditions. The dots represent the DL for each position for participants who moved in clockwise (black) and anticlockwise direction (grey). The DLs are grouped according to the position of the stimulus (left panel) or according the movement direction (right panel). D: DLs and PSEs in the static and dynamic conditions. The PSEs and DLs In the dynamic condition

Figure 3.7C shows the DLs for all participants grouped according to the bar position (left panel) and movement direction (right panel). Separate one-way repeated-measure ANOVA indicated that neither the position of the bar relative to the body influenced the discrimination threshold ($F(3, 51) = 1.72$, $\epsilon = 0.86$, $p = 0.18$, $\eta_p^2 = 0.04$), nor the direction of movement ($F(3, 51) = 2.55$, $\epsilon = 0.90$, $p = 0.07$, $\eta_p^2 = 0.06$). Similarly (data not shown in the figure), the PSE was not influenced by the bar position ($F(3, 51) = 1.15$, $\epsilon = 0.66$, $p = 0.33$, $\eta_p^2 = 0.05$) or the movement direction ($F(3, 51) = 0.02$, $\epsilon = 0.86$, $p = 0.99$, $\eta_p^2 < 0.01$).

Since these analyses show that neither the position of the bar or the direction of the movement affect the PSE and DL, we recomputed the PSE and DL for each subject from a unique psychometric function that was fitted to all trials in the dynamic conditions (e.g., Figure 3.7B, thick grey line). We performed a two-way factorial ANOVA on the DLs and PSEs with movement condition (static vs dynamic) as within-subject factor and movement direction (clockwise vs anti-clockwise) as between-subject factor (see Fig. 3.7D). All the participants discriminated the direction of change of the bar length much better in the static (0.18 ± 0.05 cm) than in the dynamic (1.37 ± 0.53 cm) condition ($F(1, 16) = 98.21$, $p < 0.001$, $\eta_p^2 = 0.74$). The direction of movement ($F(1, 16) = 0.50$, $p = 0.49$, $\eta_p^2 = 0.02$) and interaction ($F(1, 16) = 0.62$, $p = 0.44$; $\eta_p^2 = 0.02$) were not statistically significant.

The Points of Subject Equality (PSEs) did not differ markedly from zero, indicating an absence of bias in the perception of the direction of the bar length change (see Fig. 3.7B, right panel). The average PSE was -0.06 ± 0.09 cm in the static condition and -0.07 ± 0.45 cm in the dynamic condition. A two-way factorial ANOVA confirmed that neither the movement condition ($F(1, 16) = 0.05$, $p = 0.81$, $\eta_p^2 < 0.01$), nor the movement direction ($F(1, 16) = 2.59$, $p = 0.13$, $\eta_p^2 = 0.08$) or the interaction ($F(1, 16) = 0.35$; $p = 0.56$; $\eta_p^2 = 0.01$) affected the PSEs.

Physical interaction

Figure 3.8 illustrates the physical interaction happening during the stimulus period for a typical subject. The distance between the two hands was in general slightly less than the virtual bar length, indicating that the participant compressed the bar between the two hands. The actual change of the bar length Δ_L between the beginning and middle of the stimulus period matched very closely the stimulus value δ (Fig. 3.8A). The grasp force increased when the bar lengthened, and decreased when the bar shortened (Fig. 3.8B). As a result, the change of grasp force between the first and second halves of the stimulus period was negative ($\Delta_F < 0$) in the trials where the bar had momentarily shortened ($\delta < 0$) and positive in the other trials ($\Delta_F > 0$ when $\delta > 0$). Notably, the grasp force change Δ_L was proportional to the change of bar length δ (Fig. 3.8 right panel). To analyze this relationship further, we regressed the grasp force change Δ_F on the bar length change Δ_L to estimate the *grasp stiffness* k_G for each subject in the static and dynamic conditions (i.e., the slope of the regression line $\Delta_F = k_G \Delta_L$, see Methods). On average, the bar length change Δ_L explained more than 85% of the grasp force change Δ_F during the stimulus period (average R^2 : 0.86 ± 0.13 in static condition and 0.92 ± 0.04 in dynamic condition).

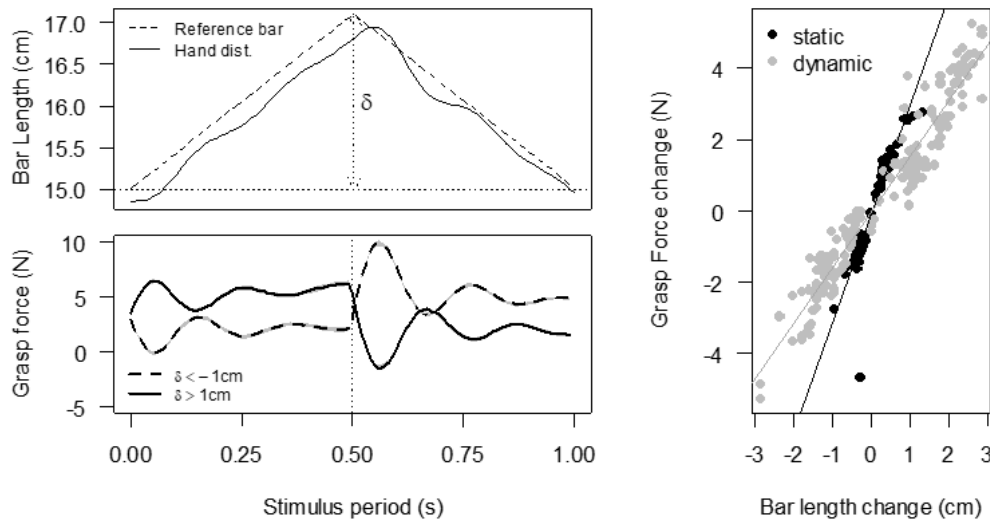


Figure 3.8. Physical interaction for a typical participant. Top left: Change of the virtual bar length and change of the distance between the two hands during the stimulus period for a typical trial ($\delta = 2.1$ cm). Bottom left: Average compression force in dynamic conditions during the stimulus period. The average force is plotted separately for bars that briefly lengthened ($\delta > 1$ cm) and shortened ($\delta < 1$ cm). Right: Effect of bar length changes on the grasp force in the static and dynamic condition.

The average grasp force (f_0) just before the stimulus was positive in the static (2.68 ± 3.18 N) and dynamic (2.69 ± 1.57 N) condition with only one exception (Fig 3.9A), indicating that the participants compressed the bar between the two hands. On average, the grasp force just before the stimulus was 2.69 ± 2.47 N, which corresponds to a difference between the hand distance and the desired bar length of 1.07 ± 0.98 mm (all subjects and conditions pooled together). The difference between the static and dynamic conditions (paired t test: $t(16) = 0.001$, $p = 0.993$) and the correlation between the two conditions ($r = 0.47$, $t(15) = 2.05$, $p = 0.058$) were not statistically significant. The grasp force variability (standard variation) during the second that preceded the stimulus was markedly smaller in the static (0.07 ± 0.01 N) than in the dynamic (0.37 ± 0.10 N) condition (paired t test: $t(16) = 12.1$, $p < 0.001$).

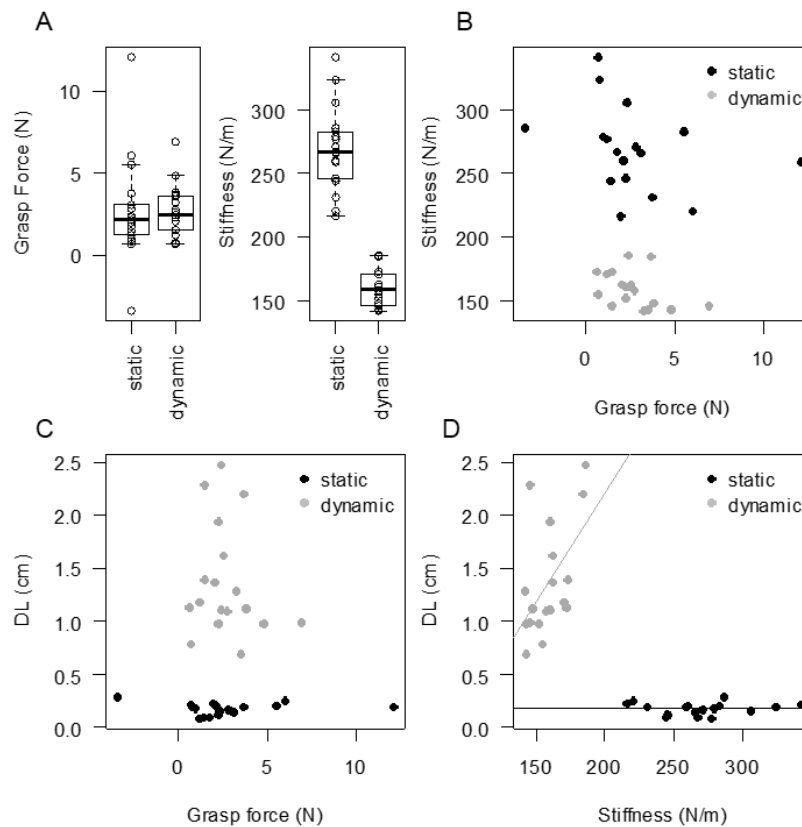


Figure 3.9. A and B: Grasp force and stiffness in static and dynamic condition. C and D: Dynamic and static discrimination thresholds as a function of grasp force and stiffness

The grasp stiffness was much smaller in the dynamic condition (159 ± 14 N/m) than in the static condition (269 ± 34 N/m). The difference was highly statistically significant paired t test: $t(16) = 12.63$, $p < 0.001$) but there was no correlation between the two conditions ($r = 0.05$, $t(15) = 0.21$, $p = 0.836$). The stimulus position and movement direction did not affect the average force or stiffness (results not shown).

Table 4 Coefficient of correlation

	Static condition		Dynamic condition	
	Grasp Force	Stiffness	Grasp force	Stiffness
Stiffness	-0.333	---	-0.412	---
DL	0.000	0.011	-0.156	0.541*

*: $p < 0.05$

The grasp force did not correlate with the stiffness in the static ($r = -0.33$, $p = 0.19$) or dynamic ($r = -0.41$, $p = 0.09$) conditions (Fig. 3.9B). It also did not correlate with the discrimination threshold in the static ($r < 0.01$, $p > 0.99$) or dynamic ($r = -0.16$, $p = 0.54$) condition (Fig. 3.9C). Interestingly, we found that the stiffness was correlated with the stiffness in the dynamic ($r = 0.54$, $p = 0.021$) but not in the static condition (right panel). In contrast, the discrimination thresholds were not correlated with the grasp force (middle panel). Table 1 summarize the coefficients of correlation between the principal variables in the static and dynamic conditions.

3.2.4 Discussion

This study measured the ability to detect a brief change of length of a bimanually held bar at rest and during movement. We found that the discrimination thresholds were about one order of magnitude larger in the dynamic condition ($DL = 1.37 \pm 0.53$ cm) than in the static condition ($DL = 0.18 \pm 0.05$ cm) in agreement with the pilot study (Baud-Bovy et al., 2010). However, we did not find an effect of the position of the stimulus and/or direction of movement on the discrimination thresholds. This result differ from the result of the pilot study where the thresholds were lower for sagittal movements (away from the body) than for lateral (leftward) movements. A difference between the two studies is the type of movement, which was continuous in this study and discrete in the pilot study. It is possible that the need to accelerate and break with discrete movements was at the origin of a pattern of interaction force that interfered with the direction of movement and

made the detection of the stimulus more difficult in the lateral direction. But given the small number of participants in the pilot study, further research is needed to confirm this effect.

Proprioceptive acuity decreases during movement

Muscle spindles are the primary contributors to the sense of position and movement with a secondary contribution of skin receptors and centrally generated motor commands (reviews in Macefield & Knellwolf, 2018; Proske & Gandevia, 2009). Muscles spindles are unique in having an efferent innervation, which allows them to maintain a response at all muscle lengths. In the static condition, the change of the length of the bar is likely to have a strong impact on the activity of spindles embedded in the muscles. As a matter of facts, spindles activity is stable in static or quasi-static conditions. Moreover, a brief lengthening and shortening of the muscle length yields a strong increase or decrease of the background activity (e.g. Cordo et al., 2002; Vallbo, 1971). In contrast, detecting the stimulus was harder in the dynamic condition. Although the fusimotor drive makes it difficult to extrapolate the activity of muscles spindles during voluntary movement, there is evidence that the muscle spindle activity reflects primarily lengthening or shortening velocity, at least in isotonic conditions (Macefield & Knellwolf, 2018). Accordingly, it is likely that muscle spindle activity varied in the dynamic condition because the lengthening or shortening velocity of the arm muscles varied during the circular movement even though the angular velocity remained constant. As a result, detecting the effect of the stimulus might be harder because the background activity is more variable in the dynamic condition.

Besides kinematic variables such as muscle length or velocity, there is considerable evidence that muscle spindles activity is also affected by the load, the activity of antagonist muscles and/or the level of co-contraction. For example, spindles activity is affected by the load in position holding task (Hulliger et al., 1982) and during a movement (Dimitriou, 2014). In our study, we measured the force applied by the hand on the bar before and during the presentation of the stimulus, which can be considered as a load from a physical point of view. We found that the grasping force before the presentation of the stimulus varied more in the dynamic condition than in the static condition. This increase of variability of the interaction force might also explain why it was more difficult to identify the stimulus in the dynamic condition.

Another possible factor that might have influenced the performance is the division of attentional resources between the motor task (moving the bar) and the perceptual task (identifying the change of length of the bar) in the dynamic condition. However, we do not believe that this factor played a large role. As a matter of facts, the discrimination thresholds obtained in this study with continuous movement did not differ much from the results obtained in a preliminary study where

the stimulus occurred during a discrete movement (Baud-Bovy et al., 2010). If divided attention were the primary cause for lower performance in the dynamic condition, one would have expected that a worse performance in the previous study because the discrete point-to-point movements requires more attention to be executed than the circular movements. In fact, we choose to use circular movements in this study because they could be executed in a highly automated way.

Grasp force and grasp stiffness

In this experiment, participants tended to compress the bar slightly throughout the trial. During the stimulus period, the grasping force increased when bar lengthened and decreased when the bar shortened. This was the case both in trials where the bar lengthening preceded the shortening ($\delta > 0$, "bar briefly lengthened") and where the shortening preceded the lengthening ($\delta < 0$, "bar briefly shortened"). The grasp force difference between the bar lengthening and shortening period was proportional to the change of length of the bar. This pattern reflects the biomechanical properties of the human arms, which can be modelled viscoelastic physical systems at least as a first approximation (Feldman & Levin, 2009). Assuming the participants do not modify the control parameter during the stimulus period, the change of hand positions caused during the stimulus will change the force in a manner that depend on the stiffness of the arm. Although measuring arm stiffness was not an objective of the study, our results can be compared to other studies where a position perturbation was used to measure the arm stiffness. In the static condition, the average grasp stiffness in our study is inside the range of endpoint stiffness measured by Mussa-Ivaldi et al. (1985). In the dynamic condition, we found that the arm stiffness decreased during the movement with respect to the static condition. This observation is in agreement with (Bennett et al., 1992) who also found that stiffness of the arm dropped during movement. It is also in agreement with Gomi & Kawato (1996, 1997) who found that stiffness increased at the beginning and end of point-to-point movement but decreased in the middle of the movement discrete movements.

Exploiting motor strategies to optimize perception

The interaction force is affected by two factors. First, the transient change of the length of the virtual bar. Second the motor state of the participant such the magnitude of the grasp force or the arm stiffness of the arm but. Unlike the stimulus, the motor state can be controlled by the participant. Since the force applied to the bar can affect the neuronal discharge of mechanoreceptors and proprioceptors and, as discussed above, the performance in this task,

participants might in principle adjust their motor state to optimize their performance in this perceptual task.

To address this possibility, we examined whether the grasp force or the grasp stiffness were correlated with the discrimination thresholds. Interestingly, we found discrimination thresholds were positively correlated with grasp stiffness in the dynamic condition only (Fig. 3.9D). Discrimination thresholds were not correlated with grasp force in either condition, or with grasp stiffness in the static condition.

It should be noted that grasp stiffness alone does not determine the performance. If this were the case, one would have expected the grasp stiffness to be smaller in the static than in the dynamic condition since the discrimination thresholds were smaller in the static condition. This pattern of results suggest that the identification of the stimulus involves different processes in the static and dynamic condition. Clearly, increasing arm stiffness seems detrimental to perceiving the change of the length of the bar in the dynamic condition but not in the static condition. To the contrary, every participant performed better in the static than in the dynamic condition despite the fact that the grasp stiffness was larger in the static condition. Whether the difference of arm stiffness across subjects in the dynamic conditions or reflect some willful or voluntary motor strategy by the subject who employed it is an open question.

A limit of this study with respect to the interpretation of this correlation is that arm stiffness was not manipulated in the experiment. A within-subject design where arm stiffness is directly manipulated might be more powerful to establish a causal relation between grasp stiffness and the performance in the perceptual task if it is possible to induce such a change in a manner that do not hamper the perceptual task.

Chapter 4

Interaction of Multiple Body Representations

After presenting results focusing on the immediate sensory and multisensory integration processing in [Chapter 2 and 3](#), here we evaluate the combination of such somatosensory signals with the cognitive representations of the body stored in the mind. In particular, we focus on the interaction between proprioception and touch which provides a powerful way to investigate the implicit body representations underlying touch (Frédérique de Vignemont et al., 2005).

In this chapter, we evaluate how different Mental Body Representation (MBRs) interact one with the other. To that aim, we combined two tasks involving different MBRs and we compare the magnitude of the biases observed in each of these. The results suggest inconsistencies between them, raising the possibility that two different metric representations of the body are devoted to these tasks. Furthermore, the potential confounds deriving from higher-level factors such as the response modality is assessed.

4.1 Introduction

In the last decade, a growing interest has been given to the investigation of the mental body representations (MBRs) which are stored in the brain. Given the interdependency between the sense of touch and the body, these cognitive maps of the body play a fundamental role in the processing of somatosensory information. As noted in the Introduction of this thesis, there is not yet a general agreement about the neuro-anatomical correlates of MBRs, which are usually defined in functional terms (see de Vignemont, 2010). In Chapter 1, I presented two models describing the interaction between the somatosensory processing and the body. The two models highlight the role of the MBRs as reference to interpret information about the surrounding environment. (Longo et al., 2010's somato-perceptual information processing model provides that immediate afferent

somatosensory signals are combined with cognitive maps of the body in order to generate the experience that we have of the body and the external world ([see Section 1.2.1](#) for more details). In particular the MBRs included in the model consists in: i) a *superficial schema* mediating the localization of tactile stimuli on the skin, ii) a *postural schema* mediating the localization of the body in space, iii) a body model which contains the metric property of the body. Noteworthy, each of these MBRs and their interactions are fundamental to generate high-level percepts. For example, to estimate the size of an object touching the skin the superficial schema is involved in order to localize the touch on the body surface. However, no skin receptors can provide metric information about the object, and the metric information stored in the body model are needed. Seemingly, the postural schema receives information about the joint angle from cutaneous receptors. But again, it is not possible to get the absolute position of the arm in the space, without the metric information of the body model (Longo, 2015). Finally, to localize the tactile information in the external world the interaction of all the MBRs is necessary. Indeed, we have to know the absolute position of the body in the space (i.e. postural schema and body model involvement) and also to localize the object onto the body surface (i.e. superficial schema).

The main objective of this preliminary study was to investigate the perceptual distortions in a task that requires combining information from the different MBRs. To that end we defined a new task, the Joint Tactile Distance and Posture Estimation Task. In a sense, this task is a combination of the Tactile Estimation Task (TET; or Tactile Distance Task), and a joint angle estimation task. In Experiment 1, participants had to estimate the distance between two tactile stimuli applied to their arm and the elbow joint posture, while the joint elbow is flexed at different angles (see Table 1). The participants verbally reported the number of estimated centimeters, referring to a millimetric scale.

Table 1. *Summary of experimental designs*

	Body Part	Joint Angle Flexion	Response Modality
Experiment 1	Arm, Forearm	From 0° to 120° by step of 30°	Visual
Experiment 2	Forearm	0°	Visual, Haptic

At each trial, differently distanced tactile stimuli could occur within the same limb segment (i.e. arm *or* forearm), or across the elbow joint angle (i.e. on the arm *and* on the forearm). When the stimuli occurred across the joint angle, the participants were explicitly asked to consider the straight-line distance between points as the crow flies. Two points located in the same area do not have the same “straight-line” distance at different flexion angles of the elbow. To give an example,

the straight-line distance between the middle of arm and the middle of the forearm is much shorter when the elbow is flexed than when it is extended.

The literature regarding tactile distance perception has often focused on shorter distances than that considered in our Experiment 1. Accordingly, one of the response modalities exploited in previous studies consisted in asking the participants to estimate the distance between the tactile stimuli by reproducing it by varying the aperture between the thumb and the index fingers (Keizer et al., 2011, 2012; Stone et al., 2018). However, such a procedure could not be employed with distances that exceed the hand width. In Experiment 1 we overcame this limitation by providing a visual reference (i.e., millimetric scale). Nonetheless, the different response estimation method being used could lead to difficulties in results interpretation. Indeed, the hand aperture response modality completely rely on somatosensory information and could be mediated by sensory-motor integration. On the other hand, the reference to a millimetric scale could be mediated by perceptual recalibration influenced by the integration of visual and somatosensory information, and thus the two could differ one from the other. Accordingly, the Experiment 2, served as a control to assess the effect of the response modality on the estimated distance. To that end, we compared the estimated distance reported using a visual analog scale, with haptic response modality where the participants used the distance between the thumb and index fingers (hand aperture) to respond (see Table 1).

4.2 Materials and Methods

4.2.1 Stimuli

Two metallic and not sharp pins (about 1 mm² tip) were used to touch the participant right arm at two of the marked positions simultaneously. The stimulus was administered manually by the experimenter at a pre-marked location on the participant's hidden arm.

4.2.3 Procedure

4.2.3.1 Experiment 1

In Exp. 1, eleven volunteer women between 18 and 24 years of age (mean $\pm$ SD: 22 $\pm$ 2.70 years) with no known neuromuscular disorders participated to the study.

The experimental setup consisted of a vertical panel, mounted on tabletop, which hid the view of the right arm of the participants. A large protractor centered on the elbow position was drawn on both sides of the panel to indicate possible flexion angles. On the left side of the panel, a 60 cm long ruler was placed horizontal on the table. The participants sat in front of the experimental setup. The right arm rested comfortably on an elevated support (see Figure. 4A), while the left arm stood along the side of the body and was hidden from view by a cloak.

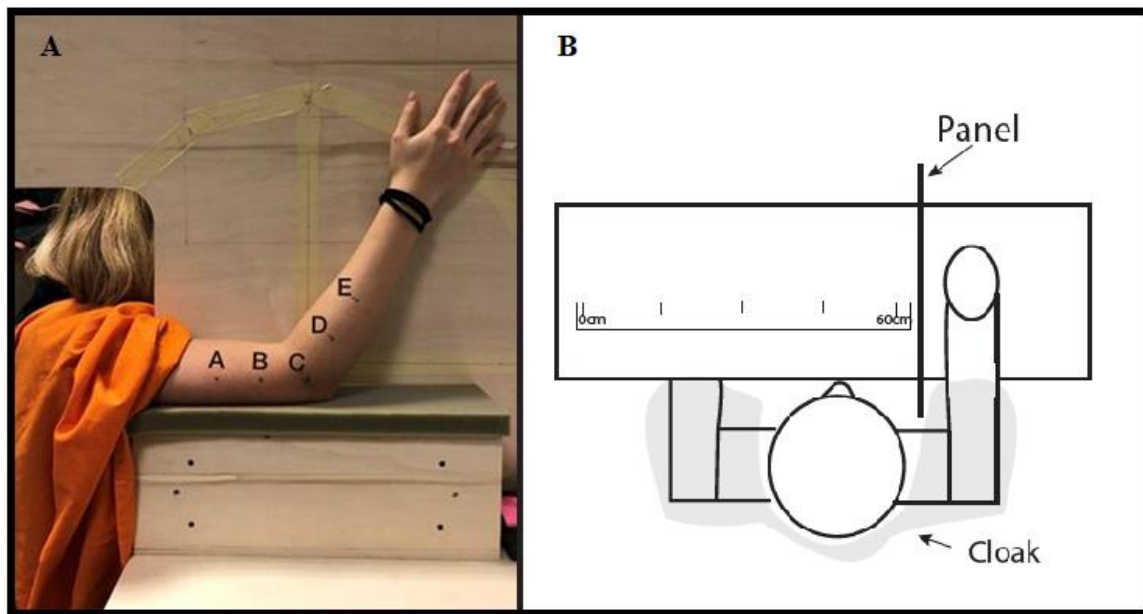


Figure 4. *Experimental Setup.* (A) The panel shows the experimental setup of Exp. 1 from the experimenter view. The black dots and letters represent the five possible stimuli locations on the arm and forearm. The black arrow highlights the angle flexion of the elbow. (B) Top view of the experimental apparatus. The participants estimated the size of the tactile objects on their hidden arm, by verbally reporting the number of estimated centimeters, referring to a millimetric scale.

Each trial started with the experimenter moving the subject's right forearm and hand to one of five possible arm postures (elbow flexion angles of 0, 30, 60, 90 or 120 degrees with 0 degree corresponding to the extended arm posture). After positioning the arm, the experimenter used the two pins to briefly touch two of five possible points on the lateral side of the arm. The contact

points were separated by 5 cm and were marked on the skin with a pen before the beginning of the experiment. The points are identified by the letters (A; B; C; D; E) in Figure 4. During the experiment, the pair of points touched by the experimenter could be on the same limb segments (pair A-B, B-C or A-C on the arm or pair C-D, D-E or C-E on the forearm) or cross the elbow joint (pairs A-E, B-D, A-D or B-E). The distance between two contact points on the skin could be 5 cm (pairs A-B or B-C on the arm; pairs C-D or D-E on the forearm), 10 cm (pairs A-C on the arm; C-E on the forearm or B-D across the joint), 15 cm (pair A-D or B-E across the joint) or 20 cm (pair A-E across the joint).

The task for the participant was to report verbally three perceptions. First, the participant had to report the perceived joint angle of flexion of their arm in degrees. Participants could look at the protractor with marked angles ranging from 0° to 130° by step of 5° drawn on the left (visible) side of the wooden panel that hid their right arm. Second, they had to report whether they had perceived one or two contacts and the corresponding body segment (on the arm, on the forearm or crossing the joint). Finally, in case they perceived two tactile stimuli, they had to look at a 60-cm long millimeter scale placed on the table and verbally report the distance in centimeters between the two contacted points. At the beginning of the experiment, participants were instructed to report the straight line "as-the-crow-flies" distance between the two contact points when the arm was flexed, and not the distance on the skin. The ten possible pairs of points were combined with the five elbow flexion angles to form a block of 50 trials. The order of presentation of the stimuli within a block was randomized. The experiments included five blocks for a total of 250 trials. The experiment lasted approximatively 90 minutes.

4.2.3.2 Experiment 2

Eight volunteer women between 20 and 30 years of age (mean $\pm$ SD: 23 $\pm$ 3.21 years) with no known neuromuscular disorders participated in the study. The participants sat at a table with their stimulated arm hidden from view, comfortably resting on the table, while the counter lateral arm stood, unseen, along the side.

At each trial, the experimenter used a custom-made piece with two parallel pins to touch the forearm of the participants in a region of the forearm 5 cm below the elbow joint. The stimulated arm was the right arm for half of the participants, and the left arm for the other half. The metallic pins had a flat ending with a surface of about 1 mm². The distance between two pins ranged from 3 to 7 cm (3, 4, 5, 6 or 7 cm). Because of the constraints placed by the hand-aperture condition, the maximal distance between two contact points was limited to 7 cm.

The main objective of this control experiment was to examine the effect of the response method on the perceived distance between two contact points. Accordingly, we provided two different response modalities. In the *visual scale condition*, participants had to report the distance in cm between the two contact points, while being able to see the millimeter scale. In the *hand-aperture condition*, the participants were blindfolded and reported the answer by opening the hand so that the distance between the thumb and index finger would correspond to the perceived distance between the two contact points.

A second objective of this experiment was to examine if there was an effect of the orientation of the contact points on the perceived distance. For this reason, the two contact points depending on the trial could be aligned with the axis of the limb segment (proximo-distal orientation) or perpendicular to it (medio-lateral orientation).

The experiment was divided into two parts with half of the participants performing the visuo-analog scale response modality first, and the other half performing the hand-aperture response modality first. Each response modality included five block of 20 trials. Each block included 4 presentations of each stimulus (i.e. 3, 4, 5, 6, or 7 cm) in each orientation (i.e. proximo-distal or medio-lateral), in random order. Due to a technical problem, the fifth block included only the half of the planned trials, with missing trials corresponding to a random subset of trials in the block that varied across participants.

4.2.4 Data analysis

The statistical analyses of the dependent variables are detailed in the results section. For repeated-measure ANOVAs, we report the partial eta squared for each effect. We used Greenhouse-Geisser epsilon to adjust P values of effects with more than two levels for the sphericity condition. For linear mixed effect (LME) and generalized linear mixed effect models (GLMM), we used the Likelihood Ratio tests (LRTs) to select the most complex matrix supported by the data set, following the approach described in (Matuschek et al., 2017). The reported values for fixed effects, correspond to Type III Wald chi-square tests. P values for post-hoc contrasts were adjusted with Holm's method. All analyses were conducted in R (*R Core Team, 2020*).

4.3 Results

4.3.1 Experiment 1

We report the results of the perceived elbow joint flexion angles, perceived contact points and perceived distance between the two contact points in the following sections.

Arm Posture

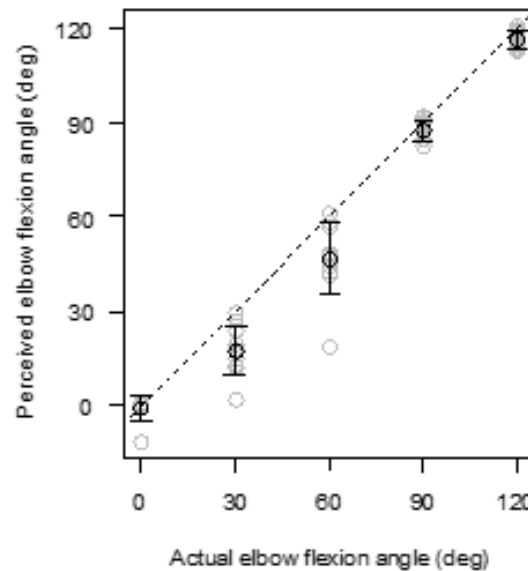


Figure 4.1. Perceived elbow flexion angles. The black dots represent the average values across all participants. The grey circles represent the average value for each participant. The dashed line represents the actual flexion angle. The error bars correspond to the standard deviation of the individual means (between-subject error).

Figure 4.1 shows a tendency to underestimate the actual elbow flexion angle, in particular at 30 and 60 degrees. A one-way repeated measure ANOVA of the effect of the arm posture on the perceived angle shows a very large effect of the arm posture indicating that participants were able to distinguish the different elbow flexion angles one from the other ($F(4, 40) = 1138.2$, $\varepsilon = 0.344$, $p < .001$, $\eta^2_P = 0.99$). We computed the difference between the actual and perceived elbow flexion

angles to test if the perceptual error was affected by the arm posture. The one-way RM ANOVA of the effect of the arm posture on the perceptual error was a statistically significant ($F(4, 40) = 16.964$, $\epsilon = 0.344$, $p < .001$, $\eta^2_p = 0.63$). A post-hoc analysis of the perceptual error confirmed that perceived elbow joint angle was underestimated for elbow flexion angles of 30° and 60° ($p < 0.001$ for 30° and 60° and $p > 0.05$ for all the other angles flexion; p values were adjusted with Holm's method).

Two-points detection

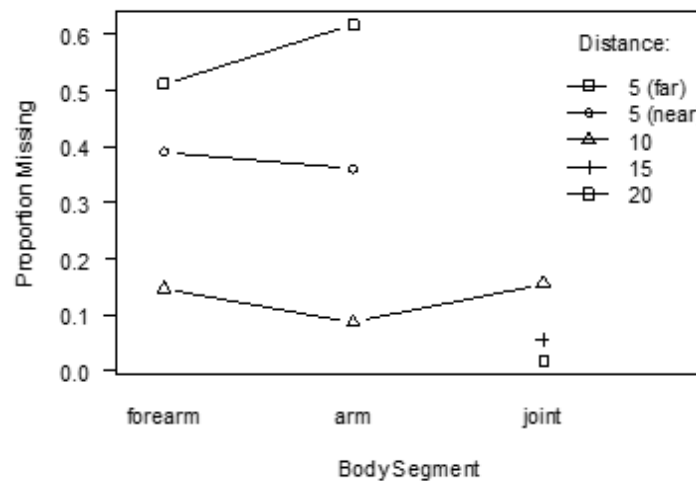


Figure 4.2. Proportion of Missing trials. The different type of dots represents the possible distances occurring between the tactile objects. On the x-axis, the different body part in which the stimuli could occur within the same body segment (forearm or arm), or across the joint (joint; i.e. one on the arm and the other on the forearm). On the y-axis, the proportion of missing trial is represented. As visible from the figure, the percentage of missing values is significantly higher for smaller stimuli distance, independently from the interested body part.

Participants did not always perceive the two contact points and were therefore unable to report a distance between them ("missing responses"). Fig. 4.2 shows that the percentage of missing responses increase for shorter distance. The figure also suggests that the percentage of missing responses for the shortest distance (5 cm) was lower when the contacts occurred near the elbow

(i.e. *near*; pairs B-C and CD), than when the contact was far from the elbow (i.e. *far*; pairs A-B or D-E) than when the contact was near the elbow (pairs B-C and C-D).

We used a Poisson Generalized Linear Mixed Model (GLMM) with a log link function to model the number of missing responses as a function of the localization of the stimulus (limb segment: arm, forearm or across the elbow joint) and the distance on the skin (5 (far), 5 (near), 10, 15, 20 cm). The GLMM included correlated random intercepts and random limb segment coefficients for each subject. The LRTs show a significant effect of the distance ($\chi^2(4) = 155.32$, $p < .001$), but no effect of the stimulus localization ($\chi^2(2) = 3.61$, $p = .165$). The interaction was also statistically significant ($\chi^2(2) = 702$, $p = .029$), reflecting the small difference in the number of missed responses between the arm and forearm. However, the effect was much smaller than the effect of the distance between the contact points. Using only the subset of trials with contact points across the joint, we also analyzed whether the number of missed responses depended on the elbow joint flexion angle. A Poisson GLMM with flexion angle and stimulus distance on the skin showed only a statistically significant effect of the distance ($\chi^2(2) = 33.668$, $p < 0.001$). The effect of the flexion angle ($\chi^2(1) = 2.862$, $p = 0.091$) and the interaction ($\chi^2(2) = 0.497$, $p = 0.778$) were not statistically significant.

We also investigated the number of responses at the individual level and we found that it ranged from 9% to 48% with 50% of the participants within the 16% to 29 % range (median = 19%). For all participants, we found the same tendency to miss more response as distance decreased. For all but two participants (81%), we also found an increased number of missed responses when the 5 cm stimulus touched the arm or forearm in the position further away from the elbow (i.e. pair A-B or D-E).

The missing responses were removed from all the subsequent analyses where we analyze the perceived distances between the two contact points.

Estimated Distance

Figure 4.3 shows a dramatic underestimation of the distance between the contact points. For the contact points crossing the elbow joint (right panel), the estimated distance varied with actual distance between the contact points on the skin and the arm posture but the latter effect appears limited.

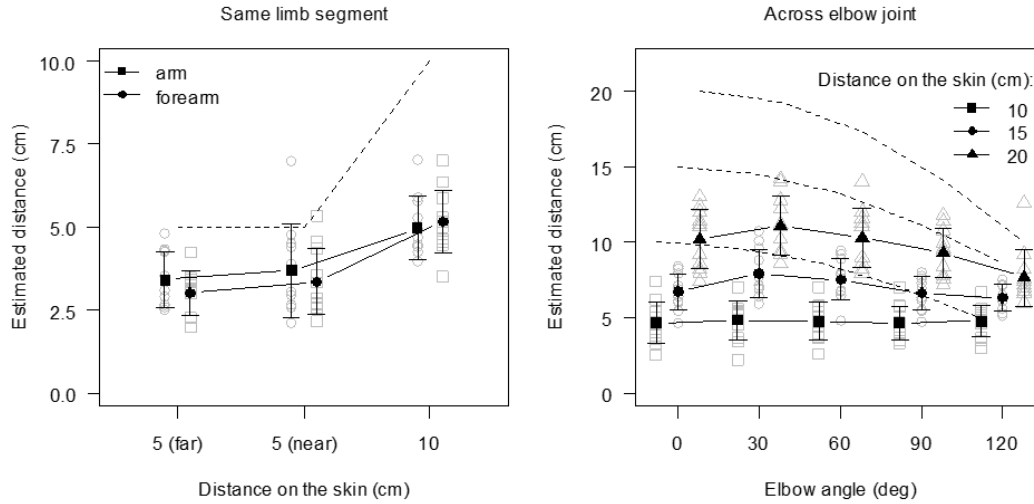


Figure 4.3. Actual (dashed lines) and perceived (black line) distance on the same limb segment (left panel) and across the elbow joint (right panel). The grey dot represents the mean values for each subject. The black dots represent the mean perceived distance across subjects. The error bars represent the standard deviations of the participants mean values. The dots positions are slight shifted on the horizontal axis to avoid overlap.

For the stimuli on the same limb segment, a two-way repeated-measure factorial ANOVA of the perceived distance with the actual distance (5 (far), 5 (near) and 10 cm) and arm segment (arm or forearm) as predictors shows a statistically significant effect of the actual distance ($F(2, 10) = 29.12$, $\epsilon = 0.805$, $p < .001$, $\eta^2_p = 0.42$). Tukey pairwise tests indicated that this effect could be entirely attributed to the difference between the 5 cm and 10 cm stimuli ($p < 0.001$). The estimated distance for 5 cm stimuli near and far from the elbow did not differ significantly ($t(20) = 1.185$, $p = 0.476$). We did not find an effect of the limb segment ($F(1, 10) = 0.902$, $p = 0.36$, $\eta^2_p = 0.01$) and the interaction was not statistically significant ($F(2, 10) = 3.341$, $p = 0.056$, $\epsilon = 0.954$, $\eta^2_p = 0.02$), which indicates that the estimation bias is the same on the arm and forearm.

For the stimuli across the elbow joint, the distance should decrease when the elbow flexion angle increases since the participants were explicitly asked to estimate in straight line. Fig. 4.3 (right panel) suggests however that the flexion angle has only a small effect on the estimated distance. In particular, this figure suggests no effect of the arm posture for the pair of contacts points B-D closest to the elbow (10 cm distance on the skin). A two-way full-factorial repeated measure ANOVA of the perceived distance revealed that the distance on the skin ($F(2, 20) = 91.59$, $p < .001$, $\epsilon = 0.657$, $\eta^2_p = 0.68$), the flexion angle ($F(4, 40) = 11.64$, $p < .001$, $\epsilon = 0.703$, $\eta^2_p = 0.14$) and the interaction ($F(8, 80) = 9.16$, $p < .001$, $\epsilon = 0.600$, $\eta^2_p = 0.11$) were statistically significant. To analyze further the interaction, we systematically compared the estimated distances for two

consecutive distances (e.g. 5 and 10 cm) on the skin with the same elbow flexion angle. These simple contrasts revealed that estimated distances for contact points separated by 10, 15 and 20 cm were different for all arm postures ($p=0.004$ for 120° elbow flexion angle $p<0.001$ for all other arm posture). We also compared the estimated distances for the same contact points at two consecutive elbow flexion angles. These simple contrasts confirmed that the elbow flexion angle had no effect for contact points separated by 10 cm on the skin (pair B-D). For the contact points separated by 15 cm on the skin (pairs A-D or B-E), there was a statistically significant difference only between elbow 0° and 30° flexion angles ($p=.005$). For the contact points separated by 20 cm, the estimated distance differed for all consecutive pairs of elbow flexion angles (0°-30°: $p=0.041$, 30°-60°: $p=0.31$, 60°-90°: $p=0.025$, 90°-120°: $p=0.001$).

As noted previously, Figure 4.3 shows a dramatic underestimation of the distance between the contact points. To compare this bias across different pairs of contact points and elbow flexion angles, we computed the ratio between the estimated and actual distance for each subject and pairs of contact points sharing the same distance. For contact points on the same limb segment, we computed these ratios separately for the arm and forearm but we pooled together all trials with different flexion angles since the arm posture does not affect the actual distance between two points on the same segment. For contact points across the elbow joint, we computed the ratio between the estimated distance and the actual straight-line distance (i.e. ratio error) for each arm posture separately.

Table 2. *Ratio error between estimated and actual distance between the contact points.* The standard deviation corresponds to standard deviations across the average values for each subject (between subjects error).

	Same limb segment		Across elbow joint		
Distance on the skin (cm)	5	10	10	15	20
Estimation (%)	68±17	51±08	63±12	58±8	62±11

Table 2 shows that the ratio error varied on average from 51% and 68% depending on the distance on the skin (grand mean = 60 ± 13 %). A one-way repeated-measure ANOVA of the average ratio values for each subject indicated that the distance on the skin had an effect on the ratio ($F(1, 4) = 5.262$, $p = 0.019$, $\epsilon = 0.433$, $\eta^2_p = 0.34$). Pairwise Tukey tests indicated that this effect could be entirely attributed to the estimated distance. For contact points on the same limb separated by 10 cm, the ratio (51%) was relatively smaller than for other contact points across the limb (>62%). Post-hoc contrasts confirmed that all ratios were smaller than 1 (one-side t-test, $p<0.001$ for all

conditions, p values adjusted with Holm's method), which confirms the large underestimation bias that can be observed in figure 4.3.

4.3.2 Experiment 2

In Exp. 2, the participants were asked to estimate the distance on the skin with different response modalities. We report the results of the perceived number of contact points and perceived distance between the two contact points in the next sections.

Two-Points Detection

Coherently with the findings from Exp. 1, Figure 4.5 shows that the percentage of missing responses increase for shorter distance. The figure also suggests that the percentage of missing responses for stimuli occurring along the proximo-distal orientation was higher than that for stimuli occurring the medio-lateral orientation, independently from the size of the stimuli.

We used a Poisson Generalized Linear Mixed Model (GLMM) with a log link function to model the number of missing responses as a function of the response modality, stimuli orientation and the distance on the skin. The variance-covariance structure of the GLMM included only a random intercept for each subject. LRTs showed a significant effect of the stimuli distance ($\chi^2(4) = 21.31$, $p < .001$) and orientation, ($\chi^2(1) = 7.22$, $p < .001$) but no effect of the response modality ($\chi^2(1) = 1.50$, $p = .221$). None of the interactions was statistically significant ($p > .5$ for all the possible interactions), which indicates that despite the trend visible in Figure 4.5, the tactile acuity did not vary between the two response modalities.

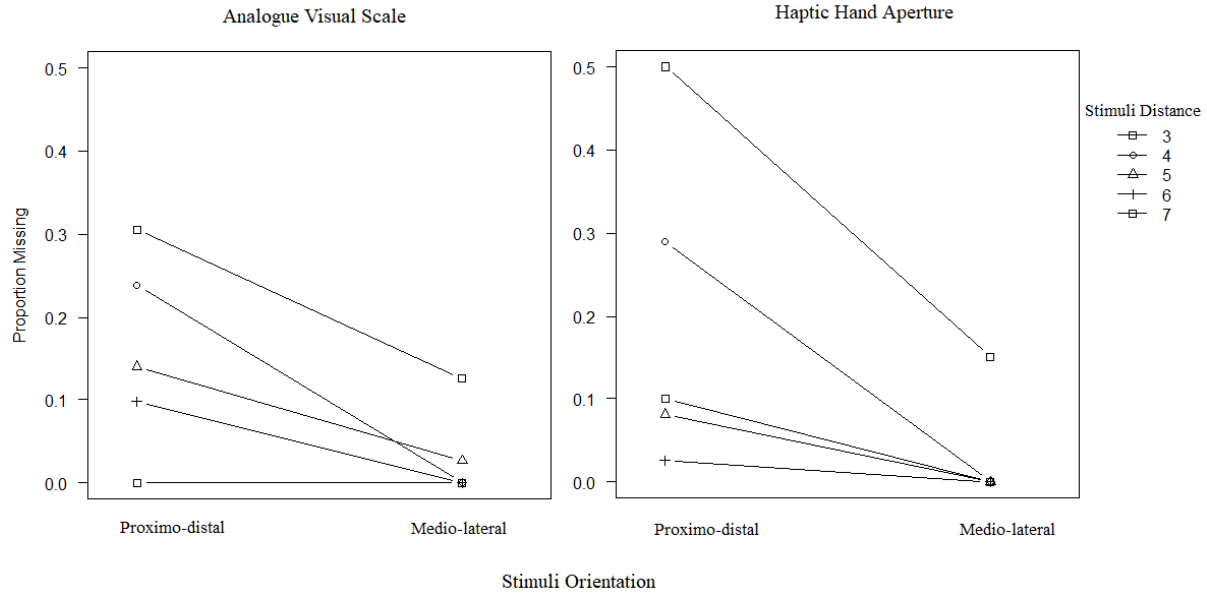


Figure 4.5. Proportion of Missing trials. Left Panel: Results for the Analogic Visual Scale response modality. Right Panel: Results for the Haptic Hand Aperture Modality. The different type of dots represents the possible distances occurring between the tactile objects. On the x-axis, the different orientations in which the stimuli could occur: proximo-distal or medio-lateral. On the y-axis, the proportion of missing trial is represented. As visible from the figure, the percentage of missing values is significantly higher for: 1) smaller stimuli distance, 2) Proximo-distal orientation of the stimulus, independently from the response modality.

Estimated Distance

Figure 4.6 shows that the participants showed significantly higher estimation in the hand aperture response modality than the visual analogic one, independently from the stimuli orientation and/or distance. We performed a three-way repeated-measure factorial ANOVA of the perceived distance with the actual distance (i.e. from 2 cm to 5 cm, by 1 cm step), the response modality (i.e. visual analogic scale or hand aperture) and the direction of stimuli orientation (i.e. proximo-distal or medio-lateral) as predictors. The response modality ($F(1, 6) = 25.24$, $\eta_p^2 = 0.81$, $p < .005$), stimuli orientation ($F(1, 6) = 78.51$, $\eta_p^2 = 0.93$, $p < .001$) and actual stimuli distance ($F(4, 24) = 65.90$, $\eta_p^2 = 0.92$, $\varepsilon = 0.54$, $p < .001$) were statistically significant. Tukey pairwise tests indicated that all the distances are different one from the others ($p < 0.05$). Furthermore, we found significant interaction effects. In particular there were a significant interaction between the actual stimuli distance and the response modality ($F(4, 24) = 6.07$, $\eta_p^2 = 0.50$, $p < .005$) or the stimuli orientation ($F(4, 24) = 10.59$, $\eta_p^2 = 0.64$, $p < .001$). This result shows that the differences between the two

response modalities and between the two stimuli orientation increased with the actual stimuli distances. Finally, the significant interaction between the response modality and the stimuli orientations ($F(1, 6) = 15.13$, $\eta^2 = 0.72$, $p < .01$) suggests that the estimation of the participants in both possible stimuli orientations are higher when they exploit the hand aperture condition, rather than the visual analogic response modality. There is no significant interaction between the three predictors considered together ($F(4, 24) = 0.61$, $\eta^2 = 0.09$, $p = .66$).

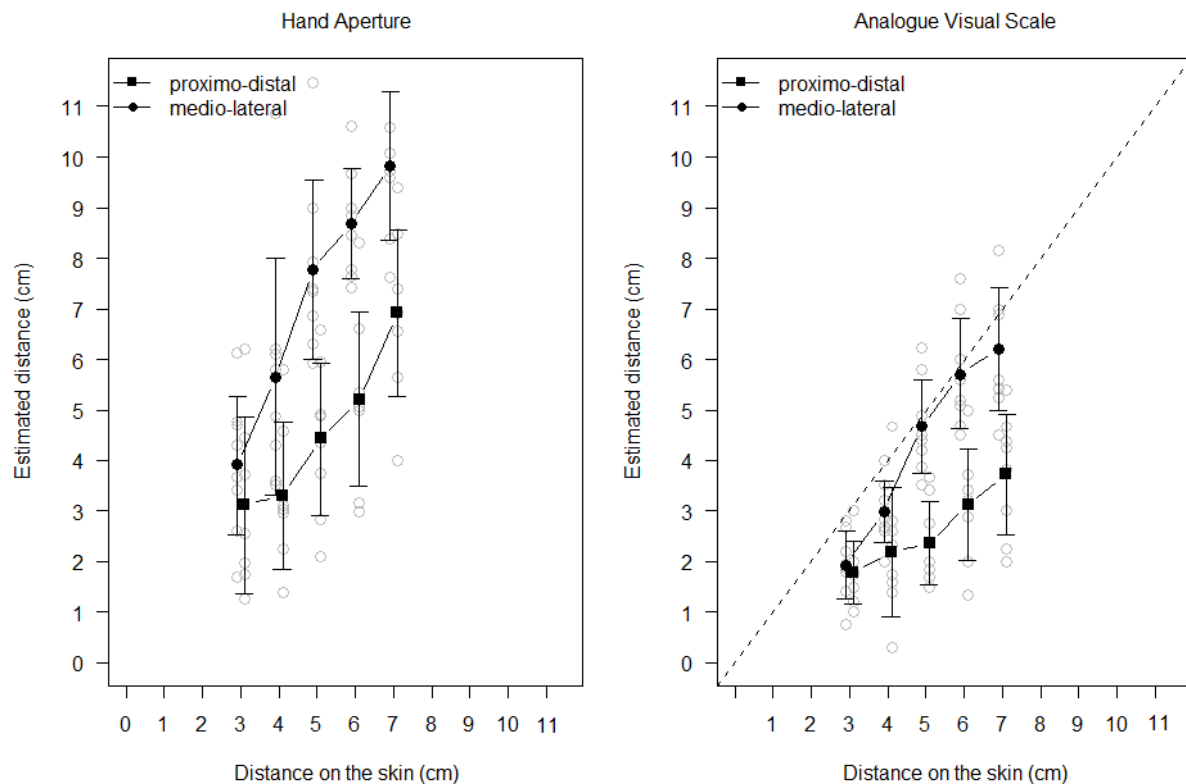


Figure 4.6. Actual (dashed lines) and perceived (black line) distance with the hand aperture (left panel) and analogic visual scale (right panel) response modalities. The grey dots represent the mean values for each subject. The black dots represent the mean perceived distance across subjects. The error bars represent the standard deviations of the participants mean values. The dots positions are slight shifted on the horizontal axis to avoid overlap.

In general, Figure 4 well represents the dramatic underestimation of the distance between the contact points. We computed the ratio between the estimated and actual distance for each stimuli orientation and response modality.

Table 3. Ratio between estimated and actual distance between the contact points. The standard deviation corresponds to standard deviations across the average values for each subjects (between subjects error).

Response Modality	Stimuli Orientation	Mean (M $\pm$ SD cm)	Ratio (Perceived/Actual Distance; M $\pm$ SD %)
Visuo Analogic	Medio-lateral	4.24 $\pm$ 2.19	0.83 $\pm$ 0.18
	Proximo-distal	3.93 $\pm$ 3.08	0.53 $\pm$ 0.21
Hand Aperture	Medio-lateral	7.10 $\pm$ 3.13	1.42 $\pm$ 0.36
	Proximo-distal	2.33 $\pm$ 1.73	0.92 $\pm$ 0.36

Table 3. shows the ratio error for all the actual distances, response modality and stimulus orientation. A one-way repeated measure ANOVA of the average ratio values for each subject indicated a main effect of the stimuli orientation ($F(1, 6) = 51.28$, $\eta_p^2 = 0.89$, $p < .001$) and response modality ($F(1, 6) = 22.50$, $\eta_p^2 = 0.79$, $p < 0.005$). Furthermore, we found significant interaction between the condition and the method of response ($F(1, 6) = 15.13$, $\eta_p^2 = 0.72$, $p < 0.01$.66) or the actual stimuli distance ($F(4, 24) = 3.54$, $\eta_p^2 = 0.37$, $p < .05$). Suggesting that independently from the response modality, there higher distances between the medio-lateral and proximo-distal response modality for shorter actual distances than for larger ones. Post-hoc contrasts showed that in the visuo-analogic condition the ratios were significantly smaller than (one-side t-test, $p < 0.001$) in all the distances of the proximo-distal condition, and only for smaller stimuli distance in the proximo-distal condition (i.e. 3 and 4 cm). On the contrary, in the hand aperture response modality the ratio error is not significant for any of the experimental conditions except for larger contact point distances occurring along the medio-lateral axis. In these cases, the ratio is positive, suggesting a significant overestimation of distance estimations.

4.4 Discussion

The main objective of this work was to investigate how information about the position of tactile objects on the skin surface of a limb segment was integrated with information about the arm posture.

In this study, we used an adaptation of the Tactile Estimation Task (TET), which has been identified as an experimental procedure to assess the metric property of the body. In particular, in Exp. 1 we performed the TET on different segments of the arm (i.e. arm and/or forearm), while varying the elbow angle flexion of the participants. In Exp. 2, the TET could relates stimuli oriented along proximo-distal or mediolateral orientation of the forearm, and provides two different response estimation methods (i.e. the visual analogic scale and the hand aperture). In both the experiment the TET adaptations allowed us to measure two different but complementary aspects of perception. The estimated distance (Exp 1 & 2) and arm posture (Exp. 1) measure the accuracy, veridicality or bias of the perception. The number of tactile stimuli which was reported to be felt as just one (i.e. missing responses) measures the precision of the perception. The first section focused on the large tactile biases observed in both experiment for the different i) body segments ii) response modalities. The next section focused on the discussion of the tactile acuity impact. Finally, we discussed the arm posture neglect observed in our control participants during the Exp.1.

4.4.1 The effect of response modality on tactile distance estimation.

A notable result of Exp. 1 is the extent to which participants underestimated the distance between the two contact points in the two first experiments. For contact points on the same limb segment, the task is comparable to the Tactile Estimation Task (TET), which has been used in various studies on tactile perception (Keizer et al., 2011, 2012). The amount of underestimation in our study is much higher to the one typically reported in the literature. For example, the average ratio between perceived and actual distance was about 60% while other studies report a ratio of 83% (Keizer et

al., 2011) or 93% (Keizer et al., 2012). However, it should be noted that Keizer and colleague used hand aperture, and not a visual scale, as response method.

The role played by the response method has been recently investigated by Tosi and Romano (2020). In their study, the authors compared three different response modalities. In the "verbal" response modality the participants had to report the number of centimeters they believe were occurring between the two contacts points with their eyes closed. In the others two conditions, the participants were able to see a horizontal reference line on a computer screen. In the "analogic" response modality, a number was display above each extremity of the (e.g. 0 cm and 15 cm) and the participant had to touch line at the location corresponding to the estimated distance. Finally, in the "discrete" condition, the line was divided by 28 landmarks consisting of different symbols and the participant had report verbally the symbol corresponding to the perceived distance. They found that the reported distances were markedly shorter when using a visual scale (i.e. in the "analogic" or "discrete" condition) than in the "verbal" response condition. Although the "discrete" condition also involved a verbal response, the results in this condition were close to the "analogic" condition, which involved a motor response, then to their "verbal" condition.

In our Exp. 1 the participants were asked to report verbally the perceived distance using a number like in Tosi and Romano(2020) "verbal condition". However, they were also asked to estimate the distance using a visual scale like in Tosi & Romano (2020) "analogic" and "discrete" condition. Moreover, the visual scale used in Exp. 1 similar to the one used in Tosi & Romano (2020) "discrete" condition except for the fact that the divisions were marked with numbers instead of symbols. Given the strength of the underestimation in our study, we hypothesize that participants in our study used the numbers like the marks above the ruler in Tosi & Romano (2020) discrete condition.

To confirm that the strong bias in Exp. 1 could be at least in part because by the response method, we performed a control experiment (Exp. 2) that compared the response modality used in Exp. 1 with the hand aperture method used in Keizer et al. (2011, 2012). The result of this experiment confirm that at least a part of the underestimation in Exp. 1 reflects the use of a visual scale. As matter of fact, the results of Exp. 2 ratio confirm that participants strongly underestimated distance in the proximo-distal direction (the average perceived/actual ratio: 53 %, see Table 3) when using the visuo-analogic scale method. In contrast, the average ration in the same direction was 92 % when using the hand aperture method, which is very similar to the results found by Keizer et al (2010 and 2012).

4.4.2 The effect of the orientation on distance estimation

In Experiment 2, we also found that reported distance were shorter along the proximo-lateral direction than along the medio-lateral direction. This direction effect found again higher underestimation when using the visuo-analogic scale than the hand aperture response modality. In this condition, we found an underestimation of 17 % with the visuo-analogic response modality and on overestimation of 42 % with the hand aperture response modality. In other words, the distances in the medio-lateral orientation are overestimated with respect to the proximo-distal orientation.

This finding is in agreement with the results of several previous studies (Longo & Golubova, 2017; Tosi & Romano, 2020). Like in our Exp. 2, Tosi and Romano (2020) found that this effect was present in all response modalities, which strongly suggests that this effect has a perceptual origin. More generally, this finding is in agreement with respect to the idea that the mental representations of the limb and the hand are wider than their actual (see for example Longo, 2017; Spitoni et al., 2015). It is also in agreement with the results showing that the shape of an object placed on the skin is distorted in the same manner in the general population (Peviani et al., 2019; Risso et al., 2020, [see Section 2.1 Chapter 2](#) of this thesis)

4.4.3 The impact of tactile acuity

It is well known that tactile acuity varies across body parts (Mancini et al., 2014; Weinstein, 1968) and that it affects the ability to distinguish the positions of two contact points that close one to another (Weber, 1996). In fact, in both experiments of this study, we found that participants did not always perceive the two contact points and that this issue occurred much more often when the two stimuli were close together. For example, in Exp. 1, this bias happened in general when the points are separated by 5 cm. It should be noted that 5 cm is not far from tactile thresholds for the forearm and arm as reported in the literature. For example, Keizer et al. (2012) report tactile threshold of 3.7 ± 0.52 cm for proximo-distal stimuli on the arm. Spitoni et al. (2015) also assessed the two-point discrimination thresholds on the arm and report mean value of 5.76 ± 1.90 cm in proximo-distal direction.

Interestingly, we found that the proportion of trials where the participants did not perceive two points were affected by other factors beyond the distance between the contact points, albeit to a lesser extent.

First, in Exp. 1, we found evidence that the proportion of missing responses was reduced when the contact points separated by 5 cm were near the elbow with respect to a more central position within the arm or forearm. This finding suggests that tactile acuity might also be higher near the elbow than in the central part of the arm or forearm. Coherently with this hypothesis, Vierordt (1870) measured 2-point discrimination thresholds on several locations on the arm from the finger to the shoulder and found a proximal-distal gradient of increasing acuity (English description of Vierordt's work in Boring., 1949). Cody et al. (2008), found that tactile acuity was higher near the wrist than at either the forearm or hand. Furthermore, previous studies showed that throughout most of the range of joint motion, the great majority of myelinated articular afferents are silent (Burgess & Clark, 1969; Clark, 1975). However, the joint tissue is well innervated with mechanoreceptors. The evidence demonstrates that the discharge of joint receptors can produce perceived signals of joint movement (Ferrell et al., 1987). We make the hypothesis that the observed higher sensitivity to tactile stimuli around the joint angle rather than in the central part of the limb segments, could reflect the higher mechanoreceptors density around joints which are involved in the boosting of the kinesthetic input from muscle spindle endings (Proske & Gandevia, 2012). Noteworthy, this difference in tactile sensitivity did not affect distance estimation performance (see previous section on Distance Estimation). This is somehow surprising given the well-known observation of an inverse relation between distance estimation and tactile sensitivity (Weber, 1996). Accordingly, future studies should shed lights on this aspect and make it clear whether higher-level factors could have a role to explain this behavior.

Second, in Exp. 2, we found that proportion of missing responses was generally higher for stimuli oriented medio-laterally than proximo-distally. Interestingly, tactile acuity appears to be affected by the direction of the stimuli. For example, Spitoni et al. (2015) found that discrimination thresholds on the thigh, abdomen and sternum are higher for tactile stimuli perceived along the medio-lateral direction (grand mean = 6.72 ± 1.57 cm) than along the proximo-distal direction (grand mean: 5.76 ± 1.90 cm). However, these results do not match with our results on the arm in Exp. 2, in which independently from the response modality we found a significantly higher number of missing responses for stimuli oriented in the proximo-distal direction than the medio-lateral one.

4.1.4 Arm posture neglect in tactile estimation task: one or two body schema?

The results of experiment 1 show that participants perceived quite accurately elbow joint position, except for 30 and 60 degrees angles where it was underestimated (Fig 4.1). In other words, this result suggests that participants can access a relatively correct representation of the arm posture, which by corresponds to a part of their body schema. However, participants appear to neglect or strongly underestimate elbow flexion angle when estimating the distance (as-the-crow-flies) between two points on their arm with a flexed elbow joint posture. Figure 4.3 right panel, shows how the posture of the angle flexion produces no or very little modulation of the estimated distance. This result suggests that proprioceptive information about the arm posture is processed differently in the two tasks. While there is a tendency to underestimate the elbow flexion angle when asked to estimate this angle directly (the arm posture estimation task), the very “flatness” of the estimated distance suggests that elbow flexion angle is much more underestimated in this distance estimation task (across joint).

As mentioned in the Introduction of this Chapter, the to estimate the distance between two points located on different body segments and successfully accomplish this task participants need to: 1) localize the position of each contact point onto the body (reference Mental Body Representation (MBR): superficial schema), 2) perceive the arm posture, which is defined by the joint angles, (reference MBR: postural schema), 3) refer both information to a metric representation of the body (reference MBR: body model). According to Longo & Haggard (2010)’s model, the body model contains metric information about the dimension of the body segments, which would be relatively static and change principally during development (see also long-term body representation, Gadsby, 2017). This information is crucial to process the quickly time-varying tactile and proprioceptive signals that change during movement and/or the physical interaction with object and yield high-level percepts such as the position of the hand in space or the distance between two tactile stimuli in space.

Although the essential features of this model of processing of haptic information are widely shared (e.g. Gadsby, 2017; Longo, 2015; Longo & Haggard, 2010; Serino & Haggard, 2010), it does not fully explain the aforementioned inconsistency between the two tasks and, in particular, why would arm posture be underestimated more in the tactile estimation task than in the joint posture estimation task.

A possible explanation is that the elbow flexion angle information used in the distance estimation task is different than the elbow flexion angle information used in the joint posture estimation task.

In other words, this explanation would assume the existence of two different task-specific representations of the arm posture. This hypothesis is consistent with Longo & Morcom (2016)'s results. The authors investigated whether the magnitude of the distortions observed in distance perception and position sense are shared. In particular, they performed a tactile distance perception task and a proprioceptive mapping task on the hand dorsum. Critically, they found no correlation between the magnitudes of the distortion observed in the two tasks.

While such explanation needs more experimental support, it might be useful to recall first that mental body representations are defined functionally and that the neuronal correlated have yet to be identified.

Another possible explanation is that participants did not take fully into account the arm posture during the distance estimation because they have a hard time computing the straight line distance between the contact points when the elbow is flexed. If we assume that such the straight-line estimate is not directly accessible from a mental representation but requires some ulterior mental computation. This explanation however does not seem to be well supported by our results. In particular, we did not find marked difference in accuracy or precision when comparing the performance in trials where the contact points were on the same limb segment and trials where the contact points crossed the joint. If the elbow flexion angle was relatively well estimated in this task, it is not clear why it would be neglected at a later stage when estimating the straight-line distance between two contact points on the same segments.

4.1.5 Conclusion and Perspectives

In the chapter, we provided a preliminary analysis and discussion of the results of our experiment. One open question is whether a generalized underestimation of the limb dimension (see Fig. 4.3 and Table 2) together with the observed underestimation of elbow flexion angle (see Fig. 4.1) can explain the limited effect of arm posture on the perceived distance observed in the “across joint condition”. To address this question, we plan to measure tactile distance underestimation on the same limb segment and use the responses about the perceived elbow flexion angle to predict the effect of arm posture on the perceived tactile distance for stimuli crossing the elbow joint. If these

predictions are incompatible with our data, this would support our hypothesis that the representations underlying tactile distance perception and position sense are distinct.

Chapter 5

Conclusions and Perspectives

The goal of this PhD dissertation was to investigate the interactions between different aspects featuring somatosensory perception. The thesis presents multiple studies on somatosensory integration processing. In particular, these mechanisms were assessed in healthy controls at the “baseline”, and in different clinical populations in which the processing of somatosensory information has been demonstrated to be deficient. The *neuroscientific aim* was to understand under what conditions an optimal integration of multisensory information is achievable. The *applicative aim* was to acquire principles that could be relevant for the technological development and clinical rehabilitation and diagnosis. The thesis also tackles the topic of multiple Mental Body Representations (MBRs) underlying the sense of touch. In addition, in this case, the research focused on the interactions mechanisms. In particular, the interest was directed toward understanding the way in which different MBRs interact with each other during a complex task requiring their synergy.

The thesis combines several breakthroughs. In this chapter, firstly I briefly summarize the main findings of this work, then I discuss in detail current and future works in perspective of these results.

5.1 Summary

In [Chapter 2](#), I presented two studies on the visuo-tactile integration processing of objects’ size and shape in two populations of clinical interest, i.e. an amputee individual and women with body concerns, including patients with Anorexia Nervosa disease (AN). The highlights of the first study:

- (i) The presentation of the first study on multisensory integration in a hand amputated individual with a bionic limb capable of returning artificial somatosensory feedback via a neural implant connected to the peripheral nervous system.

- (ii) The combination of artificial touch (using intraneural stimulation) and vision can lead to optimal multisensory integration of visuo-tactile information in an upper-limb amputee provided with a bidirectional hand prosthesis.
- (iii) The uniqueness of neuromodulation, which elicits sensations perceived directly on the phantom limb, allows the perceptual experience of the subject to be manipulated independently of the physical characteristics of the stimulus.
- (iv) Our results open new scenarios towards the application of fully integrated neurotechnologies for the total restoration of the perceptive abilities lost by subjects with amputations.
- (v) In the field of cognitive sciences and experimental psychology, the study, given the intimate connection between technology and the nervous system, shows an original and promising method for investigating optimal integration processes.

The highlights of the second study are:

- (i) Patients with Anorexia Nervosa (AN) show somatosensory distortion of shape along the medio-lateral axis (i.e. objects enlargement). This tendency is observed also in healthy women with body concerns. The result suggests that metric biases in body representation could extend to objects, and that higher level factor such as body dissatisfaction could play a role in such a bias.
- (ii) The visual and somatosensory discrimination of shape perception are significantly impaired in a sample of patients suffering from restricting type AN, in a severe state of malnutrition.
- (iii) Results provide evidence against the hypothesis of a generalized impairment in visuo-tactile integration processing in patients with AN.
- (iv) Psychophysical variables can categorize patients with AN, healthy controls with body concerns and healthy controls in their respective group. The results suggest that evaluating the perceptual abilities of the patients could provide information that might be clinically relevant.

In [Chapter 3](#), I presented two studies on bimanual size discrimination in static and dynamic motor conditions. The main finding for the first study are:

- (i) Positional information from the two hand is optimally integrated in static and moving conditions.
- (ii) Integration occurred independently of the visual appearance of the seized object, which could resemble to a box or formed by two movable vertical panels, and whether the subject had seen the object or not.

- (iii) Optimal integration in the static condition is somewhat difficult to reconcile with the results of other studies but is established and confirmed with three different groups of subjects in the three experiments performed in this study.

For the second study, the highlights are:

- (i) The accuracy of the hand relative position sense is decreased by an order of magnitude during upper-limb continuous movements.
- (ii) The size-change detection thresholds of a hand-held virtual bar does not depend on bar position movement or direction.
- (iii) The ability to discriminate the objects perceived length are not related to grasp force or arm stiffness.
- (iv) Results suggest that static and dynamic conditions require different mechanisms of information processing.

Finally, in [Chapter 4](#), I presented a work that we recently conducted to characterize the internal mental representations of the body. The principal achievements of the chapter are:

- (i) The presentation of a new experimental paradigm allowing to simultaneously investigate the different representations individually and during their interaction.
- (ii) Positional and body metric perception of the arm are distorted in healthy individuals.
- (iii) Cognitive factors such as the response modality methods affect tactile distance estimation.

Putting this research in the context, our studies suggest that multisensory integration involving touch contributes to body representations. Furthermore, this work highlights the importance of find new ways to investigate how many body representations we use, and how. Nevertheless, the presence of altered body representation also in healthy populations should rise questions about their functional role in our everyday routine. Besides providing several findings, these works give rise many questions on the human cognitive functioning and clinical and technological future perspectives arising from the study of the somatosensory information processing.

5.2 Perspectives

Taken together, results from [Chapter 2](#) open up new opportunities towards the perceptual and cognitive rehabilitations of individuals with somatosensory deficits. Interestingly, regarding the methodology, the use of a rigorous psychophysical method, pioneered by Ernst & Banks (2002) allows the verification of two independent predictions (using JND and PSE) of the optimal multisensory integration model. In addition, the careful selection of stimuli through: the use of a double QUEST for each condition; randomization of the presentation of experimental conditions, comparison stimuli, order of stimuli within each trial; use of an advanced electrode mapping algorithm to identify optimal stimulation parameters represent the strengths of the adopted method. The multisensory bionic limbs have broad implications for studying and enhancing prosthetic acceptance and advancing the adoption of artificial limbs that feel like real limbs. The translation to clinical settings is extremely noteworthy for individuals with amputation, who would hugely benefit by the restoration of a proper sensory experience: they do not engage themselves fully in activities of everyday life because they are afraid of actions failure, and do not feel the prosthesis as part of the body. Our study sheds light on the mechanisms underlying optimal integration in amputee individual. However, it is of a paramount importance to investigate deeply the cognitive mechanisms of such a man-robot interface, in order to develop therapeutic strategies that can have beneficial impacts on the quality of life of these patients. Up to now, optimal integration of an artificial sensory feedback has been shown with invasive approaches, which require a surgery and elicit somatotopic (i.e. perceived in the phantom limb) and homologous (i.e., same typology of elicited visuo-tactile percept, such as pressure or vibration) sensations. Future studies should investigate whether this evidence could be extended to non-invasive approach providing a remapped feedback, hence non-somatotopic feedback. In addition, the evidences up to this point have been shown in the upper-limb, which has its own peculiar neural structure and brain representation. Accordingly, the finding of an optimal integrated sensory feedback should be tested on other body parts (e.g. lower limb). Furthermore, since the present study provided a successful proof-of-concept that the optimal integration model can be applied also to explain the interaction between natural and artificial sensory signals, further studies should investigate the functional and cognitive benefits emerging from such an optimal integration.

Likewise, the results of the study on objects shape perception in patients with Anorexia Nervosa disease (AN) provides encouraging results for clinical applications. Treatment trials with patients with AN are challenging. To date the interventions for this type of disease consists mainly in the restoration of normal eating patterns and the resolution of the associated psychological, and

behavioral problems. Advances of the literature on neurocognition, biomarkers, and genetics of eating disorders are needed to achieve a deeper comprehension of the challenges that prevent the treatment of the disease core symptoms (H. J. Watson & Bulik, 2013). In the context of this study, we suggest that the exploiting of psychophysical variables could be a support for the diagnosis, which up to date is entirely based on the clinicians' evaluation and scoring with subjective questionnaires. Future studies should invest some effort not only to confirm this preliminary result, but also to investigate other possible applications of such an approach. For example, it should be explored what opportunities could arise from the assessment of sensory processing to identify individuals at risk. The early identification of the pathology has been demonstrated of crucial interest to reduce the severity or duration of eating disorders. Finally and foremost, our results suggest that rather than having a generally oversized somatosensory body representation, these patients exhibit a specific pattern of distortion coherent with a wider representation of the body. Noteworthy, the participants in this study were unaware that the body representations were the object of investigation, preventing the possibility that other variables (i.e. demand characteristics or participants' attitude) could affect their performances. Our results prompt the idea that the metric biases in AN body representations extend to object perception (see also (Peviani et al., 2019), thus highlighting the pervasiveness of body representations' disturbances to different cognitive maps underlying the sense of touch. Albeit to a lesser extent, the distortion is showed also by healthy individual with concerns towards the body, but not by healthy individual with no concerns. The evidence supports previous hypothesis that affects might play a role in distorting the metric properties of the body representations (Gadsby, 2017). This finding renews the importance of early evaluation and identification of negative mood during the psychological assessment of individuals with or without clinically relevant pathology. Noteworthy, we also found visual and tactile discrimination deficits specific for the population of individuals with AN involved in this study. We hypothesized that the low BMI and/or the severe status of malnutrition of our patients could offer an explanation for the impairment in sensory acuity. Accordingly, we suggest that is of relevant importance for future studies to provide a precise characterization of the sample also in term of body weight, specific type of Eating Disorder and eating habits. Otherwise, it would be much harder to disentangle between the effects of the body distortion that might be linked with a lack of sensory sensitivity (Weber, 1996) and those that might be linked to others higher-order variables (i.e. the body satisfaction).

Findings of this study also fit into a broader framework attempting to understand how the body is tracked and represented in humans' cognition. A wider discussion about it, is provided in the following lines, also in reference to the results of the other Chapters.

[Chapters 3](#) presents numerous yet-to-be-fully understood questions. In the first part of this chapter, I presented the results of three separate experiments, which coherently demonstrated the optimal integration of information from the two hands. Our results are in line with the naïve observation that in many daily-life circumstances people have to use both hands to manipulate objects and gather information about their shape. However, the set-up of the last of the three experiment had been designed with the precise purpose to resemble the one provided by a previous study in which the integration of bimanual integration was found to be not optimal (Panday, Bergmann Tiest, et al., 2013). The only knowledgeable difference between the two studies consists in the fact that we allowed the participants to observe the experimental setup before starting the task. The divergence between our and the other study is not an exception, and well reflect the heterogeneity of literature on bimanual integration. A simple explanation to account these differences is lacking. However, we align with the proposal by Ivry et al. (2004), which propose that cognitive representations of the action plays a critical role on bimanual coordination and interference (for a review see Ivry et al., 2004). Accordingly, in the discussion of our results (of this and also another study on bimanual integration that we recently run; (Xu et al., submitted); [see Appendix A](#) for the complete manuscript), we referred to the “Unity Assumption”. While the unity assumption figures prominently in sensory integration research, it is a confusing concept. Welch & Warren (1980) define the unity assumption in this way: *“the stronger the observers' assumption that they are in the presence of a single distal object, the greater will be the magnitude of intersensory bias”*. The strength of this assumption is presumed to be a function of the number of physical properties (e.g., shape, size, motion) that are redundantly represented in the stimulus situation, as well as the relative weighting assigned by the observer to these properties” (Welch, 1999a). This definition suggests that the unity assumption corresponds to an internal state of the observer, which can be influenced by many factors. However, it does not provide a practical way to characterize or assess the unity assumption. Functionally, it is not clear whether the unity assumption is a factor that has an independent effect of its own on sensory integration; or whether it is simply a way of referring to the observer's internal state, which unfortunately cannot be directly observed. Several attempts have been made to use instructions to manipulate the “unity assumption” independently of sensory inputs (Helbig & Ernst, 2007; Miller, 1972; Misceo et al., 2014). In this context, the unity assumption is considered an independent cognitive factor that modulates sensory integration. In this respect, future studies should consider replicating same bimanual tasks but providing the participants with different instructions. Also, the cognitive belief of the participants could be more easily manipulated in a virtual reality context (see Plaisier & Ernst, 2012). Noteworthy, the unity assumption could have profound implications also in relation to the theme presented in Chapter 2 (i.e. multisensory integration) and Chapter 4 (i.e. body representations). The fact that the processing of multisensory cues is modulated by the observers’ belief that the unisensory cues

belong to a same object or event (Ernst & Bühlhoff, 2004), suggests that optimal integration of information could be used as a powerful way to investigate embodiment *quantitatively*. For example, the successful optimal integration of information related to a body part, nay, a prosthetic body part, would suggest that the perceiver is likely to believe that the integrated multisensory cues belong to a unique object, which in turn could be considered as a good sign of prosthesis embodiment. An extremely encouraging result in this sense is given by (Rognini et al., 2018). The authors, not only demonstrate that a multisensory bionic limb is well embodied, but also that its use reduced distorted phantom limb perception. An example of quantitative approach to the study of embodiment has been offered by (Fang et al., 2019). The authors presented a video-based system in a reaching task in monkeys, and combined a casual inference model to establish an objective and quantitative signature for the monkey's body representation. This result should encourage future studies to apply the same task purpose on humans. It would be of great scientific interest to understand the specific contribution of each sensory signal in task assessing the embodiment.

Turning to the literature on bimanual perception, another important aspect that we evaluated in Chapter 3 is the effect of movement on bimanual perceptions. In the first study, we hypothesized that participants would not integrate proprioceptive positional information used to assess the size of the box in the grounded condition. On the contrary, we hypothesized that bimanual integration would have occurred in the dynamic conditions, because lifting the object would promote the idea that they are touching a unique object. Surprisingly, the results indicated that individuals were able to integrate bimanual information optimally also in the grounded condition. According to the optimal integration principle, the optimal threshold corresponds to the best estimate concerning the attribute of interest. As a consequence, the potential benefit of lifting the object is limited and hard to see, and we found only little evidence of better performances in the dynamic condition.

In the second study, we found apparently exactly the opposite result. As a matter of fact, also the second study provides that participants discriminate the size of objects. In particular, at each trial the participants have to report whether the length of a virtual bar had lengthened or shortened, and they made their estimation in static and dynamic conditions. At a first sight, the results of this experiment could appear inconsistent with that of previous experiments of the chapter. However, there are several important differences that should be highlighted. The first difference consists in the type of haptic cues that provides information about the size of the object. In this second experiment, estimating the size change of a virtual bar depends on the change of orientation of the hand occurring during the widening and shortening of the virtual stimulus. In contrast, in the first study on bimanual size discrimination of box-like objects the hand position is directly related to box size, and it is invariants during the grounded or the free condition. Another difference consists

in the type and moment of movement that was involved in the two experiments. In the experiment with box-like objects the participants made short and slow movements. As matter of facts, it is sufficient to slightly lift the box to perceive that the two hands are holding the same object and, possibly, further enhance bimanual integration. In addition, at the beginning of the trial the box is grounded to the table, and the participant makes a stable grip with his hands. Then, once the objects are lifted the position between the hands never change. In a sense, the lifting condition was a quasi-static condition, with the only difference being that the object was ungrounded. On the contrary, in the second experiment involving the bimanual manipulandum, the participants have to make continuous circular movements for all the duration of the experiment. In other words, during the dynamic condition they have to estimate a change in the position of the hands while the arm are simultaneously engaged in circular movement. Accordingly, it is not surprising that estimating the size of the virtual bar might requires a more sophisticated processing of proprioceptive signals than the simple comparison of hand positions in box size estimation.

However, focusing on the results of the second experiment, the finding that our proprioceptive acuity markedly decreases during movement was not granted. The large difference between the static and dynamic conditions in this study suggests the difficulty for the perceptual system to extract information about the ongoing movement from information about the length of the bar and/or additional noise present in afferent signals during movement (Baud-Bovy et al., 2010; Wise et al., 1996). Moreover, a difference between static and dynamic condition is that the movement was continuous, and that the stimulus was superimposed on the top of a time-varying background in the dynamic condition.

[Chapter 4](#) presented a paradigm to investigate the interaction between the different Mental Body Representations (MBRs). The results suggest that the stored body representations underlying both the position sense and the tactile size estimation are distorted. Noteworthy, the magnitude of the distortions observed in the two tasks used to assess them, was inconsistent. The first future step of the study will be to use the bias observed to make a prediction of the expected performance in a third task which requires their interaction. If it is not be the case, the hypothesis would be that the MBRs underlying the position sense and the tactile distance estimation do not share a common body model, as previously suggested (Longo, 2015; M. R. Longo & Haggard, 2010). A similar hypothesis had been raised also by Longo & Morcom (2016) that found similar inconsistencies. Further studies should provide more experimental support to the hypothesis. Taking a cue from the present experimental paradigm, future studies could try to include an experimental manipulation, (such as tendon vibration illusion for example) to investigate its effect on the arm posture in both the tasks.

Awards, Papers & Posters:

Awards

Franco Purghé Award 2020, discerned by the Experiment Psychology Section of the Italian Association of Psychology, for behavioral research in psychology of perception and psychophysics.

Publications

Published

Risso G., Martoni R.M., Erzegovesi S., Bellodi L., Baud-Bovy G. Visuo-tactile shape perception in women with Anorexia Nervosa and healthy women with and without body concerns. **Neuropsychologia 2020**

Risso, G., Valle, G., Iberite, F., Strauss, I., Stieglitz, T., Controzzi, M., ... Micera S. & Baud-Bovy, G. Optimal integration of intraneural somatosensory

Martoni R.M.; de Filippis R., Cammino S., Giuliani M., **Risso G.**, Cavallini M.C., Bellodi L. Planning functioning and impulsiveness in obsessive-compulsive disorder. In **European Archives of Psychiatry and Clinical Neuroscience 2018**

Martoni R.M., **Risso G.**, Giuliani M., de Filippis R., Cammino S., Cavallini M.C., Laura B. Evaluating Proactive Strategy in Patients with OCD During Stop Signal Task. In **Journal of the International Neuropsychological Society 2017**

Under Review

Giuliani M., **Risso G.**, Cammino S., Bellodi L., Erzegovesi S., Martoni R.M.. Proactive Adjustment Strategy and Temperament in Obsessive-Compulsive Disorder: A Stop Signal Task Explorative Study.

In submission

Risso G., Xu Q., Baud-Bovy G., Bimanual Integration in the Haptic Discrimination of Size.

Baud-Bovy G., **Risso G.**, Zenzeri J., Size-Change Detection Thresholds of a Hand-Held Virtual Bar at Rest and during Continuous Movement.

Xu Q., **Risso G.**, Baud-Bovy G., The Effect of Free Manipulation on Bimanual Integration in the Haptic Discrimination of the Size of a Pair of Large Pliers.

Posters

Risso G., Martoni R. M., Calzone G., Bellodi L., Baud Bovy G. Sensitivity, biases and multisensory integration in the visual and haptic perception of elliptical shapes in patients with anorexia nervosa. (Neuroscience 2019), Chicago, 19-23 October.

Risso G., Xu Q., Baud Bovy G., The Effect of Free Manipulation on Bimanual Integration in Size Discrimination Tasks with Boxes and Pliers Neuroscience 2019), Chicago, 19-23 October.

Risso G., Crippa F., Martoni R., Bellodi L., Baud Bovy G. Visuo Haptic Integration of Shape in Healthy People and Anorexia Nervosa Patients. In 14th Karniel Computational Motor Control Workshop (CMCW 2018), Israel, 13-15 March

Risso G., Baud-Bovy G., Bimanual integration of distance information in haptic perception. In 3rd Perception and Action in Complex Environments PACE 2017), Genoa, Italy, 9-11 October 2017

Risso G., Martoni R.M., Cavallini M.C., Erzegovesi S., Baud Bovy G. Visuo haptic information processing in patients suffering of Anorexia Nervosa. In 25th European Congress of Psychiatry (EPA 2017), Florence, Italy, 1-4 April

Teaching

Correlator of a Master Thesis work titled: “Dispercezione dell’immagine corporea e integrazione multisensoriale: studio di confronto tra un campione di pazienti anoressiche e un campione non clinico” thesis relator: Prof. Gabriel Baud-Bovy. September, 2019. **Università Vita-Salute San Raffaele**

Correlator of a Master Thesis work titled: “Joint Posture And Distance Estimation Task. un nuovo paradigma sperimentale per studiare i disturbi delle rappresentazioni corporee attraverso propriocezione e percezione tattile: uno studio preliminare sulla popolazione generale”, thesis relator: Prof. Gabriel Baud-Bovy. September, 2020. **Università Vita-Salute San Raffaele**

Training related to the PhD programme

Human Robot Interaction, Francesco Rea & Alessandra Sciutti, from 28th May to 8th June 2018, Italian Institute of Technology (Genova, Erzelli), exam passed

Robotic technologies for sensorimotor rehabilitation, Jacopo Zenzeri & Pietro Morasso, from 8th May to 24th May 2018, Italian Institute of Technology (Genova, Morego & Erzelli), exam passed

Introduction to physical human-robot interaction, Jacopo Zenzeri, from 3rd April to 6th April 2018, Italian Institute of Technology (Genova, Morego & Erzelli), exam passed

Research oriented structural and functional neuroimaging, Alberto Inuggi & Franco Bertora, from 12nd June to date of the exam to be defined, Italian Institute of Technology (Genova, Morego), exam passed

Science writing & Presentation skills, Alberto Diaspro & Antonio Sgorbissa, from 15th March to 21st May 2018, DIBRIS (Genova, Villa Bonino), exam passed

“Ethical, Bioethical and Legal Issues in Bioengineering and Robotics” Dott. Linda Battistuzzi and Prof. Valentina Di Gregorio (5 CFUs), exam passed

International Winter School “Beyond $p < .05$. Modern statistical approaches in psychological science” University of Padova, 18-22 February 2019, exam passed

Course: An introduction to Mixed Effect Models in R, Gabriel Baud Bovy, from 28th February to 16th April 2018, Italian Institute of Technology Genova, Erzelli (3 CFU), exam passed

Neuroprosthetics, July 20-23, 2020; Virtual Summer School, approved.

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Appendix A

The Effect of Free Manipulation on Bimanual Integration in the Haptic Discrimination of the Size of a Pair of Large Pliers

The contents of this section are adapted from the following under manuscript in submission: Xu, Q., **Risso, G.**, Baud-Bovy, G. The Effect of Free Manipulation on Bimanual Integration in the Haptic Discrimination of the Size of a Pair of Large Pliers.

The work was presented at Neuroscience, 2020, Society for Neuroscience (SfN), Chicago.

Personal contributions as second author: I participated to the data acquisition, data discussion and manuscript revision.

Abstract

In general, the brain tends to integrate optimal redundant sensory information about an object or event in the environment to obtain a more robust estimate. Despite the fact that people often use both hands to manipulate objects, previous studies have shown little evidence that proprioceptive information from the two hands is integrated when apprehending the size of an object bimanually. The main objective of this study was to find out whether information from the two hands was integrated in a haptic size discrimination task where participants had to judge the size of a pair of large pliers held with one or two hands. We found that information from the two hands is optimally integrated when the bimanually-held pliers are free to move. In contrast, we did not find bimanual integration when the pliers were fixed to a structure. In agreement with classic accounts on sensory-motor integration, we propose that the physical interaction between the two hands occurring during free manipulation might promote bimanual integration by strengthening the assumption that information is coming from the same object. More speculatively, we also propose

that free manipulation might activate predictive motor processes that rely on signals of both hands to estimate the current state of the motor system and control the hand movements in this condition.

Introduction

Multiple sensory systems provide information about the environment. The brain must continuously process and organize this information, selecting and possibly merging it in a coherent whole. While many studies have explored how information from different sensory modalities is combined or merged, fewer studies have investigated how different cues are integrated within the same modality, specifically the haptic modality. In particular, relatively little is known about how people integrate information from the two hands when exploring the shape and size of an object bimanually. In this study, we focus on the perception of the size of a large plier held by both hand by just open and closing it. We investigate how well people can perform this task and whether information from the two hands is integrated when subjects estimating the size of the pliers. In the following, we start by reviewing previous work on multi-sensory integration in order to introduce the theoretical issues, which are the same whether the information comes from one or more sensory modalities. In particular, understanding how the brain deals with potentially conflictual information and/or when it decides to merge it together are long-standing research questions. We then review the literature on bimanual integration and introduce the objectives of our study.

Multi-modal sensory integration

Early research on multi modal sensory integration focused on situations where there was a conflict between pieces of information provided by different sensory modalities. A classic illustration is "ventriloquism", where the words pronounced by the puppeteer appear to come from the mouth of the puppet in conflict with the audio cues about the sound source (Vroomen et al., 2001). Initial findings led to the view that the brain might accommodate such a conflict by simply ignoring one of the two sensory modalities (the stimulus or modality dominance hypothesis). In the case of a conflict between the visual and audio or proprioceptive modality, it was initially suggested that the visual modality dominates (Rock & Victor, 1964), but successive studies revealed a residual influence of the other modalities (e.g., Hershberger & Misceo, 1996; McDonnell & Duffett, 1972). This research line revealed that the direction and strength of the inter-sensory bias toward one or the other sensory modality depended on a variety of factors. In a review of this literature, Welch and Warren (1980) discussed evidence that the direction of the inter-sensory bias might depend on directed attention and/or on the accuracy or appropriateness of each modality. They also propose that the magnitude of the bias depends on the observers' assumption that they are in the presence of a single distal object (the *unity assumption*) and that the strength of this assumption is also a function of the number of physical properties (e.g., shape, size motion) that are redundantly

represented in the stimulus situation (Welch, 1999b). When the sensory signals are thought to refer to different objects or events, there would be no inter-sensory conflict and thus no inter-sensory bias.

These early observations have since been reinterpreted in light of Bayesian integration principles, a mathematical framework that allows one to define the best estimate that can be obtained by combining redundant information (Ernst & Banks, 2002). In brief, the optimal integration hypothesis prescribes that the best estimate s_{12} corresponds to a weighted average between the two sensory cues s_1 and s_2 and the reliability $R_i = 1/\sigma_i^2$ is simply the inverse of the noise (variance) of the corresponding cue.

$$s_{12} = w_1 s_1 + w_2 s_2 \quad (1)$$

where the weights w_1 and w_2 ($w_1 + w_2 = 1$) are proportional to the reliability of the stimulus:

$$w_1 = \frac{R_1}{R_1 + R_2} \quad w_2 = \frac{R_2}{R_1 + R_2} \quad (2)$$

Assuming that the information provided by each cue is independent and normally distributed, it can be shown that the optimal or Maximum Likelihood estimate s_{12} that combines the two cues has a variance:

$$\sigma_{12}^2 = \frac{\sigma_1^2 \sigma_2^2}{\sigma_1^2 + \sigma_2^2} \quad (3)$$

which is not only lower than that of the single cues but the lowest possible given the noise associated with each cue. This noise can be determined in behavioral experiments measuring the discrimination thresholds. A consequence of this framework is that, in the presence of a conflict, the bimodal estimate should be biased toward the most reliable sense, and many past observations have been reinterpreted accordingly. In addition, it is also generally held that the two cues are merged together before a decision is made (Ernst & Bühlhoff, 2004a).

More recently, Bayesian models have been extended to also address the question of when the brain should integrate information. For example, Körding et al. (2007b) include the likelihood of two co-occurring signals having a "common cause" in their modelling of causal inference processes. Similarly, Ernst proposed reformulating the problem of integration in terms of a "coupling prior" representing the a priori relation between the sensory signals (Ernst, 2007b).

The plier size discrimination task

The haptic sense combines proprioceptive inputs coming from muscles, tendons and joints and tactile inputs coming from mechanoreceptors in the skin and provides important information to control movement as well as information about our physical environment, especially the objects that we manipulate (Johansson & Flanagan, 2009a). Previous research has identified several cues for haptic shape perception (Pont et al., 1997, 1999). First, the size or shape of the object might be derived from the movement of the hand over the object's surface. Second, touch also provides information about the orientation of the object's surface at the contact point (tangent plane). Finally, touch, especially finger pad deformation, might provide information about the local curvature at the contact point. In the literature, position, tangent plane and curvature are known 0th, 1st- and 2nd-order cues (Pont et al., 1997). As noted above, the principles of multimodal integration apply not only to cues from different sensory modalities but also to different but redundant cues within one sensory modality. For example, previous research has shown that positional information and the contact force influence the perceived shape of the object (Robles-De-La-Torre & Hayward, 2001). In a later study, Drewing & Ernst (2006b) showed that these two cues are integrated optimally. Other studies on haptic curvature perception suggest that the weight given to various haptic cues each cue depend on the size of the object, with 0th-order cues playing a major role for large objects, 1st-order cues playing a major role for medium size objects and 2nd-order cues for small objects (Wijntjes et al., 2009).

This study investigated how well blindfolded people can discriminate the size of a large pliers held with both and whether redundant information from the two hands is integrated optimally. The pliers were two wooden sticks about 80 cm long connected at the apex by a hinge joint and the task required that the blindfolded participants estimated the distance between the two handles and joint, just by opening and closing the pliers. In principle, the size of the plier can be estimated both unimanually and bimanually. If the fulcrum is fixed, the task is akin to a curvature discrimination task, since the hand(s) holding the stick(s) of the plier move along an arc of circle in this case.

While this is the first study conducted with pliers, several studies have investigated bimanual integration previously in related tasks. Squeri et al. (2012a) investigated whether information from the two hands was integrated optimally in a curvature perception task, where a bilateral robot moved the observer's hand(s) passively along the arc of a circle. They found no significantly different performance in the bimanual conditions with respect to the unimanual conditions. Panday et al. (2013) asked observers to discriminate the size of large cylinders, with a diameter that varied from 19 to 45 cm (Panday et al., 2013). The cylinders lay on a table and the side(s) was/were explored with one or both hands. Contrary to Squeri et al.'s (2012b) experiment, they found better performance in the bimanual condition. However, in a control condition where the observers had to report the distance between two flat surfaces, they found no difference between the

performances in the unimanual and bimanual conditions. To explain these results, Panday et al. (2013) proposed that 2nd-order cues related to the deformation of the hand on the cylinder might be integrated but not 0th-order cues related to the position of the hand in space. They hypothesized that 2nd-order cues consistent with cylindrical shape would suggest to the observer that the hands were touching the same object while 0th-order cues only would not be able to elicit this impression. They also attributed the absence of integration in Squeri et al. (2012b) to the fact that participants experienced only 0th-order position cues while the robot moved one or both of their hands along the curved trajectory. This conclusion is also in line with the results of Wong et al. (2014) more recent study in which bimanual proprioceptive acuity was not found to be significantly better than the best unimanual performance.

As reviewed above, previous studies on haptic bimanual perception tasks have given contrasting results and surprisingly weak evidence of bimanual integration despite the fact that many motor tasks involve both hands. The absence of integration also stands in contrast with the tight integration in the control of the two hands as demonstrated by the difficulty in accomplishing truly independent movements with only one hand (reviews in Ivry et al., 2004; Swinnen & Wenderoth, 2004).

A critical feature of previous studies on bimanual integration that might be relevant in this context is that they all involved grounded objects. In other words, the objects could not be moved and no force was transmitted between hands. In contrast, the position of the hand-held objects involved in bimanual tasks is typically not constrained. This is the case when holding a tray or driving for example. In this type of bimanual action, the movement of the hand-held object and the hand are usually coupled, and the force applied by one hand to the object is transmitted to the other hand and vice-versa (internal force). In this study, we surmise that grounding might influence bimanual integration because holding the same object with the two hands could enhance the assumption that both hands are holding the same object when the object is free to move. The idea is that the motion coupling and force transmitted between the two hands might be used by the brain as a sign that two hands are holding the same object, thus triggering or enhancing bimanual integration.

In the following, we report the results of three experiments that investigated whether information from the two hands is integrated when estimating the size of large pliers held with both hands (see also Xu & Baud-Bovy, 2017 for a preliminary report of the results of the first experiment). In the first experiment, two groups of participants performed the task in three conditions: an unimanual condition and two bimanual conditions. In the bimanual conditions, the fulcrum of the pliers could be fixed or free to move. The order of the conditions was counter-balanced across participants. The first group of participants had no training with the task was often unable to perform the task,

in particular in the first experimental condition. In contrast, all participants in the second group were familiarized with the task, and almost all of them were able to perform it satisfactorily from the onset. In the second experiment, the three conditions were mixed together to avoid serial effects across conditions and replicate the results of the first experiment with a new group of participants. The third experiment is a control experiment to insure that the performance in the unimanual condition did not depend on whether the joint position was fixed or not.

Experiment I

Methods

Participants. The first experiment involved two groups of participants who performed the same task with small methodological differences. The first group included 18 participants (ten females and eight males, aged 28.1 ± 6.7 years). The second group included 20 participants (seven females and thirteen males, aged 29.7 ± 9.9 years), including nine participants from the first group. All participants were right-handed. None of the participants reported any known hand or neurological deficits. The experimental protocol was approved by the Ethic Committee of the Region of Liguria, and all the participants gave their informed consent prior to the task.

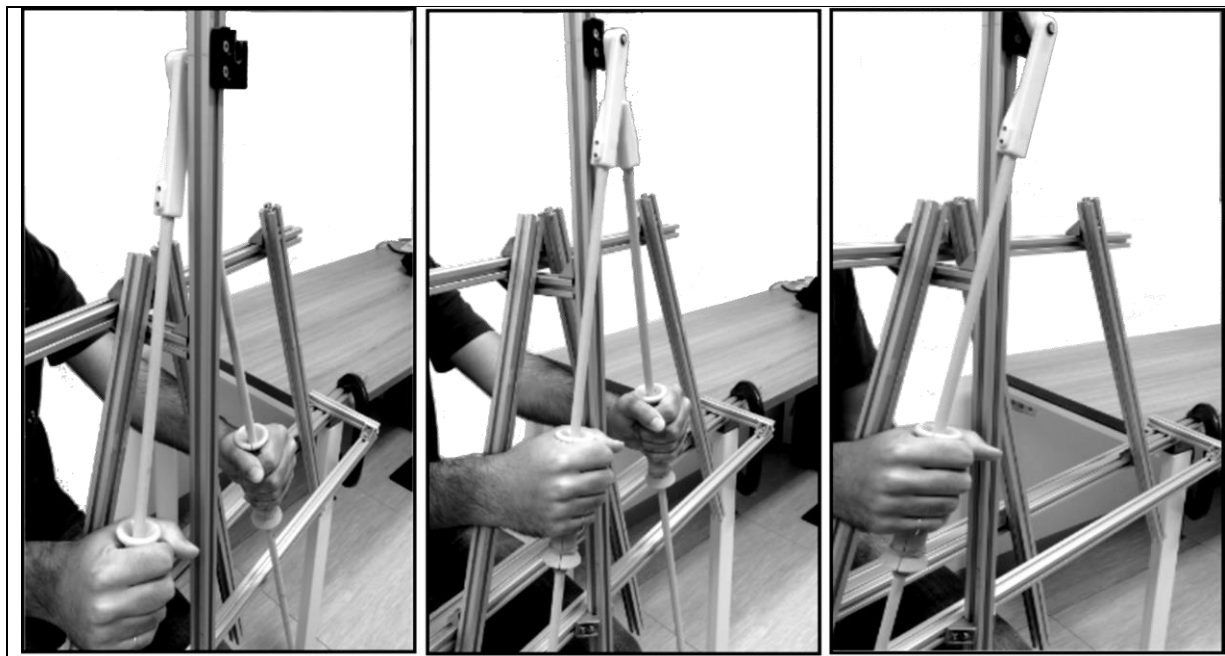
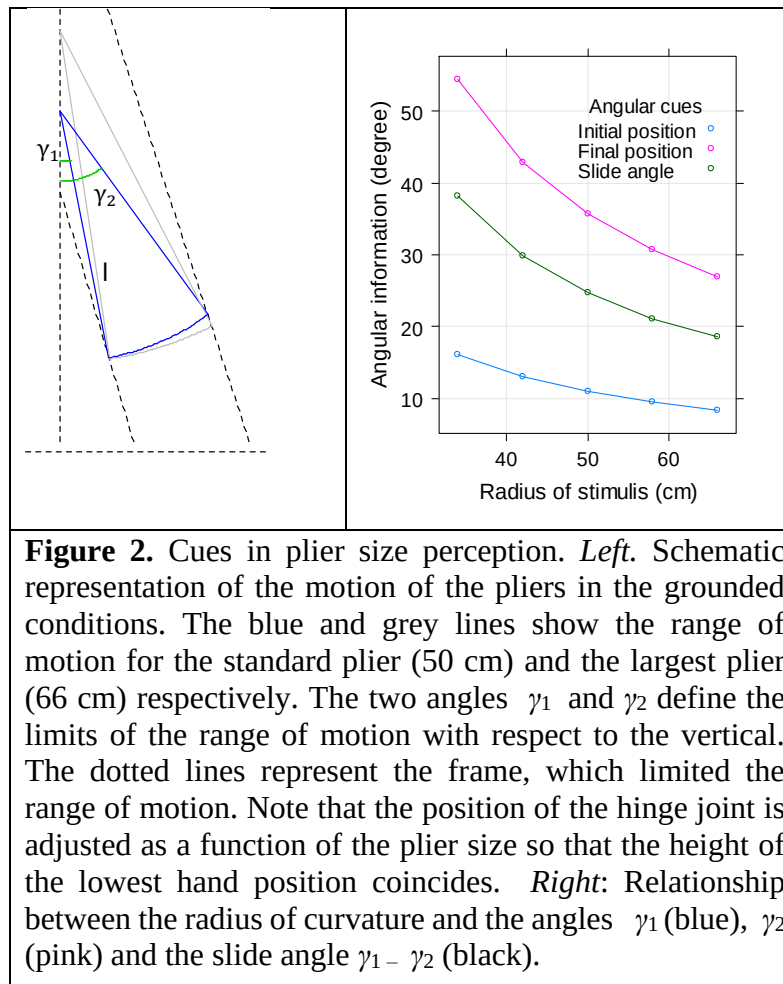


Figure 1. Experimental setup. *Left:* bimanual free condition. *Middle:* bimanual grounded. *Right:* unimanual grounded condition. The plier peg is inserted in the groove of the metallic beam and allowed to slide vertically in the bimanual free condition. It is immobilized in a fixture it in the grounded conditions.

Apparatus. The participant sat in front of a metallic frame, which was used to limit the range of motion of the hand(s) and to fix the pliers' rotation axis when needed (see Figure 1). The pliers used in these experiments were formed by two wooden sticks (diameter = 10 mm, length=80 cm) connected by a revolute joint at one extremity. A peg aligned with the revolute joint could be inserted in or fixed to the rail structure depending on the experimental condition. Ergonomically designed 3D printed handles were fixed on the wooden sticks at a distance that varied for different pliers. The size of the plier is defined by the distance between the fulcrum and the index position on the handle. The distance between the revolute joint and the handle was fixed at 50 cm for the standard stimulus and varied from 36 to 64 cm for the comparison stimulus (36, 43, 50, 57, 64 cm). All pliers had the same weight (0.128kg) to remove any possible kinetic cues that could be used to discriminate between pliers during their manipulation.



The local attitude γ corresponds to the angle between the plier and the vertical. The limits of movement restricted by the mental frame define a circular sector, whose arc corresponds to the

slide angle ($\gamma_s = \gamma_2 - \gamma_1$), i.e. to the difference between the local attitude at the initial (γ_1) and final (γ_2) positions. As noted above, the position of the center of rotation was adjusted so that the initial hand position would be the same for all plier sizes in the grounded condition. The difference in height between the two ends of the motion curvature is termed, unsurprisingly, as difference-in-height (h). Over the range of motion allowed by the setup, the relationship between the pliers' size and angular cues are approximatively linear (see Figure 2).

Task and experimental procedure. The task was a size-discrimination two-alternative-forced-choice task. For each trial, the experimenter put the standard and a comparison plier successively in the participant's hands. The participants were required to hold the plier with a power grasp. A groove on the handle constrained the index finger position to fix the hand positions on the handles. Participants were instructed to open and close each plier three times. The hand movement range was limited by the metallic frame, which was fixed on the table (see Figure 1). At the end of the trial, the subjects had to report which plier appeared to be larger.

The participants in the first group read the instructions, which showed a drawing of the pliers and explained the task. Then they were blindfolded before the beginning of the experiment to prevent them seeing the pliers. No feedback about their responses was given during the experiment. Because several subjects in the first group had difficulties in performing the task satisfactorily, a training section was introduced before the beginning of the experiment for the second group of participants. First, the participants were shown the pliers and could manipulate them before being blindfolded. Second, the participants were given two blocks of practice trials including all the comparison stimuli before starting the experiment. Feedback about the correctness of their responses was given during the practice trials. If the participants had responded erroneously during a practice trial, they were given back the two pliers so that they could manipulate them a second time. No feedback was given during the rest of the experiment.

Experimental conditions. The experiment included three conditions: the *bimanual free* condition, the *bimanual grounded* condition, and the *unimanual grounded* condition. In the unimanual and bimanual grounded conditions, the rotation axis of the pliers was fixed to the metallic frame. The height of the rotation axis was adjusted as a function of the size of the pliers, so as to keep the initial hand position at the same height. In the unimanual condition, the right hand was used to the right link of the plier. In the bimanual conditions, the participants grasp the plier with the two hands. In the bimanual free condition, a peg aligned with the fulcrum was free to move vertically. In the third experiment, the plier was free to move in the fronto-prarallel plane but still prevented from moving outside this plane by the metallic structure, thus eliminating possible kinetic cues such as static torque about the plier size.

The order of presentation of the three conditions was counterbalanced across participants. Each comparison stimulus was presented 10 times in each condition, yielding a total of 150 trials (method of constant stimuli). Inside each condition, the order of presentation of the five comparison stimuli was randomized within successive blocks of five trials.

Data analysis

The participants' responses were fitted with a cumulative normal probability distribution using maximum likelihood estimation to obtain a psychometric function as in Experiments 1 and 2. For each participant and condition, we computed the PSE and 75% discrimination threshold (DL). To estimate variability in a robust manner, we used the Median Absolute Deviation (MAD) scaled to yield an estimate of the standard error. We excluded participants who had a negative or a very large discrimination threshold in one of the conditions. The exclusion criterion ($DL > 24$ cm) was identified visually to include the main lobe of the threshold distribution. It also corresponds to choosing the median + 3 MAD = 23.6 cm.

We used a non-parametric Friedman test for repeated measures on the discrimination thresholds DLs and PSEs to test the differences between the unimanual and bimanual conditions. Whenever a statistically significant effect was found, we tested the difference between conditions pairwise with a two-tailed Wilcoxon signed-rank tests. To test whether integration took place, we computed the bimanual threshold predicted by optimal integration principles (Maximum Likelihood Estimation) for each participant and we tested whether the observed bimanual discrimination thresholds were smaller than or equal to the predicted MLE thresholds with a one-tailed Wilcoxon signed-rank tests. Finally, we also examined if individual bimanual thresholds were well associated with the predicted MLE thresholds. In particular, we used Pearson-product-moment correlation to test the relationship between the observed values and the MLE predictions. For all tests, the level of statistical significance was set at 5% (Error Type I $\alpha = 0.05$). For all Wilcoxon signed-rank tests, we report Siegel T statistic and the rank biserial correlation r_{rb} as a measure of the effect size.

Results

Table 1. Analysis of unsatisfactory performances. The rows separate participants who performed badly in one, two or three conditions. The first three columns identify whether the bad performance(s) occurred for the first, second or third condition, and whether it corresponded to the unimanual, bimanual grounded or bimanual free conditions. The results for the second group are between parentheses.

	First	Second	Third	One-hand	Grounded	Free
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One condition	2 (1)	1 (2)	0	2 (1)	1 (2)	0
Two conditions	4	2	2	4	3	1
Three conditions	2	2	2	2	2	2
Total	8 (1)	5 (2)	4	8 (1)	6 (2)	3

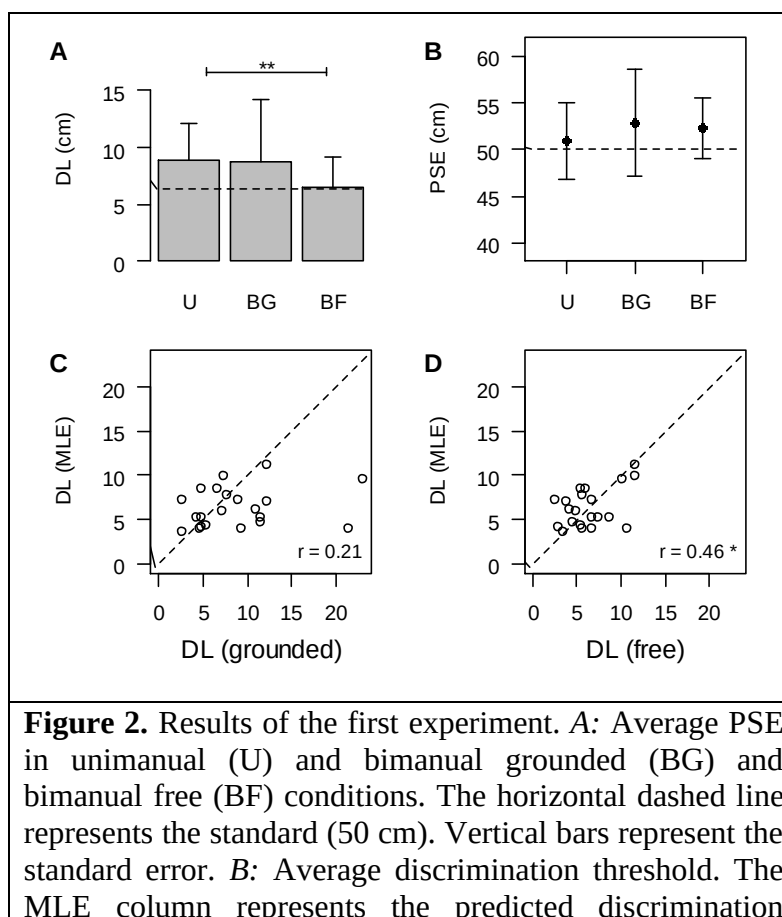
For the first group, nine (50%) participants had a large ($DL > 24$) or negative discrimination threshold in one of the conditions. Unsatisfactory performance happened more often at the beginning of the experiment. Table 1 shows that the first condition was not performed satisfactorily for eight of the nine participants. The unsatisfactory performance also happened more often in the one-hand condition (8 times, 44.4 %) and bimanual grounded condition (6 times, 33.3 %) than in the bimanual free condition (3 times, 16.7 %). The relative large number of participants who had problems with the task initially led us to introduce a training phase at the beginning of the experiment. For the second group, only three participants (15%) had a negative or unsatisfactory threshold in one of the conditions. All nine participants in this group who were repeating the experiment performed satisfactorily, including four participants who had not performed satisfactorily the first time. Note that the results of groups 1 and 2 are reported as Experiment 1 and 2 in Xu & Baud-Bovy, 2017.

Table 2. Thresholds expressed in four cues.

Cue	Free	Grounded	Unimanual
Plier size (cm)	6.59±2.25	9.22±4.27	10.33±3.10
Slide angle ($\gamma_2 - \gamma_1$, deg)	3.66±1.76	5.51±3.25	5.81±2.23
Angular attitude (γ_2 , deg)	5.12±2.42	7.65±4.43	8.15±3.10
Difference-in-height (h, cm)	1.18±0.57	1.77±1.03	1.90±0.73

For simplicity, we analyzed together data from all participants who performed satisfactorily the three conditions. For participants in the second group who had already performed all conditions the first time ($N=5$), we retained only the second performance, which yielded a total of 21 unique participants ($N = (18 - 9) + (20 - 3) - 5 = 21$). The results are similar if the analyses are conducted only with the well-performing participants of the second group ($N = 20 - 3 = 17$). Assuming that the unimanual threshold DL_u is the same for both hands, optimal integration principles and maximum likelihood estimation predict that the bimanual threshold should correspond to $DL_b = DL_u/\sqrt{2}$ (see eq. 1). The results show that the bimanual discrimination thresholds in the free condition were well predicted by optimal integration, which was not the case for the discrimination threshold in the grounded condition, which did not differ from the discrimination thresholds in the

unimanual condition (top left panel Figure 2). The average ($\pm$ SD) discrimination thresholds were 8.9 ± 3.2 , 8.8 ± 5.4 and 6.4 ± 2.7 cm for the unimanual, bimanual grounded and bimanual free condition respectively (Table 2 also reports these thresholds expressed in terms of radius of curvature, slide angle, angular attitude and difference-in-height). A non-parametric Friedman rank test on the discrimination thresholds showed a significant effect of the condition ($\chi^2(2) = 7.714$, $p = 0.021$). Paired two-tailed Wilcoxon signed-rank tests indicated a statistically significant difference between the free bimanual condition and the unimanual condition ($T = 30$, $rrb = 0.740$, $p < 0.002$), but not between the free and grounded bimanual conditions ($T = 67$, $rrb = 0.420$, $p = 0.096$). The difference between the grounded bimanual and the unimanual conditions was not statistically significant ($T = 96$, $rrb = 0.169$, $p = 0.517$). There was no statistically significant effect of the condition on the PSE (Friedman test: $\chi^2(2) = 0.667$, $p = 0.72$). At the individual level, we found that discrimination thresholds in the free bimanual condition were well correlated with the values predicted by maximum likelihood estimation (Pearson's correlation of coefficient: $r = 0.456$, $p < 0.04$). This was not the case for the discrimination thresholds in the grounded bimanual condition, which were not correlated with the maximum likelihood estimates ($r = 0.209$, $p = 0.36$).



threshold. *C*: Comparison between individual thresholds predicted by MLE and observed ones in the bimanual grounded condition. *D*: Comparison between individual thresholds predicted by MLE and observed ones in the bimanual free condition. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$.

Experiment II

The results of the first experiment show that people can discriminate the length of hand-held pliers by simply opening and closing them, given an opportunity to familiarize themselves with the pliers and the task. While about 50% of the participants had difficulty performing the task without proper familiarization, we found a much smaller proportion of such participants in the second group (15%) who practiced the task before the beginning of the experiment. The results of this experiment also confirmed our hypothesis that grounding can influence bimanual integration. The objective of the second experiment was to confirm these results with a new group of participants, who had never performed the task except for practice trials before starting the experiment. In addition, to ensure that comparisons between conditions would not be affected by serial effects, we mixed the experimental conditions by alternating small blocks of trials of each condition during the experiment.

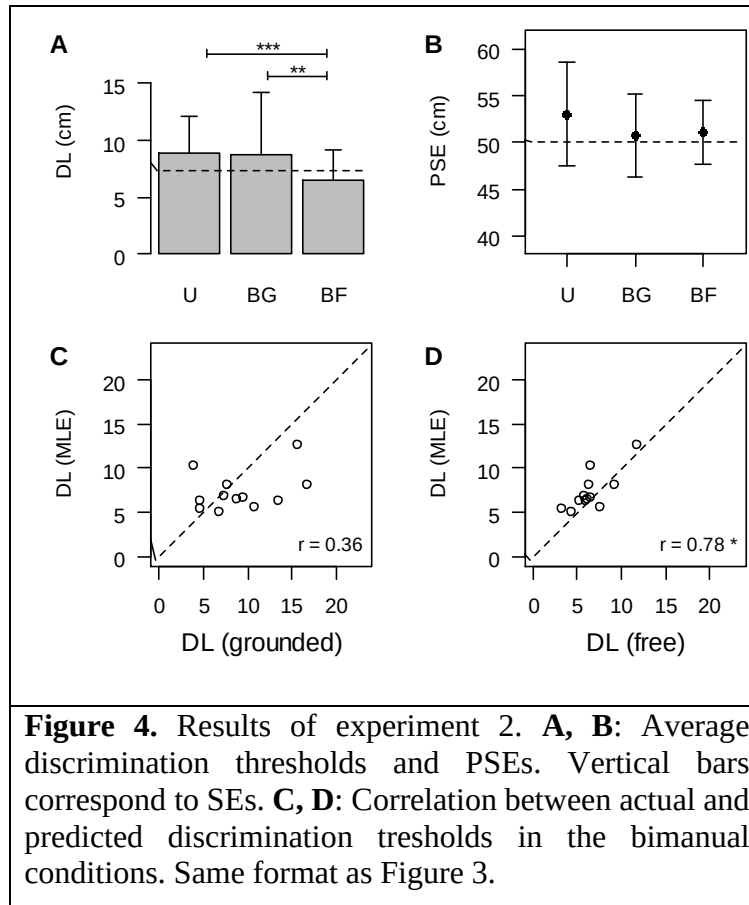
Methods

Participants. Twelve individuals (six males and six females) participated to this experiment. The group included 11 right-handed and 1 left-handed, with an average age of 30.6 ± 6.5 years. All participants were naïve with respect to the experimental task.

Experimental Procedure. The task, experimental procedure and conditions were largely similar to the one used in the previous experiment. In particular, all participants were familiarized with the pliers and the task like the second group of participants of the previous experiment. Still, there were three experimental differences with respect to the first experiment. First, we slightly extended the range of plier sizes used as comparison stimuli, which varied from 34 to 66 cm (34, 42, 47, 53, 58, and 66 cm). Second, the peg was not inserted in the rail in the free bimanual condition. This allowed the participants to move the hinge joint laterally in addition of vertically in the fronto-parallel plane in this condition. The metallic frame still prevented movement outside the fronto-parallel frame. Third, the experimental condition changed every six trials. Each block of six trials included all possible comparison stimuli in a random order. The condition corresponding to the first block and the order of the experimental conditions in the following blocks was changed for

different participants. The experiment 8 blocks of 6 trials for each condition, yielding a total of 144 trials. The experiments lasted about 90 minutes to complete.

Results



The results of this experiment essentially replicate those of the first experiment. We found a significant effect of condition on the discrimination thresholds (Friedman test: $\chi^2(2) = 15.17$, $p < 0.001$). The free bimanual condition was statistically different from the unimanual (Wilcoxon test: $T = 0$, $rrb = 1.00$, $p < 0.001$) and grounded bimanual ($T = 7$, $rrb = 0.821$, $p = 0.009$) conditions. In contrast, the difference between the unimanual and grounded bimanual conditions was not statistically significant ($T = 27$, $rrb = 0.308$, $p = 0.380$). There was no statistically significant effect of the conditions on the PSE (Friedman test: $\chi^2(2) = 1.167$, $p = 0.558$). At the individual level, the predicted (MLE) thresholds were better correlated with the thresholds measured in the free condition (Pearson coefficient of correlation: $r = 0.782$, $p < 0.01$) than those observed in the grounded condition ($r = 0.362$, $p = 0.25$) like in the previous experiment.

Experiment III

The goal of this experiment is to verify experimentally that the free manipulation of the plier does not provide a more reliable estimate of the plier size than the grounded condition in the unimanual condition. This is important to exclude the possibility that an increase of the reliability of the unimanual cues rather than bimanual integration per se causes that the improvement observed in the free bimanual condition.

Participants. The fourth group included 18 participants (nine females and nine males, average age 24.7 ± 4.4 years). All were naive to the experimental task. All participants signed a consent form.

Experimental conditions. This control experiment included two unimanual conditions. In one unimanual condition, the pliers' center of rotation was fixed to the metallic structure as in the previous experiments. As previously, the height of the fixation point was adjusted as a function of the size of the plier so that the lowest hand positions would coincide to minimize positional cues about the plier size. In the second unimanual condition, the peg of the plier was inserted into the groove of the metallic frame like in the first experiment. This constraint allowed the plier to slide vertically like in the free bimanual condition of the first experiment.

Experimental procedure. All participants practiced the task before the beginning of the experiment. We used the same six plier sizes and number of trials per repetition as in the second experiment. The two conditions alternated every six trials. For each participant and condition, we computed a fitted probit psychometric function and computed the PSE and discrimination threshold.

Results. All participants performed the two unimanual conditions satisfactorily. The average ($\pm$ SD) discrimination thresholds were 11.1 ± 4.3 and 12.9 ± 5.0 cm for the unimanual grounded and free condition respectively. Paired two-tailed Wilcoxon signed-rank tests indicated no statistically significant difference between unimanual grounded and free condition ($V = 117$, $p = 0.182$). There was no statistically significant difference between the PSEs of the two conditions ($V = 115$, $p = 0.07$).

General Discussion

The first objective of this study was to find out whether participants can estimate the size of hand-held pliers by simply opening and closing them. Geometrically, the pliers' size corresponds to the radius of curve of the circle defined by the movement of the handle around the revolute joint (instantaneous center of rotation). As noted in the introduction, various cues might give information about the length of the pliers: haptic cues about curvature or shape can be classified into position (0th-order) cues, tangent plane (1st-order) cues and local curvature (2nd-order) cues

(Pont et al., 1997). In the grounded condition where the center of rotation is fixed and the hand path corresponds to an arc of a circle, the task is akin to a curvature discrimination task. Both the hand position (0th-order cue) and the orientation of the handle (1st-order cue) provide information about the arc of circle and, indirectly, the radius of curvature. In the free conditions, the hand path is unconstrained, and the main cue is the relationship between the orientations of the two hands and the distance between them. Local curvature (2nd-order) cues are absent in this task.

The results of this study show that people can discriminate the length of hand-held pliers by simply opening and closing them. While some participants can have difficulty performing the task in absence of any training, introducing a brief training period and showing the pliers to the subjects when explaining the task allowed almost all participants to perform the task satisfactorily from the onset. The average value of the pliers' size discrimination thresholds in this task ranged from ~9 cm to 13 cm depending on the condition. These values are markedly above the discrimination thresholds (~4 cm) found by Sanders & Kappers (2006a) for a cylindrical stimulus with a radius of curvature of 40 cm. that is comparable to the ones used in this study. A likely reason for the larger discrimination thresholds observed in this study is that the participants in Sanders and Kappers (2006a) could explore the cylinders with a larger range of motion and the whole hand. In particular, the larger range of motion allowed participants to seize the size of the cylinder directly and the whole hand exploration provided 2nd-order cues that were absent when manipulating pliers.

Free plier manipulation enhances bimanual integration

The second objective of this study was to test the hypothesis that free manipulation enhances bimanual integration. As noted in the introduction, previous studies that investigated bimanual integration in tasks comparable to ours yielded little evidence of bimanual integration. Squeri et al. (2012b) did not find evidence for bimanual integration in an curvature discrimination task where a bimanual planar manipulandum moved the hand(s) along a curved trajectory. Similarly, Panday et al. (2013) did not find evidence for bimanual integration in an object size discrimination task where participants had to judge the distance between two flat panels placed symmetrically with respect to the body midline (Exp 2). Finally, Wong et al. (Wong et al., 2014), did not find lower discrimination thresholds in the bimanual condition with respect to the best unimanual discrimination threshold in a position discrimination task. In their task, a robotic manipulandum moved the hand(s) at a reference position on the body mid-line and successively to a test position on the left or right side of the reference position after a distractor movement. These results are surprising given the close physical link between the two hands in bimanual manipulations. This link is also reflected by the difficulty to move the hand independently (Ivry et al., 2004; Kelso, 1981; Swinnen & Wenderoth, 2004a) and by the strong interhemispheric connection between homologous motor and somatosensory areas at the neuronal level (Carson, 2005).

However, the hands in the previous studies explored grounded objects. The experimental setup in Panday et al. (2013) and the robotic manipulanda in Squeri et al. (2012b) and (Wong et al., 2014) did not transmit force between the two hands. As a result, it is not possible to know whether the two hands are touching the same or different objects when the touched object is grounded. We therefore hypothesized that lifting the object might provide additional cues that would signal that the two hands are holding the same object.

In the two main experiments, we found a marked difference between the bimanual free and the bimanual grounded performances, and almost no difference between the unimanual and the bimanual grounded performances. In the free condition, the performance corresponded to the optimal integration or MLE prediction. At the individual levels, we also found a good correlation between the MLE prediction and the performance in the free condition. The second experiment showed a particularly strong correlation between individual bimanual thresholds in the free condition and corresponding bimanual thresholds predicted by optimal integration, as well as a much weaker correlation in the grounded condition.

Importantly, lifting the object does not provide additional cues about the size of the plier in the free condition. First, we also took care to avoid possible additional kinetic cues in the free condition (Turvey et al., 1998; Turvey & Carello, 2011). In the first experiment, the motion of the pliers in the free condition was limited by fixing the joint in a sliding mechanism that allowed it to move in the vertical direction. For the second experiment, the motion of the plier was restricted to the fronto-parallel plane by the metallic frame. In either case, the center of mass of the pliers was above the hands and did not produce static torques. In addition, the lightness of the pliers, the fact that the pliers' links were all the same size (only the hand position changed) and the relative slowness of the aperture movement essentially suppressed any possible inertial cues which might otherwise yield information about the length of hand-held sticks when they are wielded (Turvey et al., 1998).

Second, it might be argued that the grounded condition is more informative the final hand position depended on the plier size despite the adjustment of the height of the center of rotation (see Figure 2). The hand motion is also restricted to a unidimensional arc of circle in the grounded condition, which could facilitate a comparison between the two pliers. In contrast, the hands positions were not constrained in the frontal plane in the free condition, which renders the absolute position information useless in this condition. In fact, the results of the third experiment confirms that the free condition does not provide more reliable cues than the grounded condition. There was no performance difference between the free and grounded unimanual performance. This result indicates that the performance improvement in the bimanual free condition cannot be explained

by an increase of the reliability of the unimanual cues in the free condition but is likely due to the integration of the two sensory cues available in bimanual integration.

In this respect, it is important to note that the presence of a hinge joint in the middle of the pliers does not uncouple the hand movements completely. While the joint removes the transmission of (internal) torques between the two hands, linear forces are still transmitted. For example, the plier's vertical force produced by one hand is felt by the other hand, unless either hands move vertically together or the hand orientations change. Also, when the plier is not fixed, the two hands can in principle move freely in the frontal plane even if the plier implies a constraint between the hand orientations and the distance between the two hands. In contrast, no force is transmitted between the two hands in the grounded condition where the position of the pliers' rotational fulcrum is fixed: the radial force component with respect to the revolute joint is transmitted to the structure holding the plier while the tangential force component yields a displacement of the stick without force transmission to the other hand. As a result, the two hands move completely independently along a one-dimensional curve in the grounded conditions. Therefore, the pattern of motion physical interaction while subjects manipulated the pliers in the free condition provided information that their hands held the same physical object without providing information about the size of the pliers.

Bimanual integration in current accounts of sensory integration

The goal of sensory integration is to obtain a more reliable signal by fusing together redundant but noisy information. Bayesian theory and Maximum Likelihood Estimation provide a basis to derive a quantitative prediction about the best possible performance that can be achieved under these conditions. As noted in the introduction, a major problem that the brain (or our perceptual system) must solve is to decide *when* to integrate sensory information, which makes sense only if the information is redundant (Ernst & Bühlhoff, 2004b). A related question is *how* the brain decides that multiple streams of information are redundant.

The question has been extensively studied in the past. Early research focused on the observed biases when inconsistent sensory cues were presented to the subject to find out whether one sensory modality dominated the other ones. An influential review of this literature established that inter-sensory bias was influenced by amodal properties of the sensory cues such as their spatial location or timing and by cognitive factors such as the degree to which sensory sources are familiarly related, the distribution of attention between the two modalities and the instructional and/or situational modification of the observer's assumption that they were in presence of a single distal object (Welch and Warren (1980); Welch 1999). In a more recent review, Chen and Spence (2017) proposed that the concept of common cause (Körding et al. (2007b)) or coupling prior (

Ernst, 2007b) in Bayesian integration theories could replace the unity assumption. These concepts, like the unity assumption, represent prior information about the cause and/or relation between the various sensory signals.

One question of interest is what triggers the integration of bimanual information in this task, whether it consisted of the amodal properties of the stimulus or more cognitive factors. According to Chen & Spence (2017), the unity assumption is a top-down modulation of human multi-sensory integration but the distinction is not always obvious as it might also be possible that amodal properties of the stimulus act indirectly by signaling the presence of a single distal object or that the sensory cues have common cause. For example, Plaisier and Ernst (2012) argued that visual cues showing both hands touching the same object might have strengthened unity assumption. However, it should be noted that knowledge alone of holding a single object did not suffice for this strengthening and bimanual integration to occur in our study. As a matter of fact, participants knew that they were holding pliers in the grounded and free conditions since they were shown the pliers at the beginning of the experiment and told that these pliers would be fixed in the grounded condition. Despite all this information, we did not observe bimanual integration in the grounded condition, even in Experiment 2 where the free and grounded conditions were presented in a mixed order.

A somewhat different explanation is that what is important is the level of processing of sensory information. For example, Panday et al (2013) argued that it is necessary that information be processed at a higher level, where the shape is represented for bimanual integration to occur. They also argue that 2nd order cues might play a central contribution in this process. In contrast, bimanual positional information would be processed at a lower level is not integrated even when two hands share the same position as in Squeri et al. (2012) or Wong et al (2014). This explanation is less general than the unity assumption underlying because the processes involved in size and shape processing are specific to this task. However, research on multi-sensory integration has provided other examples where the level of processing of sensory information matters. For example, numerous studies have shown that audio and visual stimuli are better integrated if they are semantically congruent such the sound of barking with the image of a dog or a female voice with a gender-matched face (Doehrmann & Naumer, 2008, for a review). In this example, semantic cues represent characteristics of objects that are presumably stored in long-term memory and that are independent from the spatial or temporal characteristics of the stimulus. Accordingly, this research has shown integration between two sensory cues is enhanced when the two cues refer to the same object in the so-called semantic memory. In our study, however, it is not clear why bimanual sensory cues would be processed in the free condition at a higher level than in the grounded condition unless one assumes that participants did not combine information from the

two hands in the grounded condition because they did not perceive, consciously or not, holding a single object in this condition.

A link to motor cognition

From a motor control point of view, the physical coupling created by an object held with both hands has important consequences because it is not possible to control the two hands independently in this case. As a matter of fact, the object transmits force between the two hands, which must be taken into account when planning and/or executing the movement. Current motor control theories posit that the motor system estimates the consequences of the action in a predictive manner (review in (Franklin & Wolpert, 2011)). To that end, it has been proposed that the motor system combine sensory feedback and forward models that simulate the actions to estimate the current state of the system, such as the position of the limbs and, presumably, the position of hand held objects. Interestingly, current motor theories also use a Bayesian framework to estimate the current state of the motor system from prior information, sensory feedback and predictions.

While most experimental studies have focused on the control of a single limb, some studies have shown that a perturbation of one hand can lead to anticipatory adjustments to both hands in bimanual tasks, which suggests that the brain might have internal models for bimanual tasks that integrate this physical coupling (Witney, 2004). An interesting question is whether the internal models that are relevant for controlling hand movements in bimanual motor tasks are also involved in the processing of sensory information in bimanual perceptual tasks. A possible but still speculative interpretation of the results of our study is bimanual integration occurs in the free condition because the motor system must integrate the information from the two hands and possibly estimate the plier size to control the movement of the hands in this condition.

To conclude, we showed that free manipulation of a large plier promotes bimanual integration when estimating their size. Crucially, we showed that free manipulation did not provide additional information about the pliers' size or improved the reliability of the sensory cues. Improved discrimination processes can be explained by the gain predicted by optimal integration model when two redundant cues are combined together. Finally, we discussed various ways free manipulation might improve bimanual integration. First, we proposed that the physical interaction between the two hands occurring during free manipulation enhances bimanual integration by strengthening the assumption that information is coming from the same object. We also proposed that free manipulation might activate predictive motor processes that rely on signals of both hands to estimate the current state of the motor system and control the hand movements in this condition. Bimanual integration would not occur in the grounded condition because the absence of physical coupling between the two hands would not require that the motor system to combine information

from the two hands in this condition. In particular, further research is needed to confirm that the motor and perceptual systems share a common estimate of the object's size.

Appendix B

Supplementary materials for Chapter 2 “Multisensory Integration of Somatosensory Feedback”

Appendix 1B. Preliminary Experiments

The goal of these preliminary experiments was to define experimental conditions that: 1) allows one to measure threshold in both sensory modalities; 2) satisfy the unity assumption in bimodal condition to promote integration (Gepshtein et al., 2005) and 3) equalize the difficulty of the unimodal conditions so that the unimodal thresholds are as close as possible. To achieve this objective, we measured discrimination thresholds in the different experimental conditions with a few subjects. As in the main experiment, we used 8 stimuli with varying eccentricities and the method of constant stimuli with 16 repetitions per stimulus. Then we fitted a logistic psychometric function and computed the 84% discrimination thresholds.

Visual stimuli

In order to adjust the visual stimuli we tested four different experimental conditions (23 healthy individuals in total; some subjects participated to more than one pilot experiment in which we changed the color of stimuli, the lightening condition and/or the distance between the blurring screen and the stimuli.

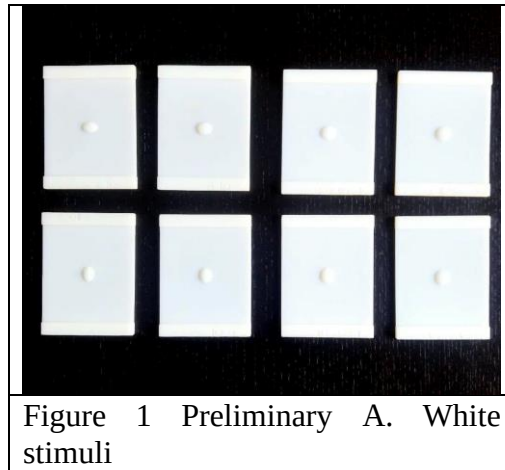
Table 5 Preliminary. Experimental Details, DLs and PSEs of the visual preliminary experiments.

Experimental Condition	Stimuli	Blurring screen distance	Lightening	Subjects	DL (M $\pm$ SD)
Helbig & Ernst (2007)	White Ellipses	Between 6-12 cm	Not reported	10	From 0.42 to 1.76*
1	White Ellipses	Blurring screen at 6 cm	No	5	2.63 $\pm$ 0.77
2	White Ellipses	Blurring screen at 3 cm	No	6	1.26 $\pm$ 0.25
3	White Ellipses	Blurring screen at 3 cm	Led lights	6	0.55 $\pm$ 0.32
4	Black Ellipses	Blurring screen at 6 cm	Led lights	9	1.67 $\pm$ 0.81

STUDY (HC, visual)	Black Ellipses	Blurring screen at 4-5 cm	Led lights	19	1.13 ± 0.45
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*: the amount of blurring was manipulated in Helbig & Ernst (2007) experiment. It varied from 0.42 to 1.76. Our goal in the visual condition was to obtain a DL similar to the haptic threshold.

In the first condition, we used white stimuli (see fig. 1 A Preliminary) and we set the blurring screen at 6 cm of distance from them (as indicated in the seminal work by (Ernst & Banks, 2002).



In this condition the participants showed very high visual thresholds (see table 1 Preliminary). The visual stimuli were very difficult to see and we decided to decrease the distance between the blurring screen and the stimulus.

In the second condition, we used the same white stimuli but we set the blurring screen at 3 cm of distance from the experimental stimuli.

Despite lowering the thresholds (see table 1 Preliminary), the task was still too difficult, and we added led lights close to the stimuli positions in order to improve the visual condition.

In the third condition, we used the same parameters as in condition 2 and we added led lights around the stimuli positions (see Figure 1 B Preliminary).

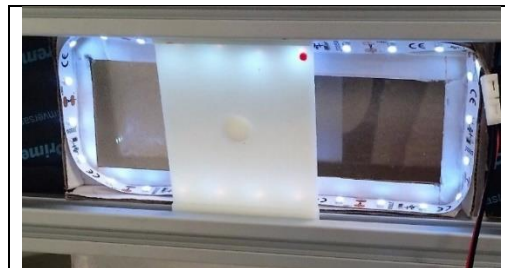


Figure 1 Preliminary B. White Stimuli with led lights added (picture from the back side)

By adding led lights, the threshold decreased markedly. However, with this lightening condition the participants were able to observe the shadow of their finger behind the stimulus in the bimodal condition. To avoid different visual cues in the bimodal condition with respect to the visual condition, we decided to print black stimuli.



Figure 1 Preliminary C. Black Stimuli (also used in the experiment)

The fourth condition was similar to the third but the distance between the blurring screen and the stimuli was 6 cm and the color of the stimuli was black rather than white (see Figure Preliminary 1 C).

In this condition, we solved the problem of the shadow of the finger but visual thresholds increased again. Importantly, these thresholds appeared to approach the tactile thresholds (see somatosensory condition below). Accordingly, for the final experiment we decided to keep these black stimuli and lightening and decrease more the distance between the stimuli and the screen.

Tactile stimuli

For the tactile stimuli, we measured the discrimination thresholds in three conditions, with two different stimulus thicknesses (2.00 mm and 1.5 mm) and two different exploration modalities.

- Free exploration of the stimulus. Participants can freely move the finger on the ellipse for the entire duration of the trial.
- In order to make the task more demanding for the participants we asked them to avoid moving the finger for the entire duration of the trial (S. J. Lederman & Klatzky, 1987).

In total, we tested 16 healthy individuals in three experimental conditions (see Table 2).

Table 6 Preliminary. Experimental Details, DLs and PSEs of the somatosensory preliminary experiments.

Experiment	Stimulus Thickness	Exploration Modality	subjects	DL mean
Helbig & Ernst (2007)	2.0 mm	With exploration	10	1.02
1	2.0 mm	With exploration	5	0.82 ± 0.26
2	2.0 mm	Without exploration	6	1.03 ± 0.83
3	1.5 mm	Without exploration	5	1.43 ± 0.37
STUDY (HC, tactile)	1.25 mm	Without exploration	19	0.84 ± 0.32

In the first condition, we used 2.0 mm thick stimuli and we allowed the participants to explore freely the ellipses for the entire duration of the trial (as in Ernst & Banks, 2007). In this condition, the haptic thresholds (0.82 ± 0.26) were lower than that of Helbig & Ernst (2007) and then in the visual condition (2.63 ± 0.77 , see Table 1).

In the second condition, we made the task more challenging by asking the participants not to move their finger when touching the stimulus for the entire duration of the trial. The thresholds in this condition (1.03 ± 0.83) were close to those found in Helbig & Ernst. However, they were still markedly smaller than the ones found in the visual conditions (see Table I).

In the third condition, we decided to decrease the thickness of the stimuli from 2.0 mm to 1.5 mm to increase the difficulty of the task (van der Horst & Kappers, 2008). The resulting DLs (1.43 ± 0.37) were closer to the visual ones (1.67 ± 0.81) but still below them. For this reason, we decided to reduce the thickness to 1.25 mm in the main experiment. Despite this reduction of thickness, the haptic DL in the main study (0.84 ± 0.32) were markedly lower than in the pilot experiment (1.43 ± 0.37) and still lower than in the visual condition (1.13 ± 0.45).

Conclusions

Reproducing experimental conditions in psychophysics experiments is challenging, in particular when using physical stimuli instead of computer images or virtual reality (e.g. Ernst and Bank, 2002). Our first attempt to reproduce Helbig and Ernst (2007) experiment used the same parameters but yielded different results. In our pilot experiment, visual thresholds were initially above the haptic thresholds. Reasons for discrepancies can be multiple. The semi-transparent plastic sheets that we and Helbig and Ernst (2007) used to blur the visual stimuli are not standardized. Lighting condition might have also differed. The posture was clearly different in

both studies (seated vs lying on the back). We believe that some amount of preliminary testing is almost unavoidable in such a context.

For this study, the pilot experiments reported here helped use to reduce an initial difference between haptic and visual condition (0.82 ± 0.26 vs 2.63 ± 0.77) to something that was more acceptable in the main study (0.84 ± 0.32 vs 1.13 ± 0.45) though not ideal.

Appendix 2B. Outlier analysis and robust statistics

Outliers

The definition of outliers is somewhat arbitrary except in extreme cases. In practice, many different criteria are used. In a box and whisker plot, outliers are defined as data points outside the whiskers, which corresponds to 1.5 times the IQR. Another often used criterion is to identify data points that differ from the group average by more than two or three times the standard deviation and removing these data points before applying the tests.

The following table reports the number of outliers for PSEs and DLs according to these three criteria in the three conditions where it happened (note that there was not a perfect overlap between the outlier definitions):

Group	Variable (condition)								
	PSE (H)			DL (V)			DL(Bimodal)		
	BP	2SD	3SD	BP	2SD	3SD	BP	2SD	3SD
HC (N=19)	1	1	0	1	1	0	0	1	0
BCHC (N=9)	1	0	0	1	0	0	0	0	0
AN (N=16)	0	1	0	2	1	1	0	1	0

The table shows that there is only one outlier with the 3 SD definition and 6 outliers with the 2 SD or boxplot (BP) definitions. However, a visual inspection of psychometric functions showed that they fitted well the data and the participants were accurate in their performances in the other conditions. In absence of specific reasons to remove these data, we believe that they can capture valuable information, which are part of the study area. For these reasons, we decided to leave them in the analyses and not consider them as outliers. Such a decision might however be a problem for statistical analyses since ANOVAs assume the normality of the distributions. A Shapiro-Wilk test of normality of the residuals of a two-way ANOVA for the PSEs (5 conditions x 3 groups) was not statistically significant ($W = 0.99$, $p = 0.49$). However, a similar test for the DLs (3 condition x 3 groups) was statistically significant, indicating that DL deviated from normality ($W = 0.86$, $p\text{-value} < 0.001$).

Robust Analyses

While we used and reported ANOVAs to analyze our results, we also used robust methods based on the 20% trimmed mean to check the validity of the main tests (R package WRS2, (Mair & Wilcox, 2020)). The tables below report the results that corresponds to the analyses of the data.

Points of Subjective Equality

Table. PSE in unimodal conditions: effect of sensory modality (H vs V) and group

PS ((unimodal)	Mixed 2-way ANOVA				Robust method (bwtrim)			
	Df1	DF2	F	P	DF1	DF2	F	P
Group	2	41	7.055	0.002	2	15.4237	6.0696	0.0114
Sensory Modality	1	41	37.888	<0.001	1	23.5803	44.7984	<0.001
Interaction	2	41	0.792	0.460	2	17.0183	0.3882	0.6842

The two-way mixed ANOVA on unimodal PSEs still showed an effect of sensory modality and group but not of the interaction between the group and condition:

Table. Haptic bias: difference from null (one-sample tests)

group	mod	co	pse.mean	pse.sd	t test			One-step estimator test	
					t	df	pval	Onestep	onesampb.pval
HC	uni	v	-0.11	0.48	-1.03	18	0.32	-0.12	0.32
BCHC	uni	v	0.03	0.31	0.34	8	0.74	0.02	0.88
AN	uni	v	0.10	0.48	0.84	15	0.41	0.15	0.35
HC	uni	h	0.54	0.53	4.45	18	0.00	0.57	0.00
BCHC	uni	h	0.71	0.35	6.13	8	0.00	0.73	0.00
AN	uni	h	1.07	0.59	7.25	15	0.00	1.10	0.00

Bootstrapped robust estimate of the mean PSEs (one step estimate, Mair & Wilcox, 2020) were significantly different from 0 in the haptic modality, but not in the visual

Table. Haptic bias: difference between haptic and visual conditions

group	Paired t test				Yuen test for paired sample		
	estimate	statistic	p.value	parameter	yuend.stat	yuend.df	yuend.pval
HC	-0.655	-3.438	0.003	18	-3.567	12	0.004
BCHC	-0.675	-3.659	0.006	8	-3.824	6	0.009
AN	-0.971	-4.649	0.000	15	-4.190	9	0.002

Robust Yuen' tests on trimmed means for paired samples confirm the statistically significant difference between the haptic and visual modality for all groups.

Table. PSE (bimodal condition): effect of the conflict (see Figure 4, left panel)

DL ((unimodal))	Mixed 2-way ANOVA				Robust method (bwtrim)			
	Df1	DF2	F	P adj	DF1	DF2	F	P
Group	2	41	2.076	0.138	2	23.1832	1.181	0.325
Sensory Modality	2	82	163.139	0.000	2	28.4107	111.957	0.000
Interaction	4	82	0.577	0.656	4	23.4356	0.853	0.507

Discrimination Thresholds

Table. DL (unimodal conditions) Haptic versus visual conditions

DL ((unimodal))	Mixed 2-way ANOVA				Robust method (bwtrim)			
	Df1	DF2	F	P	DF1	DF2	F	P
Group	2	41	9.939	<0.001	2	15.8498	6.925	0.007
Sensory Modality	1	41	10.845	0.002	1	14.7409	11.365	0.004
Interaction	2	41	1.178	0.318	2	14.8645	0.688	0.518

In this crucial analysis of the DLs in the unimodal condition, the results of the 2-way mixed ANOVA and robust methods are similar. Both tests show an effect of the sensory modality and group but no interaction.

Table. DLs: comparison across sensory conditions (see Fig. 4, right panel)

Paired t-test versus Yuen's paired sample test for trimmed means

Group	co1	co2	Paired t test			Yuen's test			Optimal Integration
			Df	t	pval	Df	stat	pval	
HC	V	H	18	2.390	0.028	12	2.070	0.061	?
HC	H	B	18	2.258	0.037	12	2.242	0.045	S
HC	V	B	18	4.266	0.000	12	4.215	0.001	S
HC	B	MLE	18	0.264	0.795	12	-0.009	0.993	NS
BCHC	V	H	8	2.117	0.067	6	1.548	0.172	?
BCHC	H	B	8	0.654	0.531	6	0.712	0.503	S
BCHC	V	B	8	2.562	0.034	6	1.861	0.112	S
BCHC	B	MLE	8	1.383	0.204	6	1.224	0.267	NS
AN	V	H	15	2.344	0.033	9	2.306	0.047	?
AN	H	B	15	1.607	0.129	9	1.269	0.236	S

AN	V	B	15	2.826	0.013	9	3.543	0.006	S
AN	B	MLE	15	0.809	0.431	9	0.642	0.537	NS

The table shows that two test yielded different results (in red). First, the comparison between V and H in HC group was not significant. As discussed in the paper, the difference between DLs in visual and tactile condition can be a problem from an experimental point of view since it makes the optimal integration harder to test. That said, the fact that this test is not statistically significant is not a problem for any interpretation of the results.

The second difference is that the difference between visual and bimodal condition was not statistically significant. In interpretative terms, the absence of any effect statistically significant test in this group indicates that we cannot reject any of the hypotheses about the integration processes. This pattern of results clearly reflects the lack of power due to the small sample size in this group.

The last column indicates the pattern of results that would reflect optimal integration (? stands for indifferent). As it can be seen, neither set of analyses corresponded exactly to these predictions. As reported in several places in our study (e.g. Limitation), the DLs (unlike the PSEs) did not provide conclusive evidence with respect to optimal integration hypotheses

Conclusion

The p values obtained with robust statistics were slightly more conservative than the p values obtained with the ANOVA but all tests were still statistically significant at the 0.05 level of significance. Two contrasts were not statistically significant when comparing DLs pairwise and our conclusions do not depend on these results, which happen not be conclusive with either set of analyses.