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Université Lumière Lyon 2

Ecole Doctorale Neurosciences et Cognition (NSCo)

INSIGHTS INTO BODY REPRESENTATION PLASTICITY FOLLOWING TOOL-USE: THE ROLE OF VISION AND PROPRIOCEPTION

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Spécialité de doctorat : Neurosciences cognitives

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قُلْ رَبِّ زِدْنِي عِلْمًا

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ABSTRACT/RÉSUMÉ

Tool-use is an essential component of the human behavioral repertory that allows us to extend the frontiers of our interaction with the environment. Several studies have shown that the use of a tool functionally extending arm length might change the arm representation toward a tool incorporation, inducing what is reported in the literature as a plasticity of the body representation for action. In my doctoral dissertation, I first investigated the contribution of proprioception in the paradigm of tool incorporation by assessing which proprioceptive modality is crucial for this incorporation in an elderly population whose online proprioception remains intact while offline, remembered proprioception is impaired. To this end, we compared the kinematic of reach and grasp movement performed before and after a tool-use session in which 60 years old participants were required to perform the same movements with a mechanical grabber. Results showed that participants modified the kinematic of the transport component of their movement to incorporate the tool as reported previously in younger adults. Most importantly, the kinematic incorporation of the tool was correlated to participant's online proprioception acuity so that a better online proprioceptive acuity give rise to larger kinematics effects of tool-use. In the second part of my thesis, I wanted to examine how the use of a tool may modify the proprioception acuity itself. To this aim, I assessed the proprioception acuity through a Joint Position Sense test (JPS) in healthy adults, before and after tool-use. Strikingly, proprioception is more precise after tool-use. To confirmed tool incorporation in the arm representation after tool-use, I ran a second experiment in which I measured proprioceptive acuity before and after tool-use and, in addition, we asked participants to localize tactile stimuli delivered to their forearm before and after the use of the tool. The results showed that using a tool induces proprioceptive improvement for the arm that manipulates it that coexist with an updated representation of the arm that used the tool to be elongated. Finally, to examine the role of vision, I assessed the kinematic behavior of two blind populations, a congenitally blind group and a group of later onset. Participants performed a reach and grasp paradigm before and after tool-use to determine whether having experienced vision during youth is an absolute requirement for body representation plasticity to occur. In the two groups alike, we observed no kinematic modifications of arm reaching after tool-use. These results are in sharp contrast with those reported previously in healthy blindfolded participants and stresses the importance of vision during childhood and adolescence to enable tool incorporation in the body state estimate. Finally, in the discussion part I will go throw all my work to relate the results under the umbrella of body representation plasticity after tool-use.

Keywords: Tool-use, body representations, plasticity, somatosensory system.

L'utilisation des outils est une composante essentielle du répertoire comportemental humain qui nous permet d'étendre les frontières de notre interaction avec l'environnement. Plusieurs études ont montré que l'utilisation d'un outil allongeant fonctionnellement le bras pouvait changer la représentation du bras dans le cerveau. L'incorporation de l'outil dans la représentation du bras est connue dans la littérature comme un phénomène de plasticité de la représentation corporelle utile à l'action. Dans ma thèse de doctorat, j'ai d'abord étudié l'apport de la proprioception dans le paradigme de l'incorporation d'outil en déterminant quelle modalité proprioceptive est cruciale pour cette incorporation. Pour cela j'ai testé une population âgée de 60 ans et établi que leur proprioception « online » restait intacte alors que leur proprioception « offline » était altérée. Nous avons ensuite comparé, pour cette population vieillissante, la cinématique du mouvement de préhension effectué avant et après une session d'utilisation d'outil. Les résultats ont montré que l'incorporation de l'outil se traduit dans cette population par les mêmes changements cinématiques que ceux déjà rapportés dans une population plus jeune. De manière particulièrement intéressante la modalité « online » de la proprioception joue un rôle important dans le maintien de la plasticité de la représentation corporelle de l'action après l'utilisation d'outils. En effet, la taille des changements cinématiques liés au phénomène d'incorporation d'outil dépend de l'acuité proprioceptive. Ainsi, la proprioception est bien liée aux phénomènes d'incorporation des outils. Dans la deuxième partie de ma thèse, j'ai entrepris d'examiner comment l'utilisation d'un outil peut modifier la proprioception elle-même. A cette fin, j'ai testé la proprioception de participants adultes sains à l'aide d'un Joint Position Sense test (JPS), avant et après, une session d'utilisation d'outil. Les résultats ont montré que la proprioception s'améliore après l'utilisation d'un outil, cette amélioration est restreinte au bras ayant utilisé l'outil. Afin de confirmer que cette modification proprioceptive coexistait avec la modification de la représentation du bras, j'ai réalisé une deuxième expérience évaluant d'une part, l'acuité proprioceptive avant et après l'utilisation de l'outil, et d'autre part, la localisation de stimulations tactiles délivrées sur l'avant-bras. Les résultats ont montré que l'utilisation d'un outil induit une amélioration proprioceptive pour le bras qui le manipule, et ceci coexiste avec une représentation actualisée du bras qui utilise l'outil (allongement de la longueur du bras). Enfin, dans la dernière partie de ma thèse, j'ai étudié le rôle de la vision dans le phénomène d'incorporation d'outil. J'ai évalué le comportement cinématique de deux populations malvoyantes/non voyantes différant de par l'âge du début des déficits visuels dans un paradigme de préhension avant et après l'utilisation d'un outil. Nous n'avons pas retrouvé de

modifications cinématiques induites par l'utilisation de l'outil dans ces deux groupes. Ces résultats soulignent l'importance de la vision au cours de l'enfance et de l'adolescence pour permettre la mise en place des phénomènes de plasticité des représentations corporelles.

Enfin, dans la partie discussion, je discuterai l'ensemble de mes résultats dans le cadre de la plasticité du schéma corporel après l'utilisation d'outil.

Mots-clés : Utilisation d'outil, représentations corporelles, plasticité, système somatosensoriel.

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TABLE OF CONTENTS

List of figures	15
List of tables	15
List of abbreviations.....	16
State of the art	18
General introduction.....	19
Chapter 1: MOTOR CONTROL.....	23
1. Theories of motor control	24
2. Internal models of action	25
3. Assessment of feedforward and feedback control	29
1. Visual effects.....	29
2. Proprioceptive effects.....	31
4. Kinematic profile of reach-to-grasp movement	32
Feedback and feedforward models in a reach-to-grasp movement.....	33
CHAPTER 2: BODY REPRESENTATIONS	36
1. Definition of body representations.....	36
2. Peripersonal space and its taxonomy	37
3. Subdivisions of body representations	37
3.1. Body Structural Description (BSD).....	38
3.2. Body Image (BI)	38
3.3. Body Schema (BS).....	39
4. The contributions of multiple sensory modalities to body representation.....	41
4.1. Visual contribution to body representation.....	42
4.2. Tactile and proprioceptive contributions to body representation.....	44
4.3. Auditory contributions to body representation	51
4.4. Vestibular contributions to body representation	52
5. Tool-use: a clue to investigate body schema plasticity	53

Chapter 3: RESEARCH QUESTIONS AND HYPOTHESES.....	61
Hypothesis	62
Experimental part	65
Chapter 4: ONLINE PROPRIOCEPTION FEEDS PLASTICITY OF ARM REPRESENTATION FOLLOWING TOOL-USE IN HEALTHY AGING.....	67
Chapter 5: TOOL-USE MODULATES PROPRIOCEPTIVE ACUITY AND REPRESENTED ARM LENGTH	91
Chapter 6: BLINDNESS ALTERS ARM REPRESENTATION PLASTICITY FOLLOWING TOOL-USE	114
GENERAL DISCUSSION.....	143
1. Insights into the role of proprioception and body representation’s plasticity.....	143
Main results.....	143
Proprioception and the update of the body estimate for the motor control of tools .	143
2. Insights into the role of vision and body representation plasticity	145
Main results.....	145
3. Balancing/calibration between visual and proprioceptive information to induce the plasticity phenomena	146
References	151

LIST OF FIGURES

FIGURE 1. A SCHEMATIC MODEL FOR GENERATING GOAL DIRECTED MOVEMENTS (SHADMEHR & KRAKAUER, 2008).....	27
FIGURE 2. KINEMATICS OF REACH-TO-GRASP MOVEMENT.	33
FIGURE 3. DIAGRAMMATIC REPRESENTATION OF THE MAMMALIAN MUSCLE SPINDLE (TAKEN FROM PROSKE, 1997).	46
FIGURE 4. DIAGRAMMATIC REPRESENTATION OF THE MAMMALIAN GOLGI TENDON ORGAN (TAKEN FROM PROSKE & GANDEVIA, 2012).....	46
FIGURE 5. TYPES OF CUTANEOUS RECEPTORS (DALY ET AL., 2013).	47
FIGURE 6. PROPRIOCEPTIVE ASSESSMENTS IN THREE DIFFERENT CONDITIONS (ADAMO ET AL., 2007).....	49
FIGURE 7. CORRELATION PLOTS BETWEEN THE ONSET OF VISUAL DEFICIENCY AND THE KINEMATIC CHANGES INDUCED BY TOOL-USE.....	146
FIGURE 8. FREE-HAND MOVEMENT KINEMATICS MODIFICATIONS AFTER TOOL-USE IN ADULTS GROUP (A) AND OLD ADULTS ONE (B).	149

LIST OF TABLES

TABLE 1. CRITERIA USED TO QUALIFY BODILY AND SPATIAL REPRESENTATIONS (MARTEL ET AL., 2016).....	41
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LIST OF ABBREVIATIONS

BR: Body Representation

BS: Body Schema

BI: Body Image

BSD: Body Structural Description

CNS: Central Nervous System

CD: Corollary Discharge

ERP: Event Related Potentials

GMP: Generalized Motor Program

JPS: Joint Position Sense

MGA: Maximum Grip Aperture

PPS: Peripersonal Space

RHI: Rubber Hand Illusion

TMS: Transcranial Magnetic Stimulation

TDJ: Tactile Distance Judgment

VET: Visual Enhancement of Touch

STATE OF THE ART

GENERAL INTRODUCTION

It is intuitive to think that the brain represents the body, this unique and extraordinary object, as a bottom-up process, where all what is needed is the processing of incoming somatosensory inputs. However, cognitive neuroscience and experimental psychology showed that this view is far too simplistic. Creating a representation of the body that is coherent and dynamic, through which we can interact properly with the environment, requires indeed the integration of information from different sensory modalities (Blanke, 2012). There is an ongoing debate concerning the exact number and type of body representations in the brain, but it is well-established that distinct, yet interacting systems are involved in representing the body. Thus, our ability to perceive our body is the product of a complex multisensory system, integrating information from vision, touch, proprioception, and vestibular systems. In addition, information from these sensory systems is tightly integrated with motor control systems, allowing us to effectively interact with the world. Finally, along with sensory and motor systems, our body is strongly related to our sense of self – including the feeling that a body part is our own, and agency, the belief that we can have control over our bodies (Medina & Coslett, 2016). In my thesis work, I focused my research activity on the body representation that is used and involved in action planning and execution, which is typically termed and referred to as the “*Body Schema*”.

The overall goal of my thesis is to gather a better understanding of the role played by sensory modalities, in particular proprioception and vision in body schema’s plasticity. A well-established approach to investigate this plastic phenomenon, and has been the focus of my research work, is the “*tool-use*” paradigm. The notion that using a tool modulates the user’s limb representation, introduced by Head and Holmes (Head & Holmes, 1911), has been around for at least a century. It is only recently that scientists uncovered empirical evidence for it (Iriki et al., 1996). It is now well documented that tool-use may update several representational aspects of the limb manipulating the tool and/or the peripersonal space around it (Farnè & Làdavas, 2000; Farnè, Serino, & Làdavas, 2007; Maravita, Spence, & Driver, 2003). In particular, tool-use has also been reported to modify the arm kinematics (Baccarini et al., 2014; Cardinali et al., 2009, 2012; Martel et al., 2019) and the spatial tactile processing (Cardinali et al., 2009; Sposito et al., 2012). Several changes across these different tasks and measures have been replicated and shown to be consistent, thus suggesting these measures can be used to characterize the concept of “tool incorporation”.

Yet, there are still several aspects of tool incorporation that have not been adequately addressed. Knowing that proprioception is thought to play a critical role in updating the body schema following tool-use, my research focused on three main unknown aspects of tool incorporation: Considering that physiological aging affects the offline submodality of proprioception 1) which proprioceptive submodality does contribute to body schema's plasticity following tool-use? Is it the online modality, which does not require any memory component, or the offline one? 2) In general, does tool-use affect forearm proprioception in the healthy and younger population? And if so, does this proprioceptive change coexist with a forearm representational lengthening after tool-use? Lastly, since vision has been recently shown to contribute to some aspects of tool-incorporation I asked: 3) does blindness affect the ability of the brain to update the body schema following tool-use?

To these aims, we developed three different studies using either kinematic measurements, proprioceptive assessment, or tactile localization task.

We first questioned the proprioceptive contribution to body schema plasticity. We tested older adults (average age 60.1 Y.O), who typically conserve their online proprioception intact, being though affected in the off-line, memory based component of proprioception; we used kinematics recording and analyses to assess the presence of the kinematic changes that are typically observed after tool-use among younger adults.

In second study, we tested the hypothesis that tool-use may induce proprioceptive changes in a healthy and young(er) adult's population: using a joint position sense test (JPS), we compared their proprioceptive acuity before and after tool-use. In addition, in the attempt to relate our results with a lengthening of forearm representation we required participants to perform a tactile localization task in order to understand the mechanism behind the plasticity of body schema following tool-use. Finally, the last axis of my thesis focused on the role of vision in the plasticity of the body schema: in particular, to test the hypothesis that the availability of vision may be critical for the body schema to be updated and possibly within certain period in life, we tested two populations of blind participants, either congenital or who lost vision later in life.

My dissertation is organized into three main sections: an introductory state of the art section, followed by the experimental work conducted during the past four years, ending with a general discussion of the work. The state of the art section will be organized into three main chapters. The first one will focus on motor control, to briefly review the internal models to which I will refer in the following sections. The second chapter will deal with the body representations, in

terms of their subdivisions, and the contribution of sensory modalities in body representations. Then it will focus on the case of tool-use and how this paradigm has been used to investigate body schema's plasticity. Finally, the third chapter will summarize the main points of this review of the literature, and introduce the dissertation's main hypotheses. The second part will then introduce the three experimental studies developed during my doctoral thesis to assess these main hypotheses. Finally, the last part will discuss the main results within the framework of body schema plasticity.

CHAPTER 1: MOTOR CONTROL

Reaching toward an object seems to be a simple action that we perform in everyday of our life. But this motor behavior is more of complex, thus relying on a relationship, and a transformation between sensory signals and motor command. This transformation is internally represented within the central nervous system (CNS) (Wolpert & Ghahramani, 2000). Thus, performing an optimal reaching movement requires the brain to turn a specific mental representation of the action into an appropriate movement with low costs. Studying motor control is an important issue to address in order to understand how mental representation of actions are built and updated into the brain in order to perform an optimal movement.

Motor control is classically described as relying on two modes of control: a feedforward mode that anticipates the properties of the overall action and a feedback mode that corrects during the execution of the movement the residual errors. Recently, models of motor control postulated that, due to some delay in sensory feedback processing, movements were likely to rely on pre-programming, and the feedback control plays a simple corrective role. More recently, models of motor control have been formalized as “internal models” and consider the forward model as predictive.

In the next part of this chapter, I will first introduce the theories of motor control, then I will focus on the new theory that led to the current “internal models” of motor control. This model suggests the presence of feedback and feedforward mode of control that I will present briefly. I will end up taking the example of a reach-to-grasp movement as I mainly examine this movement during my experimental work.

1. Theories of motor control

Different theories of motor control reflect philosophically varied views about how the brain controls movements. These theories often reflect differences in opinion about the relative importance of various neural components of the movement. For example, some theories stress peripheral influences, other may stress central influences. The first theory was the *reflex theory* proposed by the neurophysiologist Sherrington, according to which reflexes were the building blocks of complex motor behavior intended to achieve a common goal (Sherrington, 1920). This theory by designating the reflex as the basic unit of a behavior does not explain either spontaneous or voluntary movements as acceptable forms of behavior. Furthermore, it does not explain how a single stimulus may elicit a variety of responses depending on context and on descending commands or the ability to perform new movements.

Many theories were advanced after this one, from the *neuro-maturational theory* of development proposed by Gesell and McGraw in the 1940's (Gesell & Amatruda, 1947; McGraw, 1943), the *system theory* of Bernstein who states that “movements are controlled neither centrally nor peripherally, but rather are effected by interactions among multiple systems” (Bernshteĭn, 1967), the *ecological theory* proposed by Gibson (Gibson, 1979), the *dynamic action theory* that minimizes the importance of the idea that the CNS sends commands to control movements, but searches for physical explanations that may also contribute to the characteristics of actions. Progresses were made through the *motor learning theories* proposed by Adams (Adams et al., 1972) who postulated that learning relies on feedbacks, and correction of errors leads to a learning from practice in a closed-loop. However, fast or ballistic movements, such as a ball shoot, only provide feedback after completing the movement and therefore intrinsic feedback is not readily available and there is no time for it to help modify the movement.

Thus an *Open-loop Control Theory* was developed for these ballistic actions proposed by Schmidt (Schmidt, 1975). In this theory the Generalized Motor Program (GMP) is the basic form of our actions. It is called ‘generalized’ because the program can generate a variety of similar actions, such as forehand drop shots at a variety of heights or with varying amounts of power. According to this theory, four elements are stored in memory after an individual generates an action: 1) The initial conditions of the movement, such as the proprioceptive information of the limbs and body 2) The response specifications for the motor programs, which are the parameters used in the generalized motor program, such as speed and force 3) The sensory consequences of the response, which contain information about how the movement felt,

looked and sounded and the last one 4) The outcome of the generated movement or the response outcome, which contains information of the actual outcome of the movement with the knowledge of results. The recall schema of this theory provides adjustments to the GMP, the recognition schema would evaluate the response with the sensory consequences used during and after the response. The recall and recognition schema are tightly linked together, as they use the relationship between the initial conditions and response outcomes. They differ in that the recall schema is used to select a specific response with the use of response specifications prior to the action response, the recognition schema would allow us to evaluate the outcome of the response.

The follow up of Schmidt's theory (Schmidt, 1975) was made with the progression of computational sciences and math and led to the current model of motor control which is the "internal models of action" that I will be presenting in the following section of this chapter.

2. Internal models of action

Due to the extreme number of possible configurations for each human tasks (2^{600} configurations for 600 human muscles) (Lebon et al., 2013), it has been proposed that the human brain contains a simplified representations of the sensorimotor system in order to predict the future state of the body and control it. This is what is called the "internal model theory".

In this theory, sensorimotor actions are generally the contribution of feedforward and feedback control. Feedforward control occurs early before any sensory feedbacks arrive to the CNS; it is generally referred to as a predictive control. On the other side, when sensory inputs arrive, corrective adjustments will be applied to take into account possible perturbations and residual errors. This mode of control would rely on feedback processing. However, due to the long latencies of sensory feedback, instabilities persist in the system, and so to prevent such instabilities the system must include a model that predict the sensory feedback and hence the future state of the system, which is the forward model (Wolpert & Miall, 1996). In the next section of this chapter, I will be presenting some notions about feedforward and feedback control, but also the forward model.

Feedforward control: the feedforward control is a perfect schema when the perturbation is perfectly known. This type of controller prepares an adequate control for each disturbance. When a deviation from an equilibrium point is detected by the brain, feedforward control will quickly react to obtain a stable steady state. The term "feedforward" comes from the fact that this controller relies only on prediction to decide the action to be applied.

It has been largely demonstrated in the literature that the action of muscle begin before any inputs from the sensorimotor system (Lee, 1980). This anticipative control is called in the neuroscientific context the "feedforward motor control". This predictive control has been highlighted latterly during grasping and manipulating actions in 1993 by Johansson (Roland S. Johansson & Edin, 1993).

The internal model that includes association between motor commands, movements and external spaces plays a primordial role in motor control (Kawato, 1999). In the context of feedforward control, the inverse model is essential to be able to produce action based on a desired trajectory. Its main role is to generate a neural action based on the difference between the current state and the desired one. In other terms, the inverse model is exactly the inverse of the forward model. When the forward model seeks to estimate the consequence of an action on the movement, the inverse model estimates which action has to be applied to obtain the desired trajectory.

The inverse model had been experimentally highlighted via different movement of the hand with applying different mechanical perturbation (Hinder & Milner, 2003; Papaxanthis et al., 1998; Shadmehr & Mussa-Ivaldi, 1994). The movement of the hand is compared before, during and after these perturbations. It has been shown that the movement of the hand is altered after these perturbations. After some trials, the subject learn to plan the trajectory of the hand in order to make it as desired. This phenomenon has been explained by the adaptation of the inverse model of the hand.

Feedback control: As the movement proceeds, feedbacks coming from the sensory system are needed to correct movement's residual errors. However, the sensory feedbacks are too delayed to enable movement corrections, hence, to ensure on-line movement corrections sensory feedbacks are predicted through internal models (Bhushan & Shadmehr, 1999; Kawato, 1999; Wagner & Smith, 2008; Wolpert & Miall, 1996).The review of Shadmehr and Krakauer (Shadmehr & Krakauer, 2008) offers a comprehensive view on the recent internal models of motor control and their neural substrates.

As mentioned before, the inverse model is the base of the feedforward control. Yet, in the context of feedback control, two models are essential to realize this computation; the forward model and the state estimation. The need for these models comes from the facts that a considerable delay occurs in the sensory system. Feedback response could not be as accurate and fast as it is with information coming only from the sensory system. In the state estimation, both information coming from the sensory system and forward model are combined to form a belief about the state of the body and environment as shown in *figure 1*.

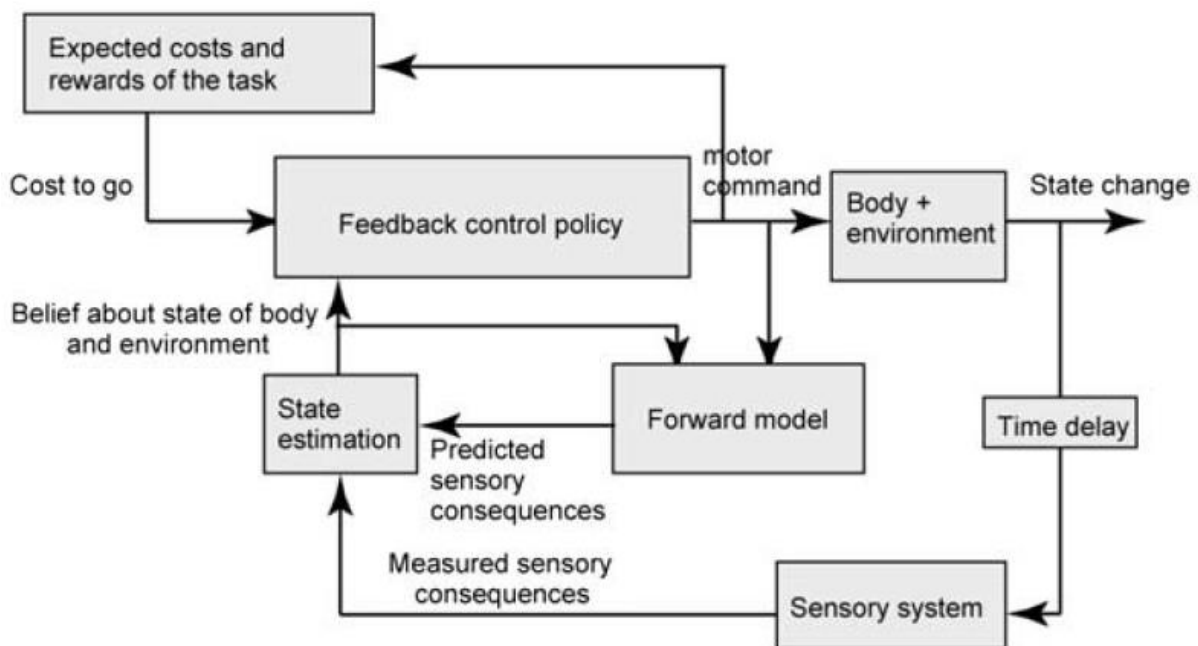


Figure 1. A schematic model for generating goal directed movements (Shadmehr & Krakauer, 2008).

The forward model mimics the behavior of the motor system in response to a motor command. It contains information about the body and the environment (Wolpert & Miall, 1996), it aims to have a model of the state of the sensorimotor system in order to predict the consequences of the actions on the current state of the body. The existence of a forward model is generally demonstrated via experiments on reaching and grasping movements. It has been highlighted that when a human manipulates an object between his index and thumb fingers, the force exerted is slightly larger than the weight of the object to prevent slipping (Flanagan & Wing, 1990; Johansson & Westling, 1984; Kawato, 1999). This force is predictive in such a way that no phase shift occurs between this force and the one caused by the weight of the object. This prediction of the sensory consequences of the action is insured via the forward model.

Based on that, the state of the body is updated and given this factor, the grip force is calculated, which is the force applied by the index and thumb fingers to grasp the object; then, by multiplying a friction coefficient and a safety factor, the necessary minimum level of grip force can be obtained (Kawato, 1999).

Lifting forces are a good illustration of the existence of the forward model and how this model is updated with experience. Eastough and collaborators (2007) showed that the mass of a to-be-grasped object can influence the action kinematics before any contact with the object. Grasping objects of increasing mass leads to a greater peak of grip aperture to ensure a secure grip position on the object, an increased lift delay to ensure appropriate grip force and finally, a reduced peak lift velocity to further ensure that the object is not dropped during the lift action (Eastough & Edwards, 2007). Before any somatosensory feedbacks are received, an adequate force is applied depending on the object, so that the more the object is heavy the more the fingers placement will be delayed (Salimi et al., 2000). Similar effects of object weight have been shown to emerge in 5 years old children to resemble the pattern observed in adults after 10 years old (Martel et al., 2020; Roy et al., 2013).

Schmitz and collaborators (2005) asked participants to lift for a light or heavy objects in several conditions. In the block condition in which objects of the same weight were repeatedly lifted, grip forces were perfectly scaled so more forces are applied for heavier objects, demonstrating the efficiency of the programmed motor output. In a second condition, in which light and heavy objects were regularly interleaved, that is when their weight could be anticipated, grip forces were still adapted but in a less precise way. In the last condition, the weights were randomly distributed. In such conditions, the grip forces could not be anticipated, participants defined a motor command for an unspecific weight. Participants used previous lifts to update the next ones, hence refining their motor command (Schmitz et al., 2005). In sum, it has been well established that adults keep sensorimotor memory of their actions: accordingly, when reaching toward an object a second time, the motor program will be updated and the prediction of the force to apply will be more precise (Chouinard et al., 2005; Gordon et al., 1993; R.S. Johansson & Westling, 1984; Schmitz et al., 2005).

To reduce noise inherent to both the sensory and motor signals and to take into account the uncertainty in the forward model, information coming from forward model are compared with those coming from sensory system to form a "state estimator". The difference between the predicted and sensed consequences of movement will serve as an indicator to tune the internal models and to adapt the motor control. The adaptation of motor control is realized by the inverse

model represented by feedback control policy in *figure 1*. Among all possible configurations that could accomplish the tasks, only the one who minimizes a cost function is selected (Cruse, 1986; Shadmehr & Krakauer, 2008).

3. Assessment of feedforward and feedback control

The contribution of feedforward and feedback control to the movement generation has been the subject of much debate. The last century saw the pendulum oscillate constantly between these two extreme conceptions. In this section, I am far from concluding the debate that dissociate them. In order to investigate the difference between feedback and feedforward control, many authors used specific paradigm to isolate one of them. Therefore, studying only the feedforward control, one has to cancel every sensory signal that goes to the feedback controller. In a reach-to-grasp manipulation, two sensory signals contribute to the feedback nature of the motor control: visual information about the hand and the object, and the proprioceptive information.

1. Visual effects

By canceling some visual inputs, we can isolate either the feedforward or feedback control. If the vision of the target is not allowed, no feedback is supposed to be present and no correction of the movement should be possible (isolating the feedforward).

Relatively preserved reaching movement in dark condition compared to reaching in normal one, indicates an efficient feedforward control. When a subject is asked to reach in the dark, he must rely on the mental representation of the target object and how much it is far from his body. Kinematic analysis where used in order to study the profile of movements in the dark in order to isolate the feedforward control (Desmurget & Grafton, 2003). The first contribution concerning this behavior was provided by Woodworth more than a century ago (Woodworth, 1899). He asked participants to perform repetitive movements with a hand-held pencil, and he reported three main results: (1) Movement accuracy degraded significantly with hand velocity when vision of the movement was allowed; (2) Movements executed with visual feedback involved small corrective movements at the end of the trajectory; (3) movement accuracy was not affected by hand velocity when participants executed the movement with their eyes closed. In an interesting development, Woodworth suggested that motor mastery was achieved by progressively eliminating final adjustments to rely exclusively on the "first impulse". Many studies confirmed and generalized his conclusion.

The influence of the vision of the hand initial position has been also investigated in many works (Desmurget & Prablanc, 1997; Prablanc et al., 1979; Rossetti et al., 1995). First studied by Prablanc and his collaborators in 1979 by comparing movement under two conditions: 1) Full open loop in which vision of the hand is not permitted and 2) Dynamic open loop in which static vision of the initial position of the hand is permitted. The authors reported that movement accuracy is better when initial vision of the hand is allowed. As mentioned in the review of Desmurget (Desmurget & Grafton, 2003), seeing the hand in its initial position allow to reset the bias of proprioceptive signals and by consequence the feedforward control aspect which occurs at the first moment of the movement (Desmurget, Rossetti, Prablanc, Jeannerod, & Stelmach, 1995; Desmurget, Vindras, Gréa, Viviani, & Grafton, 2000).

The role of dynamic vision on the feedback control has been studied in 80's (Beaubaton & Hay, 1986; Carlton, 1981) and results showed that the vision of the hand during the first part of the movement does not affect the accuracy of the movement compared to the condition where the hand is invisible. Carlton asked participants to point to a visual target with a stylus (Carlton, 1981). Five conditions were investigated based on the part of the trajectory physically occluded by a shield (0%, 25%, 50%, 75%, and 93%). No improvement have been signaled between 0 and 50 % conditions (Carlton, 1981). However, the work of Bard and collaborators (Bard et al., 1985) showed that an early effect of vision on the accuracy of the movement is present. The authors reported that even when the second half of the movement was occluded, a positive effect of the vision is detected. To separate the effects of hand vision in the initial position (feedforward control contribution) and the vision of the movement of the hand, light was turned on just after the movement onset (Blouin et al., 1993). Early effect was detected even when participants were not able to see their hand at rest, but only after the onset of the movement. It is also highlighted, that after the first half of the movement, visual feedback loop could be robust enough to correct error caused by the non-vision of the hand in the first half of movement (Desmurget & Grafton, 2003). Vision of the target allows making anticipatory action depending on the geometry of the object. For example the maximum grip aperture is directly depending on the size of the object, the bigger the object, the larger the maximum grip aperture will be (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Jeannerod, 1984; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991). Indeed, Sarlegna and collaborators highlighted the importance of the target position information to the online control of arm movements. The authors suggested that since proprioceptive information offers cues on hand position, visual input of

the hand might contribute to a lesser extent, as compared to vision of the target (see for review Sarlegna & Mutha, 2015).

It is difficult to make a real assessment of feedforward and feedback control just by modulating the vision of the target due to the fact that online correction occurs as soon as the subject receives visual feedbacks, preventing a clear dichotomy between feedback and feedforward (Desmurget & Grafton, 2003). The online corrections of motor control has been investigated by changing the target characteristics after the hand left its initial position. The delay between visual integration and the effect on the motor control is estimated at about 100 ms (Paulignan et al., 1991), and the delay for proprioceptive feedback integration appears to be around 80-100 ms (Desmurget & Grafton, 2000). Thus if we consider these values in regard to the movement duration typically around 400-600 ms in experimental set-up, then it seems impossible to use sensory feedback during the fastest part of the trajectory during a reaching movement (Desmurget & Grafton, 2003). Yet, the processing of visual and proprioceptive inputs are too slow to allow sensory feedback control when the hand location is changing rapidly. Thus, sensory feedback loop improves movement final accuracy by allowing fine control of the hand displacement at the very end of the trajectory of the movement when velocity is low. However at the same time, this sensory feedback will help human to gain experience and updating their forward models repertory (Calvo-Merino et al., 2006).

2. Proprioceptive effects

The assessment of feedforward and feedback motor control has also been studied through proprioceptive feedbacks either by examining movements in deafferented participants or in healthy subjects by modulating the object's weight. The earliest work (for review see Desmurget & Grafton, 2003) on this topic concluded that proprioception has limited effects on movements (Kelso et al., 1980). Kelso and colleagues asked participants to reach to a previously learned position with their thumb and index, a load could be unexpectedly applied during the displacement of their finger. Their results showed that subjects were easily able to perform the reaching, even when the thumb and index finger were temporarily deafferented by applying an inflated strap around the wrist joint. Several observations confirmed that deafferented patients are able to realize a wide range of finger movements with a remarkable accuracy (Rothwell et al., 1982). Desmurget & Grafton, in their review pointed on the important role of proprioception during movement planning, and reported that its absence during the movement itself produces limited effects on the overall goal of the movement (Desmurget & Grafton, 2003).

4. Kinematic profile of reach-to-grasp movement

Prehension is an everyday movement including two main components: a reaching component (also reported as “*transport component*”), and a grasping component (also reported as “*grip component*”). Each responds separately to different object properties remaining however tightly coordinated (Jeannerod, 1981, 1984). Kinematics (or the analysis of motion) was generalized in the early eighties by the neurologist and neurophysiologist Marc Jeannerod and led to revolutionary insights about the motor organization of the human prehension movements. Despite inter subjects variability, the kinematic of prehension movement appears highly reproducible. Several technical improvements were established in order to improve the measurement of the wrist velocity, acceleration and deceleration profile and the opening of the thumb and index during the grip phase. The sampling rate initially at 50Hz increased potentially to 3000Hz.

1. The reaching component of the hand toward the target-object involves a fast-velocity initial phase and a low-velocity final phase. The profile of the wrist velocity is characterized by a single bell-shaped peak, attesting the displacement of the arm toward the object. This peak starts with an increasing velocity that reaches a maximum value at about 40% of the total movement time (Chieffi et al., 1993; Jakobson et al., 1991; Jeannerod, 1984). The velocity peak divides the asymmetrical reaching-velocity profile into an acceleration phase and a deceleration phase. The acceleration peak reflects the maximum positive peak of the velocity’s derivative, and the deceleration peak is the maximum negative one that began after about 75% of movement time (Jeannerod, 1984) (see *Figure 2*). This phase involves proximal muscle activity of the shoulder and elbow, and during this phase the extrinsic object properties such as the position and distance of the object, together with object orientation are extracted (Smeets & Brenner, 1999).

2. The grasping component represents the shaping of the thumb and index as a function of the target object. The fingers start to progressively open from the starting position until they reach their maximum aperture (referred to as the maximum grip aperture) at about 60-80% of the movement time, that is during the wrist deceleration phase (Jeannerod, 1984; Paulignan et al., 1991). Then, the fingers close on the object, indicating the end of the movement. During this phase the intrinsic object properties, such as its size, shape, and weight are processed, distal muscle activity is particularly involved (Jeannerod, 1981, 1984). *Figure 2* summarize the kinematic profile of a classical reaching movement starting from a pinch grip position (at least in the majority of prehension studies) in order to reach and grasp a target on the table (here is a small white ball).

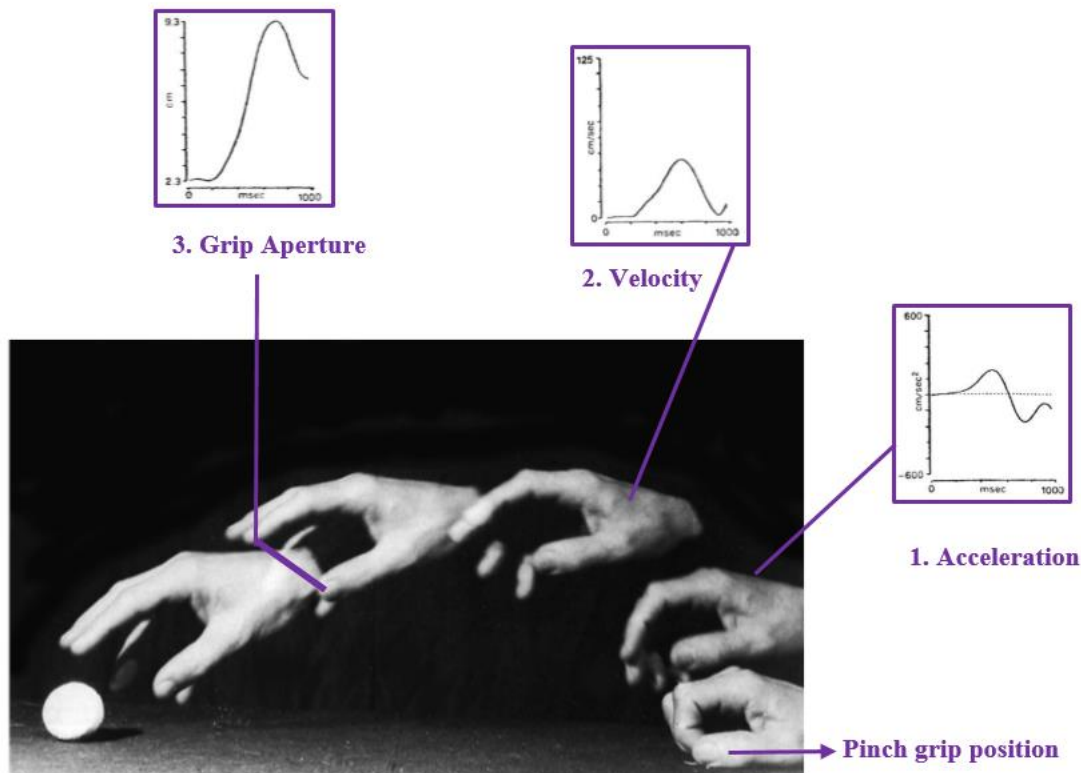


Figure 2. Kinematics of reach-to-grasp movement. Starting from a pinch grip position (index and thumb closed) 1. Acceleration and deceleration peaks profile of the wrist 2. Velocity peak profile of the wrist 3. Grip aperture profile corresponding to the grip component of the movement. *This illustration was used in several publications introducing the analysis of the movement of the hand* (from Marc Jeannerod, 1998, cover page of the French scientific magazine "La Recherche").

Feedback and feedforward models in a reach-to-grasp movement

During a reach-to-grasp movement toward an object, the feedforward system has to compute the size, form, shape, and texture of the object as well as its distance from the body in order to feed the motor program and execute the reaching movement. However, because residual errors remain in the motor program, feedbacks are use is in flight to adjust the action. Now, let's imagine the situation where the object is sliding off the table. In this case, the feedback control comes into play in order to give inputs about the direction and velocity of the object to allow an online correction of the motor command and grasp the object before it falls. During this movement, the acceleration of the wrist portrays the feedforward control while the deceleration portrays the feedback control. The online control occurs as soon as the system receives visual feedbacks, and online adjustments of the trajectory of the hand moving toward the object would appear very early after the acceleration peak, suggesting that accuracy is improved through feedback mechanisms (Desmurget et al., 2005).

In addition, during the grasping phase of the movement, visual feedbacks of the target object can be used to adjust the progressive closing of the fingers on the object, and this occurs in the deceleration phase of the reaching phase of the movement (Paulignan et al., 1991). According to Fitt's law movement duration increases as function of its difficulty (Fitts, 1954) and the width of the target (Bootsma et al., 1994) such that an decrease in object width increases the spatial accuracy demands on the transport component increasing in turn movement time.

CHAPTER 2: BODY REPRESENTATIONS

It is largely believed that in everyday life activities, humans rely on internal representations of the current spatial configuration of their body in order to appropriately guide movements and to make perceptual judgements about the location of the different body parts with respect to each other (Kammers et al., 2006). These body representations and the distinction between their different types has become the stock in trade of much recent work in cognitive neuroscience and philosophy (Gallagher, 1986; Pitron & de Vignemont, 2017; Schwoebel et al., 2004; Schwoebel & Coslett, 2005; Sirigu et al., 1991). The first part of this chapter will review the literature concerning the different types of body representations, the potential confusion between them, and how they are built. I will also consider the debate concerning the relationship between the different types of body representations. In the second part of this chapter, I will go through the multisensory contributions to the construction of body representations. In the last part of this chapter, I will report on the plasticity of body representations phenomena, focusing on the case of tool-use.

1. Definition of body representations

Different yet interacting systems are involved in representing our bodies in the brain. Hence, our ability to perceive our bodies is the product of a complex multisensory system, integrating information from vision, touch, proprioception, and vestibular systems. These information are tightly integrated with systems for motor control, allowing us to effectively act on our environment (Medina & Coslett, 2016). Along with sensory and motor systems, our bodies are strongly related to our sense of self, and hence including the feeling that a body part is our own, and so we can have control over it. Thus, in order to guide the movement of the body through space, the brain must constantly supervise the position and movement of the body parts in relation to nearby objects (Holmes & Spence, 2004). Such a monitoring requires integration of neural representation of the body or the “body representation” and of the space around the body or “peripersonal space”. The main interest of my review here is about “body representation”, but I will first recall here some essential notions of the “peripersonal space” in terms of definition and the triadic space taxonomy.

2. Peripersonal space and its taxonomy

The peripersonal space (PPS) is defined as the space immediately surrounding our bodies and in which objects can be grasped and manipulated (di Pellegrino & Làdavas, 2015; Rizzolatti et al., 1998). PPS is well accepted as the region of integration of somatosensory, visual and auditory information (Graziano & Cooke, 2006). The neurophysiological properties of PPS have been first discovered in non-human primates (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). Then numerous studies proposed similar representation of the PPS in humans (Brozzoli et al., 2006; di Pellegrino & Làdavas, 2015). The PPS can be added to the triadic space taxonomy described via a sensorimotor criterion: *the personal space*, occupied by the body itself, whose representation is mainly built by proprioceptive and tactile information, but also with the contribution of visual input about body-parts in the space; *the extra-personal space*, mainly based on visual and auditory inputs that convey information from the far space; *the peripersonal space*, mainly based on the integration of tactile and visual information coming from the body and the space immediately around the body, constitutes a privileged interface for the body to interact with nearby objects.

3. Subdivisions of body representations

The existence of mental several representations of the body, called body schema but also body image is widely accepted. However, there has been an extensive confusion about the number, nature and the properties of these notions due to the variety of ways we have of relating to our body (e.g. vision, touch, proprioception, motor behavior, semantic understanding, emotional affect etc.) and the variety of disorders of bodily awareness (De Vignemont, 2010). The dyadic taxonomy dichotomizes body representations (BR) into the Body Schema (BS), a sensorimotor representation of the body that guide actions, and the Body Image (BI), a representation not critical for action but rather perceptual, conceptual or emotional in nature (De Vignemont, 2006, 2010). The triadic taxonomy proposed by Schwoebel and others on the basis of dissociated symptoms and task performance among patients with different brain lesions, separates the Body Image into two distinct representations: the Body Semantics, which constitutes the conceptual and linguistic level of body parts for a functional purpose, and the Body Structural Description, which is a visuo-spatial map of body parts and their topological relationships, based primarily on vision, but also somatic perception (Schwoebel & Coslett, 2005; Sirigu et al., 1991). The description of clinical case patients, with specific cerebral lesion and different symptomatology, has largely contributed to establish the existence and define the critical features of different body representations. In the next section, I will present a review of the three main subdivisions

of the body representation; the body schema (BS), the body image (BI), and the Body Structural Description (BSD), with reference to their main sensory inputs, their properties and the accessibility of each, as reported in the existing literature.

3.1. Body Structural Description (BSD)

The body structural description is a topological map of locations derived primarily from visual information (Buxbaum & Coslett, 2001; Sirigu et al., 1991). Body Structural Description gathers structural information about location of body parts and is considered as mainly visuospatial and conscious (Martel et al., 2016). Recent findings suggest that autotopagnosia, a deficit following which patients have difficulties to localize and orient different parts of the body, may be attributable to a selectively impaired representation of the structure of the human body (here termed body structural description). Buxbaum and Coslett (2001) observed an autotopagnosic case of a patient with diffuse left hemisphere damage who had an impairment when asked to point to named or visually identified body parts on himself or others and when asked to match pictured body parts across changes in viewing perspective. Interestingly, though, this patient was able to perform the same task when asked to point to parts of animals and inanimate objects. These findings suggest that the ability to access structural descriptions of human body parts might be selectively disrupted (Buxbaum & Coslett, 2001). Vision plays an important role in building and updating this topological representation of the body (Tessari et al., 2012). Schwoebel and Coslett (2005) have reported the neural bases of the body structural description in the lateral left hemisphere, particularly in the left temporal lobe and in the posterior intraparietal sulcus. However, all authors agree on the difficulty in dissociating the neural bases of the different body representations, which might be due to the limited number of studies. As for example, both body structural description and the body image seem to be impaired following left temporal brain damage (Schwoebel & Coslett, 2005).

3.2. Body Image (BI)

The term Body Image was first coined by the Austrian neurologist and psychoanalyst Paul Schilder, in his book "*The Image and Appearance of the Human Body*" (Schilder, 1935). Body Image is characterized as a conscious, semantic and lexical representation of the body and its relationship with external objects, such as body part names, association between body parts and artifacts, and the function of body parts (Schwoebel & Coslett, 2005). Sirigu and his collaborators reported a selective preservation of the body image in an autotopagnosic patient who had a diffuse cerebral atrophy (Sirigu et al., 1991). This patient was able to view her own body, and was able to correctly answer questions that required her to indicate the body part's

function, as for example, what is the mouth for. Buxbaum and Coslett also noted that an autotopagnosic patient, reported selective preservation of body image because he perfectly performed when asked to point to body parts on himself when they were associated with items of clothing or grooming tools (Buxbaum & Coslett, 2001).

Body image appears to rely heavily on visual inputs, for that, the term body image is more and more generally employed to refer to the visually based representation of the body shape and size, in other words, the visually based metrics of the body (Martel et al., 2016). Body image is conceptualized as an offline representation that structures first-person body perception in the visual modality, but also in the somatosensory one (Miller et al., 2014). Concerning the neural basis of body image, studies revealed impaired body image following temporal lesions (Schwoebel & Coslett, 2005). Body image has been mainly referred to the concept of body ownership in studies of the rubber hand illusion, which consists in tricking the subjects to believe that a fake rubber hand is their own, by brushing their unseen hand synchronously with a fake hand (Kilteni et al., 2015).

3.3. Body Schema (BS)

Head and Holmes were the first to introduce the term of “postural schemata” (Head & Holmes, 1911), to refer to a continuously updated representation of the posture of the body:

“By means of perceptual alterations in position we are always building up 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 brings every fresh group of sensations evoked by altered posture into relation with it. Immediate postural recognition follows as soon as the relation is complete” (p.187).

Since then, several studies used the term of body schema to referred to the body representation for action (Baccarini et al., 2014; Cardinali et al., 2009; Maravita et al., 2003; Martel et al., 2019; Sposito et al., 2012). Cardinali and colleagues defined the body schema as the body representation that the brain uses to plan and execute an action, by storing the information about the body for appropriate motor control, as, for example, the position in the space of the different body segments, their structure, and their size (Cardinali et al., 2012). Body parts’ spatial positions and dimensions are computed by afferent information coming essentially from somatosensory modalities, such as proprioception, kinesthesia and touch, in a sensory-motor schema (Cardinali et al., 2009; Martel, Cardinali, Roy, & Farnè, 2016). For that, no successful action is possible without a representation of one’s bodily parameters (De Vignemont, 2010).

Body schema is conceptualized as an online sensorimotor representation of the body that is continuously updated by postural changes (Miller et al., 2014) mainly unconscious (Martel et al., 2016).

Many neurological clinical cases were explained as a consequence of a disruption of the Body Schema. Deafferentation is one of them (Brochier et al., 1994; Halligan et al., 1995). This clinical condition is characterized by a loss of somatosensory information that can affect a portion of the body. There are two types of deafferentation; a central one that arises after a lesion of the cortical/subcortical areas devoted to somatosensory processing, and a peripheral one that is a consequence of a lesion in the peripheral nerves. In both cases, body-parts localization in space, as well as appreciation of postural changes, are no more possible without constant visual control. Also, apraxia which is a disorder of skilled movements that cannot be explained by peripheral deficits or motor weakness and deafferentation (De Vignemont, 2010) may be also considered as a Body Schema disruption (Buxbaum, Giovannetti, & Libon, 2000; Schwoebel & Coslett, 2005). Patients with apraxia show mislocalisations of the goal of their actions (e.g., brushing chin rather than teeth), and demonstrate greater deficits in locating the hand that will carry the action (e.g., difficulty to wave hello, tying shoes, typing on a computer) (Haaland et al., 1999). Concerning the neuroanatomical bases of body schema, few studies reported that the body schema depends on the activity of the somatosensory cortices, the intraparietal sulcus (Corradi-Dell'Acqua et al., 2009) and the dorsolateral frontal cortices (Schwoebel & Coslett, 2005).

In summary, the body schema allows us to locate our body and its part in space, and is constantly updated in an unconscious way. Thus, the body schema is essentially sensorimotor in nature (Martel et al., 2016), and studies characterized it with either somatosensory or motor tasks. Body schema is thought to be a highly plastic representation of the body parts that can be used to execute or imagine executing movements (Medina & Coslett, 2010). Several paradigms have been proposed to test the body schema and to assess its plastic properties, such as kinematics recording (Cardinali et al., 2009; Cardinali et al., 2012; Martel et al., 2019), arm bisection (Sposito et al., 2012), tactile localization (Cardinali et al., 2009; Sposito et al., 2012), tactile distance perception (Anema et al., 2009; Canzoneri, Ubaldi, et al., 2013), motor imagery (Baccarini et al., 2014; Schwoebel & Coslett, 2005) or ballistic movements by pointing to proprioceptive or tactile targets on the insensate arm (Rossetti et al., 2001). Table 1 summarize the criteria that differentiate the three types of body representations adopted by Martel and

collaborators in their review, namely the sensory inputs, the format and the functional properties, and the accessibility to each representation.

	Body Schema	Body Image	Body Structural Description
Sensory inputs	Proprioception Kinesthesia Touch	Multisensory (Vision, Audition)	Somatosensory Vision Verbal
Format	Somatosensorimotor	Visuospatial	Visuospatial
Functional properties	Metric body knowledge for action (Body part's position and size)	Body percept, Concept and affect; Visual metrics of the body	Structural information about body parts location
Accessibility	Mainly unconscious	Conscious	Conscious

Table 1. Criteria used to qualify bodily and spatial representations (Martel et al., 2016).

With this overview about the subdivisions of body representations in mind, I will now turn the focus in the next part on the contributions of the sensory modalities to body representations.

4. The contributions of multiple sensory modalities to body representation

By interacting with the environment, we are constantly confronted with information related to our own body. Bodily sensations originating from tactile, vestibular and proprioceptive senses contribute a major information flow about the way we are constituted as a living being (Longo & Haggard, 2010), providing information about the posture and the location of our body parts at a certain moment in time. By exploring the world and moving through the environment, we are exposed also to relevant exteroceptive visual and auditory inputs that can additionally contribute to inform our brain about our body features, such as its length and thickness, and also interoceptive senses such as heart beat and respiration (Covarrubias et al., 2017). Altogether, this flow of inputs constructs the variety of body representations (De Vignemont, 2010; Schwoebel & Coslett, 2005) detailed in the section above. Indeed, given the multisensory nature

of body representations, in the next part, I will nevertheless try presenting each sensory modality separately, and its contribution to body representations. I will stress the role played by visual and proprioceptive inputs because these two modalities are of interest in the experimental part of my thesis.

4.1. Visual contribution to body representation

In humans, vision has been considered traditionally as the dominant sense, as well as the most reliable in terms of spatial perception (Rock & Victor, 1964). Several studies have shown that the visual information about the body influences body representations at several stages of visual processing. Visual enhancement of touch (VET) is a perceptual phenomenon by which tactile acuity is enhanced when viewing the body but not when viewing the non-body object. In experiments VET is typically done by measuring the tactile acuity of the participants by asking them to judge the orientation of tactile gratings (Kennett et al., 2001; Konen & Haggard, 2014; Serino et al., 2007). In the experimental condition, participants can view their hand but not the orientation of the grating, and in a control condition they view a non-body object appearing at the same location of their hand, along with a visual event corresponding to the grating approaching the hand. The VET effect is reported by an enhancement of the tactile acuity when viewing the body and not when viewing the non-body object. Evidence emerging from event related potentials (ERP) (Cardini et al., 2011), transcranial magnetic stimulation (TMS) studies (Fiorio & Haggard, 2005) and somatotopic specificity (Serino et al., 2007) suggest that VET involves visual modulation of early somatosensory processing.

Most interestingly, visual experience during development seems to shape the way in which touch is processed in adulthood (Röder et al., 2004). Touch is coded in anatomical but also in environmental external spatial reference frame, in such a way that one can study the existence and weight attributed to either reference frame by comparing performance in uncrossed (the typical hand posture) with that of crossed-hand posture. In one of their studies on this issue, Röder and collaborators found that the tactile localization performance of late, but not of congenitally blind people was impaired by crossing the hands, a behavioral effect that is considered to depend upon the normal development of a spatial sense of touch. Thus, the performance of the late blind group was indistinguishable from that of sighted participants. Their study showed that blind people who had never had any visual experience were unaffected by changes in hand posture, and they suggested that the possibly default localization of touch in external space is dependent upon visual experience though independent of the instantaneously availability of vision. Because late-blind adults experienced the same crossed-

hands effect of the sighted ones, this study also indicates that once established, the existence of a visual frame of reference may stay for life.

Vision can also have remarkable effects in a situation like the rubber hand illusion (RHI) where a visuo-tactile-proprioceptive conflict is introduced (Botvinick & Cohen, 1998). It consists in inducing the illusion of owning a fake rubber hand, by brushing the participants' unseen hand synchronously with a fake hand (see, for review Kilteni et al., 2015; Tsakiris, 2010). This illusion occurs only when the rubber hand is placed in an anatomically plausible posture (Tsakiris & Haggard, 2005), suggesting that the illusion is modulated by top-down signals originating from the representation of one's own body (Pavani & Zampini, 2007). Interestingly, blind individuals are immune to this illusion (Nava et al., 2014; Petkova et al., 2012). Here they used a "non-visual version of the rubber hand illusion" where the experimenter moves the participant's left index finger so that it touches the rubber right hand while simultaneously touching the corresponding site on the participant's right hand. Petkova and colleagues (2012) suggested that blind individuals with impaired visual development have a more veridical percept of self-touch and a less flexible and dynamic representation of their own body in space when compared to sighted subjects. Thus, they speculated that the multisensory brain systems that re-map somatosensory signals onto external reference frames are less developed in blind individuals and therefore don't allow efficient fusion of tactile and proprioceptive signals from the two upper limbs into a single illusory experience of self-touch as in sighted individuals (Petkova et al., 2012).

Marino and collaborators showed that vision of the body not only affects somatosensory perception, but can also affect the internal model of the body used for motor control (Marino et al., 2010). They measured the maximum grip aperture (MGA) parameter of grasping movements while subjects viewed a real size, an enlarged or a shrunken image of their own hand while reaching to grasp a cylinder. Their results showed that in the enlarged view condition, the MGA decreased relative to the real size view, as if the grasping movement was actually executed with a physically larger hand, thus requiring a smaller grip aperture to grasp the cylinder. In contrast, no effect was found for the reduced view condition. This asymmetry may reflect the fact that enlargement of body parts is experienced more frequently than shrinkage, notably during normal growth (Pavani & Zampini, 2007). In the same vein, Bernardi and collaborators results suggested that visual information pertaining to the size of the body is accessed by the body schema and is prioritized over the proprioceptive input for motor control (Bernardi et al., 2013), by measuring the same parameter of the grasping movement (i.e, MGA),

and showing the same pattern of modification going in the same direction of Marino and collaborators (modified kinematics of grasping movement; reduction of the MGA) .

The last point that I want to address in this section is that even if visual information helps specifying our body proportions, large distortions are nevertheless present. In her famous study, Linkenauger and collaborators made a series of experiments showing that there are dramatic and systematic distortions in the perception of bodily proportions, as assessed by visual estimation tasks whereby participants were asked to compare the lengths of two body parts (Linkenauger et al., 2015). Interestingly, distortions were not observed when participants estimated the extent of a body part relative to a non-corporal object, such as a wooden cylinder. These findings also highlighted that the magnitude of distortions was correlated to the tactile sensitivity of the body part. For example, participants overestimated the length of their torso, which touch-wise is a less sensitive body part compared to the arm. This may further suggest that people perceive visually the relative size of their body parts as a function of each part's relative tactile sensitivity and physical size. In the next section, I will discuss the contribution of touch and proprioception in representing the body in the brain.

4.2. Tactile and proprioceptive contributions to body representation

Before starting addressing the contribution of touch and proprioception to body representations, I deem necessary to briefly provide some basic knowledge about proprioception and its measures. In the following section, I will present the proprioceptive system in some details because of its pivotal role in the hypothesis tested in my doctoral work. I indeed investigated the effect of tool-use on proprioception (chapter 2 of the experimental part).

4.2.1. *Proprioceptive system and its measures*

The term “proprioception” was coined by Sherrington in 1906 (Sherrington, 1920), and the history of proprioception has been subject of discussions for hundreds of years. In my work, I will be referring to proprioception as the ability to sense the position of limbs (joint position sense or stataesthesia), and the sense of limb movement (motion sense or kinaesthesia). These two senses are essential for optimal motor control, coordination and stability during movements of daily life activities (Li & Wu, 2014). I should also mention another sub-modality of proprioception which is the sensation of force (Hillier et al., 2015) that is reported in literature but remains outside the scope of my work.

4.2.2. Proprioceptive signals

Proprioception rely on the central integration of afferent and efferent signals. Among the afferent signals, there are the muscle spindles, the Golgi tendon, the cutaneous receptors and the joint receptors.

The *muscle spindles* are stretch receptors within the body of a muscle that provides an afferent input signal about the length of the muscle, but also its velocity during its contraction (Proske & Gandevia, 2012). Muscle spindles are composed by intrafusal muscle fibers of which there are three types: dynamic nuclear bag fibers (bag1 fibers), static nuclear bag fibers (bag2 fibers), and nuclear chain fibers (see figure 3). The dynamic nuclear bag fibers are sensitive mainly to the rate of change in muscle length, while the static nuclear bag fibers signal only a change in muscle length but not the rate of that change, same as for the nuclear chain fibers. The intrafusal muscle fibers are at both ends connected to either tendinous ligaments or extrafusal fiber, namely contractile proteins. So intrafusal fibers are stretched or shortened correspondingly, when extrafusal fibers change length (Proske, 2009).

Ends of the bag fibers extend beyond the capsule while chain fibers lie within the limits of the capsule. There are two types of sensory endings found in muscle spindles: group Ia afferent fibers terminate as primary endings, making spiral terminations around the nucleated portions of all three intrafusal fiber types, and group II afferent fibers terminate as secondary endings, lying to one side of the primary endings and supplying bag 2 and chain fibers. The primary endings respond to its speed and the size of a muscle length change. They belong to the fastest axons as they are myelinated. They contribute both to movement and the sense of limb position. Secondary endings are only sensitive to length and not to velocity, so they contribute only to the sense of the position. These endings have smaller axons and thus slower conduction speed. Gamma dynamic (γ dynamic) fusimotor fibers innervate bag 1 fibers, while gamma static (γ static) fusimotor fibers innervate bag 2 and chain fibers (Proske, 1997).

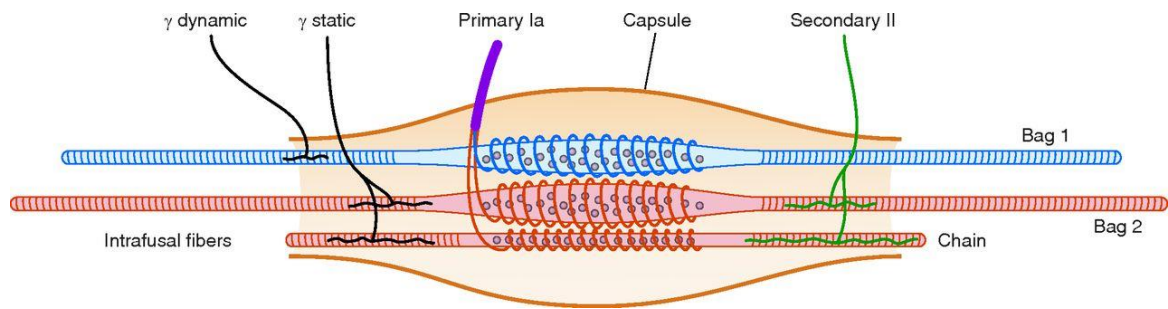


Figure 3. Diagrammatic representation of the mammalian muscle spindle (taken from Proske, 1997).

Golgi tendon organ afferents are suggested also to contribute in proprioception, by including the senses of force and heaviness (Hillier et al., 2015). The Group Ib axon penetrates the receptor capsule and branches, each branch terminating on a tendon strand that is attached to a muscle fiber. A typical tendon organ has 10 or more muscle fibers attached to it, each fiber belonging to a different motor unit. Contraction of a motor unit supplying a tendon organ stretches the tendon strand to which its muscle fiber is attached, generating activity in the Ib axon (Proske & Gandevia, 2012) (see figure 4).

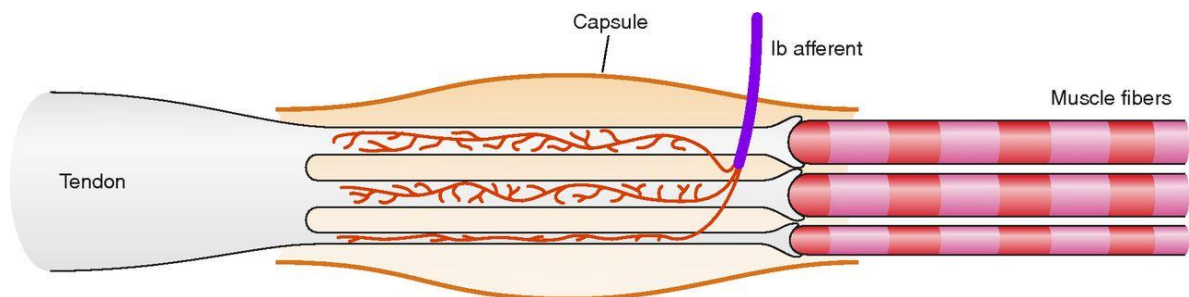


Figure 4. Diagrammatic representation of the mammalian Golgi tendon organ (taken from Proske & Gandevia, 2012).

Receptors in the skin (*cutaneous receptors*) also contribute to joint position and motion sense, including mechanoreceptors, thermoreceptors, and nociceptors and serve such modalities as touch, pressure, vibration, temperature, and nociception (pain) (Darby & Frysztak, 2014; Hillier et al., 2015) (see figure 5). It has become increasingly apparent that mechanoreceptors in the hairy dorsal skin of the human hand might also play a role with respect to proprioception

(Edin, 2001). It was reported that a large majority of the mechanoreceptors on the back of the hand are activated by movements at nearby joints (B. B. Edin & Abbs, 1991). And the way in which they respond, suggests that they provide high-fidelity information about joint movements.

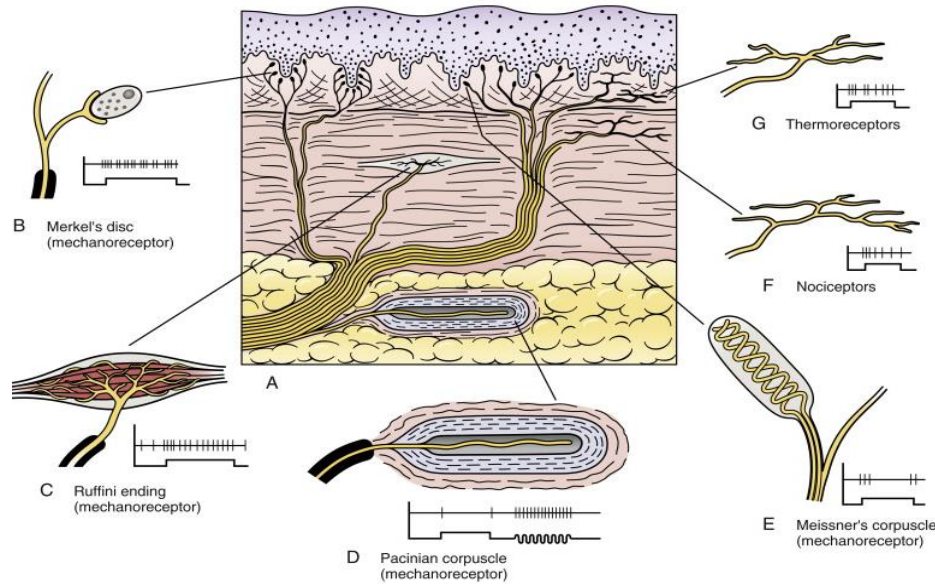


Figure 5. Types of cutaneous receptors (Daly et al., 2013).

Joints receptors also contribute to proprioception (Burke et al 1988), but this contribution is thought to be minor, and limited to provide kinesthetic information, and this is likely to be of significance only when muscle spindle afferents cannot contribute to kinaesthesia.

There is evidence that proprioception is also centrally tuned through *efferent signals*. These efferent signals have been reported under different terms such as “corollary discharge”(Crapse & Sommer, 2008; Farrer et al., 2003), motor corollary discharge (CD) (Requarth et al., 2014), all underlying the same mechanism, where the information is derived from the motor commands of cortical areas involved in planning (area 6, supplementary motor cortex and pre-motor cortex) and executing movements (area 4, primary motor cortex). These CD generated during the movement are not used to directly generate movements but, instead, interact with the processing of self-generated sensory signals. CD transiently modulate self-generated sensory responses and can help distinguish between self-generated and externally generated sensory information (Poulet & Hedwig, 2007). These internally generated CD signals and proprioceptive feedback represent separate sources of information either of which could, in

principle, be used to distinguish between external versus self-generated sensory input (Requarth et al., 2014).

4.2.3. Assessment of proprioception

Concerning the assessments of proprioception, there is no gold standard testing to date. Typically, various tests have differentiated between 2 main proprioceptive functions: detection of static position and detection and replication of motion (Hillier et al., 2015). The threshold of movement detection is also reported in some studies (Thelen et al., 1998).

Most likely due to its simplicity, the most commonly used proprioceptive assessment is the “joint position matching task”, consisting in having the participant to reproduce a given (reference) joint angular position. This test can be performed in a remembered or in a concurrent condition (Goble, 2010). In the remembered condition, the subject’s limb is actively or passively displaced to the reference position and held immobile for 2–3 s (Adamo et al., 2009; Bullock-Saxton et al., 2001), 5 s (Deshpande et al., 2003; Goble et al., 2009; Pickard et al., 2003), or 15 s (Kaplan et al., 1985) prior to being returned to its starting position. Next, the subject is asked to reproduce the reference joint position with either the same (ipsilateral) or other (contralateral) limb based on proprioceptive memory (see figure 6). In the concurrent condition, the procedure is identical, but the limb is not returned to the start position. The limb is left immobile in the reference position while the participant uses the contralateral limb to match the reference position, based on concurrent proprioceptive information coming from both limbs.

The advantage of the latter procedure is that it avoids the potential confound of decreased memory abilities, particularly in the case of testing the elderly. Yet, it should be noted that this procedure may have a limitation in the latter population: because it relies heavily on interhemispheric communication, poor performance in this task may not reflect a deficit in proprioception, but decreased integrity of the corpus callosum, a known consequence of aging process (Ota et al., 2006).

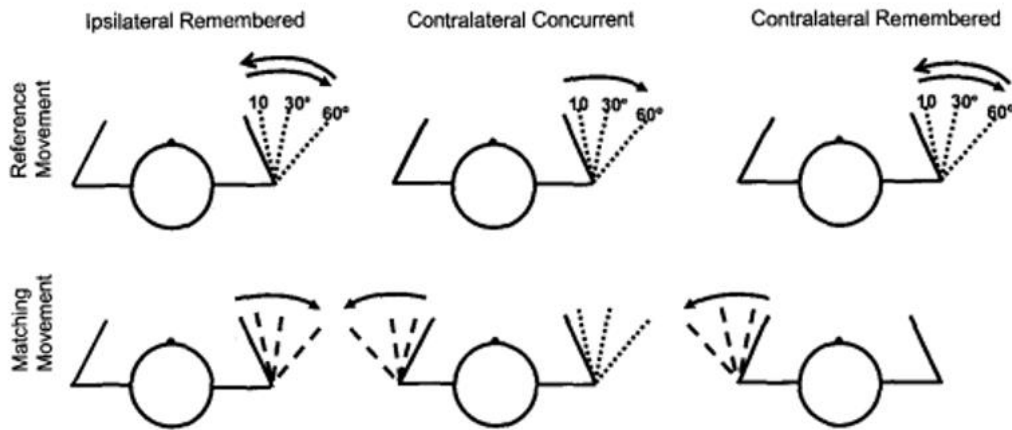


Figure 6. Proprioceptive assessments in three different conditions (Adamo et al., 2007).

The most commonly reported measure of proprioceptive acuity is the absolute error, which is the difference between the reference position and the position reproduced by the participant. This proprioceptive acuity index has been proven highly sensitive, for example, in distinguishing relatively small differences between younger and older adults (Adamo et al., 2009; Goble et al., 2009; Westlake et al., 2007). Because of the presence of a number of task-related factors in this test, though, the error values are not considered as “normative cut-offs” in the literature, but merely indicative of elderly proprioceptive acuity. For example, in studies of both young and older adults, greater errors have been observed for the matching of reference posture (i.e., angle amplitude) located farther from (i.e., larger than) the starting joint position (Kaplan et al., 1985). In addition, position matching ability appears to be enhanced under weight-bearing conditions (Bullock-Saxton et al., 2001) and when active versus passive matching occurs (Pickard et al., 2003). In the next part, I will present the available review about the contribution of touch and proprioception to body representations.

Perceiving the location of our body in the external space is essential for the interaction with the environment and for the construction of a coherent sense of self (Longo & Haggard, 2010). Proprioceptive signals generating from muscles, joints, and skin provide information about the position of the joint (Sherrington, 1920), contributing to a representation of body posture as firstly highlighted by Head & Holmes (Head & Holmes, 1911).

To perceive the absolute position of body parts in external space, however, this postural information has to be combined with information about the size and shape of the body segments that connects the joints (Longo et al., 2010) already stored in our brain as metric properties of body parts. For example, if two touches were delivered on either side of the hand, then determining the distance between the touches requires a reference to a representation of hand

size already established in the brain. Taylor-Clarkes and his collaborators used a visual distortion procedure in order to give their participants a prolonged visual experience of magnified forearm and minified hand, and found that perceived tactile distances were expanded on the forearm and compressed on the hand when comparing to baseline (Taylor-Clarke et al., 2004). Tajadura-Jiménez and his collaborators suggested that tactile perception is referenced to an implicit body-representation which can be informed also by auditory feedback (Tajadura-Jiménez et al., 2012) (See the section of auditory contribution to body representation). In contrast, several studies have shown that tactile distance perception is not solely determined by high-level representations, but is also shaped by low-level aspect of somatosensory processing and is subject to distortions. The Weber illusion is possibly the most famous example; in this illusion, the perceived distance between touches on a single skin surface is larger on regions of high tactile spatial resolution than those with lower acuity. This illusion suggests that tactile size perception involves a representation of the perceived size of body parts preserving characteristics of the somatosensory homunculus (Longo & Haggard, 2011; Taylor-Clarke et al., 2004). Similar distortions were found in proprioception. In their study, Longo and Haggard asked participants to rest their unseen hand still and point with the other hand to the locations of fingertips and knuckles (Longo & Haggard, 2010). Their results showed a distorted map of the hand, with shorter fingers, as compared to their actual size, and larger hand than it really was.

Along the same vein, muscle tendons vibration, which alters proprioceptive information about limb flexion/extension, has also been used to investigate the influence of proprioception on body representation. De Vignemont and collaborators, elicited a proprioceptive illusion, the left index of subjects was either elongating or shrinking by vibrating the tendon of the biceps or triceps muscle of their right arm while subjects grasped the tip of their left index finger (de Vignemont et al., 2005). They asked subjects to estimate the distance between two simultaneous tactile contacts on the left finger during tendon vibration, and found that tactile distances felt bigger when the touched body part felt elongated (proprioceptive illusion produced by vibration of tendon). Control tests showed that the modulation of touch was linked to the perceived index-finger size induced by tendon vibration. Their results show that the perception of tactile objects is referenced to an implicit body representation and that proprioception contributes to this body representation. In analogy to tactile distance perception, the absolute location of body parts in space also requires a reference about the state of the body. In addition, Pinocchio illusion is a great example on the influence of proprioception on body representation. In this illusion,

participants grasp their nose while a vibration is induced on either the biceps or the triceps of the grasping arm, generating an illusion that the nose was either lengthening or coming inwards the head depending on which muscle was stimulated (de Vignemont et al., 2005; Lackner, 1988).

4.3. Auditory contributions to body representation

At odds with the large body of evidence supporting the contribution of vision, touch and proprioception to the body representations, less attention has been devoted to the potential contribution of audition. Yet, in everyday life our body movements can generate impact sounds that contain 360° spatial information of high temporal resolution. Given this strong connection between auditory signals and corporeal actions, it has been proposed that audition may also plays a role in body representation. Tajadura-Jiménez and collaborators (Tajadura-Jiménez et al., 2012) asked participants to knock on a surface with their right arm while it was progressively extended sideways. In synchrony with each tap, participants listened via headphones to a knocking sound that could originate at either the real or an increased distance from the real knocking location. In the critical condition, the sound originated at twice the distance at which participants actually tapped. After exposure to this condition, tactile distances tested on the right arm, as compared to distances on the reference left arm, felt bigger than before the exposure. No evidence of changes in tactile distance was found at the quadruple tapping sound distance, or when auditory feedback was asynchronous. These results suggest that tactile perception is referenced to an implicit body representation which is also informed by auditory information.

Sound can also have an effect on the perceived body as a physical entity. Senna and her collaborators in their “hand marble illusion” showed that hearing the sound produced when an object hits marble in synchrony with the feeling of an object hitting one’s own hand, makes this hand to be felt stiffer and heavier (Senna et al., 2014). This novel bodily illusion demonstrates that the perceived material of our body, likely among the most stable attribute of our bodily self, can be quickly modified (here in the case of few minutes) through multisensory integration processes.

4.4. Vestibular contributions to body representation

The vestibular system plays a continuous role in most everyday adaptive behaviors, including motion perception, posture control and orientation in the surrounding space. Vestibular signals are widely distributed to a number of cortical regions, all multisensory and none of them seems to represent a primary “vestibular” cortex, similar to other modalities such as vision and audition (Fundamental Neuroscience for Basic and Clinical Applications, 2018). The vestibular system provides the brain sensory signals about the three-dimensional head rotations and translations movements, that are of importance for postural and oculomotor control, as well as for spatial and bodily perception and cognition (Lopez & Blanke, 2011). In addition, several somatosensory areas receive vestibular inputs and vestibular stimulation has been shown to modify the perceived length and width of the hand (Ferrè et al., 2013; Lopez et al., 2012) suggesting that vestibular signals can contribute to the building of body representations. For example, Ferré and colleagues (2013) investigated the effects of galvanic vestibular stimulation (GVS) on the localization of a stimulus on the skin of the hand (defined as somatoperception) and on the implicit representation of the hand size and shape (defined as somatopresentation) (Serino & Haggard, 2010). Vestibular inputs influenced the localisation of tactile stimuli on the hand: touches on the dorsum of the hand were perceived as shifted toward the wrist (Ferrè et al., 2013). In the same vein, Lopez and collaborators (Lopez et al., 2012) performed an experiment using a tactile distance comparison task between two body segments (hand and forehead) during caloric vestibular stimulation. They found that objects contacting the hand were judged longer during the stimulation compared to a control stimulation. In a second experiment, they asked participants to localize four anatomical landmarks on their left hand by pointing with their right hand, and found that the perceived length and width of the left hand increased during caloric vestibular stimulation with respect to a control thermal stimulation. The overall results thus seem to suggest that the body representation temporarily adjusts as a function of vestibular signals, modifying the representation of the hand size. They further indicate the need for current models of body representations and bodily self-consciousness to take vestibular signals into account.

I will now turn the focus on the plasticity of body representations and particularly on the updating of the body representation for action, which I will refer to as “body schema” hereafter. I will consider specifically the plasticity of body schema that has been reported to follow the use of tools: skillful tool-use is of outmost importance for several animal species and particularly for humans. Understanding the cognitive processes that may underpin body schema

plasticity following tools, also referred to as tool incorporation, or tool incorporation, and may help understanding the reasons why humans are highly sophisticated tool masters.

5. Tool-use: a clue to investigate body schema plasticity

A well-established approach to understanding the mechanisms underlying the construction of body representations consists in characterizing the conditions that modulates them. Through my research work, I adopted the tool-use paradigm to manipulate the body representation. The idea that tool-use may provoke the incorporation of the used tool in the users' body representation has been known for longer than a century (Head & Holmes, 1911). And thus, in recent years neuroscientists provided empirical evidence supporting it (Iriki et al., 1996).

In the following section, I will particularly review three main approaches used to investigate tool incorporation and its behavioral consequences: action kinematics, tactile localization, and forearm bisection tasks.

Our group has contributed converging evidence for the plasticity of body schema following tool-use by leveraging the kinematic analysis of reach-to-grasp movements (Cardinali et al., 2009; Cardinali, Brozzoli, Finos, et al., 2016; Cardinali et al., 2012; Martel et al., 2019). The seminal work of Cardinali and colleagues reported that tools modulate the kinematics of the limb that manipulates it (Cardinali et al., 2009); they recorded free-hand reach-to-grasp movement toward an object in neurologically healthy participants, before and after 10 minutes of tool-use. The session consists on using a tool composed by an ergonomic handle (9 cm) with a lever, a 33 cm-long rigid shaft and an articulated 'hand', composed by two curved fingers (10 cm each), for a total weight of 300 grams. Overall, holding the grabber allowed a functional elongation of the arm by approximately 40 cm that allow to reach and grasp an object located 40 cm further away than the subject's reachable space. Squeezing the lever (vertically) made the "fingers" of the tool closing (horizontally). The kinematics profile of participants' subsequent free-hand movements was modified after a single, brief tool-use session. Indeed, kinematics allows to precisely characterize both the temporal and spatial features of a hand action, which typically requires some time to start (reaction time), to achieve a maximum of acceleration (latency of the acceleration peak), velocity (latency of the velocity peak) and deceleration (latency of the deceleration peak). Together with these so-called transport parameters of the action (as they characterize the displacement of the hand in vicinity of the target object), kinematics allows for defining the grasping parameters (opening and closing of the fingers on the object to be grasped) on both the temporal and spatial domain (e.g., the latency

to achieve the maximum ginger opening). Once the object stably in hand (no further change in finger's aperture), kinematics also allows defining the end, and thus the total duration, of a movement (movement time). When considering Cardinali et al's study, free-hand movement kinematics after tool-use (as compared to before tool-use) displayed longer latencies of velocity and deceleration peaks, which were in addition reduced in amplitude, and a longer movement time. The grasping component of reach-to-grasp movement (maximum grip aperture of the thumb and index finger) was immune to any change induced by the tool-use session, suggesting a modification of the representation of the forearm, but not of the hand. Interestingly, these changes parallel the kinematics differences displayed by subjects having long(er) arms, when compare to those having short(er) arms. Indeed, people with longer arm showed longer latencies and reduced peaks of velocity and deceleration, as well as longer movement time (Cardinali et al, 2009; Martel et al, 2019). These results provided evidence for tool incorporation into the arm representation and thus body schema plasticity. Remarkably, tool-use effects generalized to pointing movements, despite the absence of specific pointing training using the tool, further supporting the conclusion that the tool was incorporated in the representation of an elongated arm in the body schema.

Converging evidence was provided within the same study (Cardinali et al., 2009) by asking participants to quickly point with their left index fingertip to an anatomical landmark of their right arm (elbow, wrist, or middle fingertip) which was randomly touched by the experimenter. Results showed that subjects pointed to the elbow and wrist as if they were farther apart from each other after the tool-use session. Interestingly, the distance between the wrist and the middle fingertip did not change. This results are in line with those observed from the kinematic pattern of results, a change being present in the transport component of the free-hand reach-to-grasp movement, but not in the grip component.

In more recent works, Baccarini and colleagues found that mere mental simulation of tool-use induced a similar change in (part of the same) kinematic parameters found in overt motor execution (Baccarini et al., 2014). In their study, they asked neurologically healthy participants to perform free-hand reach-to-grasp movements before and after a session of motor imagery performed with either a tool elongating their arm length or, as a control, with their hand alone. Crucially, kinematics of free-hand movements was affected after tool-use imagery, but not hand-use imagery, in a way similar to that previously documented after actual tool-use (Cardinali et al., 2009) with longer latencies and reduced peaks of transport component of the movement. These findings constitute the first evidence that tool-use imagery may be sufficient

to affect the representation of the user's arm. Noteworthy, participants were briefly familiarized with the tool, they could see it and handle it the day before the experiment, and so both visual and proprioceptive information's were possibly at stake in producing the effect following mental tool-use imagery.

In a related study, Cardinali and coworkers leveraged the tool-use paradigm to ascertain whether a given sensory input modality may guarantee a privileged access to body representation (Cardinali et al., 2011). To this aim, they asked healthy subjects to localize three anatomical landmarks on their right arm, before and after using the same arm to manipulate a tool. In addition to this classical task-dependency approach, they assessed whether preferential access to the body schema could depend upon the way positional information about forearm targets was provided. Participants performed either a verbally or a tactually driven version of a motor and a perceptual localization task. Results showed that both the motor and perceptual tasks were sensitive to the update of the forearm representation, but only when the localization task (perceptual or motor) was driven by a tactile input. This pattern reveals that the motor output is not sufficient per se, but has to be coupled with tactually mediated information to guarantee access to the body schema. These findings shade light on the action–perception models of body representations and underlie how functional plasticity may be a useful tool to clarify their operational definition.

Indeed, studies on representational plasticity following tool-use have primarily focused on the act of using the tool, but whether the tool's morphology also serves to constrain plasticity needs investigation. Miller and collaborators ran two experiments that varied in term of tool morphology; one tool was similar to the hand in the first experiment, while the tool in the second experiment was similar to the arm (Miller et al., 2014). They asked participants to perform a tactile distance judgement task (TDJ) between pairs of points applied to their tool-using target body surface and forehead (control surface) before and after tool-use. When considered in the framework put forward by Cardinali (2011) reported above, this combination of task and modality (i.e., tactile input and a perceptual output) might be considered as granting access to the body schema. They reported a significant representational plasticity in hand shape when the tool was morphologically similar to a hand but not when the tool was arm-shaped. Conversely, significant representational plasticity was found on the arm when the tool was arm-shaped, but not when it was hand-shaped. These results indicate that morphological similarity between the tool and the effector may constrain the body representational plasticity that is induced by tool-use. In addition, the results of Miller (2014) are in keeping with that finding that kinematic

changes have been reported to be selective for transport component when a mechanical grabber elongating the arm by some 40 cm was used (Cardinali et al, 2009). They also suggest that the grasping component of the movement could be selectively affected, after using a hand-shaped tool. This prediction was confirmed by our group, by asking participants to reach and grasp an object using tools that elongated the hand, but not the arm. Cardinali and colleagues (2016) asked participants to use Pliers, to be acted upon by the index and thumb fingertips, and Sticks, taped to the same two digits, to grasp the same sized object. The two tools were equivalent in terms of morpho-functional characteristics, providing both fingertips the same amount of elongation. However, they imposed different sensori-motor constraints on the acting fingers. They used kinematic analysis to compare the profile of free-hand movements performed before and after the use of both tools. Their results showed that both tools were effective in inducing changes in the grip component, which in addition were compatible with the hand being represented as bigger. Importantly, these effects were selective for the grasping, as the transport component parameters were not affected by the use of either tool. Furthermore, the different sensori-motor constraints imposed by Pliers and Sticks over the hand, induced differential updates of the hand representation: Sticks selectively affected the kinematics of the two fingers they were taped on, whereas Pliers had a more global effect, affecting the kinematics of fingers not recruited during the use of the tool. Altogether, these results suggest that tool-use induces a rapid update of the hand representation in the brain, not only on the basis of the morpho-functional characteristics of the tool, but also depending on the specific sensori-motor constraints imposed by the tool.

More recently, a study by Miller and colleagues supported the idea that incorporation phenomena are body-part specific (Miller, Cawley-Bennett, et al., 2017). Their study investigated whether tool-induced recalibration of tactile perception on the hand transfers to the cheek. This hypothesis was postulated based on the proximity of the representation of the hand and face in the primary somatosensory cortex (Farnè et al, 2002, Muret et al, 2014). He used the same task (TDJ) used in his previous work (Miller et al., 2014) and asked participants to verbally estimate the distance between two tactile points applied to either their hand or face, before and after using a hand-shaped tool. His results showed that tool-use recalibrated tactile distance perception on the hand but left perception on the cheek unchanged. This finding provides support for the idea that incorporation of the tool into the body representation of action is body-part specific.

On the other hand, Maravita and collaborators introduced a novel behavioral task to assess for tool-incorporation effects on the plasticity of the body schema. They used a forearm bisection task, consisting in having participants to estimate the mid-point of their forearm before and after 15 minutes of tool-use (Sposito et al., 2012). The results showed that the mid-point was estimated to be more distal (toward the hand) following tool-use as compared to pre tool-use training. This pattern of result is compatible with an increased representation of the participants' forearm length. Control experiments showed that this result was not due to a mere distal proprioceptive shift induced by tool-use, and failed to appear following the use of a 20 cm-long, non-functional tool. These results strongly support the point that, body-space interactions requiring the use of tools that extend the natural range of action, entail measurable dynamic changes in the representation of body metrics. Interestingly, Maravita and collaborators recently used the same paradigm to investigate the impact of different actions onto tool incorporation (Romano et al., 2019). In this study, they tested how different actions using the same tool can impact on subjective metric representation of the body. They hypothesized that any specific modulation effects of the subjective metric of the limb using the tool is critically determined by the pattern of motor programs required by the use of the specific tool. They adopted the same paradigm of forearm bisection mentioned above, and they did it before and after two different types of training that selectively maximized either proximal or distal movements of the arm, while the other hand was kept stationary. Their results showed that the perceived midline didn't change for the stationary arm, while a proximal shift was observed when the training involved more movements of the shoulder, and a distal shift when the training with the tool induce more movements of the wrist and fingers. Control experiments confirmed that different types of motor training induce different effects on body representation. These results suggest that the motor pattern is important to determine the direction of the perceived changes in body metric representation, and the morphological and functional aspects of the tool and the goals of the task further affect such changes.

Recently our group investigated the role of proprioception and vision in the plasticity of body schema, through a kinematic analysis approach applied to a deafferented patient (Cardinali, Brozzoli, Luauté, et al., 2016), or to healthy, blindfolded participants (Martel et al., 2019). In the following section I will relate on these two studies that opened several questions that I addressed during my doctoral work.

5.1. The role of proprioception

Cardinali and colleagues tested whether the phenomenon of tool incorporation is possible in the absence of proprioception. To this aim, they studied a patient with right upper-limb deafferentation (Cardinali, Brozzoli, Luauté, et al., 2016). They analyzed the kinematics of free-hand reach-to-grasp movements before and after tool-use session, in three sessions over a period of 2 years. In the first session, before tool-use, the kinematics of the deafferented hand was disrupted. Similarly, the first movements with the tool showed an abnormal profile that tended to normalize at the end of the session. Subsequent free-hand movements were also normalized. At session 2, 6 months later, the patient exhibited recovered free-hand kinematic profile, additionally showing changes in grasping kinematics after tool-use, but no sign of tool incorporation. A follow-up 2 years later, further confirmed the normalized kinematic profile and the absence of the typical pattern taken as an indication of tool incorporation.

This study provided evidence for the fundamental role of proprioception in the update of the body schema. But does tool-use affect proprioception of the limb using the tool? Proprioception has indeed been advocated as the main contributing sensory modality to the building of the body schema and the deafferented case study reported above seems to indicate its presence is indeed crucial. Yet, whether physiological changes in proprioception may affect the tool-use dependent plasticity of the body schema remains unknown. Indeed, proprioception is known to undergo modifications with healthy age (Boisgontier et al., 2012; Bullock-Saxton et al., 2001),

Physiological aging of the proprioceptive system

Structural and functional decline of the somatosensory system occur with aging and contribute to possible postural instability, which may have catastrophic and disabling consequences of high fall-risk and their related injuries (Shaffer & Harrison, 2007). Sensory information about the status of the body flows primarily from the proprioceptive, hearing, cutaneous, visual and vestibular systems.

Age has an impact on proprioception (Bullock-Saxton et al., 2001), and if degraded or lost, it may contribute to a loss of movement control where the person must then rely on visual input for feedback and feedforward process, resulting in a difficulty of learning novel tasks, improving or even maintaining the quality of movements (Shumway-Cook & Woollacott, 2007). Presbypropria or the age-related proprioceptive impairment as defined by Boisgontier (Boisgontier et al., 2012) might be due to a change in muscle architecture, such as loss of intrafusal fibers and fusimotor neurons and denervated spindles. Presbypropria might influence the responses of spindles to passive and active lengthening, hence changes in tendon

properties, are likely to alter tendon organ responses and change therefore the equilibrium between muscle tension and tendon organ discharge (Narici & Maganaris, 2007).

When it comes to assessing the proprioception of elderly population, the contralateral concurrent matching test should be the one preferred to the remembered conditions in order to get more specific results (Boisgontier et al., 2012), and eliminate the extra variable of memory implicated in the remembered conditions.

In the light of these age-dependent physiological changes in proprioception, one could enquire about the contribution of proprioceptive modalities in the update of arm representation following tool-use. In trying answering this question, I developed the first of the studies that I will present in the experimental part of this dissertation.

5.2. The role of vision

The most recent study from our group on this issue, provided empirical evidence that the plasticity of body schema can take place without resorting to any visual inputs (Martel et al., 2019), thus suggesting that somatosensation may be sufficient to trigger body schema plasticity. In this study, they compared movement's kinematics in healthy but blindfolded participants when reaching to grasp an object before and after the same type of tool-use used in previous work (Cardinali et al., 2009). The results showed longer latencies and reduced peaks in the arm transport component parameters after the tool-use session, consistent with an increased length of arm representation. Also similarly to the previously reported work, whereby visual feedback was available to subjects, no changes were found in the hand grip component parameters. In addition, correlation analyses revealed similar kinematic signatures in naturally long-armed participants. Moreover, as no effect was observed on a task requiring the explicit estimate of the participants' forearm, these findings were taken to indicate that tool-use effects are specific for the implicit level of arm representation (i.e., the body schema). These findings demonstrate that somatosensation is sufficient for incorporating a tool that has never been seen, nor used before (Martel et al., 2019).

Yet, to my knowledge there is no study investigating tool incorporation phenomena in a blind population, whereby the possible role played by vision in in the development of body estimate updating during tool-use. In trying answering this question, I developed the last of the studies that I will present in the experimental part of this dissertation.

CHAPTER 3: RESEARCH QUESTIONS AND HYPOTHESES

Along this non-exhaustive review of the literature on motor control and the body representations, we recalled that, to efficiently and accurately control our actions, a coordination between the body and the external world is necessary, including an efficient integration of feedback information. Models of motor control posit that information about the predicted position of the body, provided by copies of motor plans, is integrated with estimates of current body position using feedback from the body estimates (Shadmehr & Krakauer, 2008) or the body representations as suggested recently in the cognitive neuroscience field (Martel et al., 2019). Therefore, there seems to be a tight link between body representations and motor control. Thus, performing actions accurately requires the integration of information about not only the environment and the goal of our action, but also about our body size, position and shape. That means that our body representation should be quickly updated to integrate such information.

It has been proposed that one way to understand this updating phenomenon may consist in studying the kinematics consequences of performing actions with tools. Tool-mediated actions indeed require transferring motor control from the body to the artifact, thus allowing to test for the potential updates in the body estimate, used for motor control. Tool-use has been used in several studies, not only using kinematics as an index, but also the effects of tool-use on tactile perception and body size perception, and has since proven a viable way to assess the plasticity of body representations.

As reported in detail in the previous section, using a tool that extends arm length leads to its (at least partial) incorporation into the representation of the arm that manipulates it. Accordingly, after reaching actions done with a tool, the difference in subject's kinematics profile of their own hand, freed from the just used tool, was comparable to that observed when comparing the actions of persons having long arms and short arms. Kinematics profile displayed longer latencies and decreased peaks of the transport component of the reach-to-grasp movement, similar to people having physiologically longer arms. Across several studies, tactile localization tasks also revealed that subjects tended to localize points on the arm more farther apart after tool-use, and tended to localize the midpoint of their forearm as being more distal, reflecting (at least partial) incorporation of the tool into the representation of their arm that used it.

Still, the precise role and relative contribution of sensory inputs from vision and somatosensation for such plasticity to take place, is not well understood. If proprioception

seems necessary to update the body representation for motor control, it remains unclear whether different aspects of proprioception may contribute, and to what relative extent, to this plasticity. Indeed, older adults around 50/60 years of age are known to lose at least part of the memory-based component of proprioception: Yet, tool-use ability has not been reported to be hampered in the typical population and this age, suggesting that tool-use plasticity may rely more on the online aspect of proprioception, known to be spared till old age (Adamo et al., 2009). More generally, does tool-use affect proprioception per se? Finally, while blindfolding sighted subjects can reveal whether proprioception is sufficient for body schema plasticity following tool-use (Martel et al., 2019) it cannot answer the question of the role possibly played by vision in a conclusive way, as by definition sighted subjects have had a life-long history of visual perception. Is the lack of visual experience detrimental to the development of this body representation plasticity? These are the questions that have motivated the experimental work of my doctoral thesis.

Hypotheses

The next part will present the work I have done for these past three years. It will be organized in three different experimental chapters. The general objective of my doctoral work was to investigate the role of vision and proprioception in body schema plasticity through kinematic analyses and tactile localization task.

First, as proprioception plays a crucial role in the update of body schema, we aimed to question which modality of proprioception contributes more to this update. We tested older adult's population, and after assessing their proprioceptive modalities through a joint position sense test, we analyzed the kinematics of their free-hand reach-to-grasp movements before and after the use of long-mechanical grabber that extends their arm length during reaching movements toward an object.

We expected that older adult's would conserve their online proprioceptive modality knowing that this one does not require a memory component that might be affected by age, and thus the offline one would be impaired. Moreover, we hypothesized that if kinematics of free-hand reach-to-grasp movements changed after tool-use session in the same way as in the adults population (longer latencies and decreased peak of transport component of the movement), then the online modality of proprioception is crucial for body schema plasticity. Also, we expected that the control condition, which rules out the effect of fatigue due to test-retest effect, would not show the same kinematic patterns, and thus that the effect would be specific to our tool condition.

The second experimental chapter presents a study on the effect of tool-use on the proprioception per se. The motivation of this study was to investigate proprioception closely knowing that it plays an important role in the update of body schema. We tested the proprioception of healthy adult's population (through a JPS test) before and after tool-use session and a control weighted wrist session. Given the importance of proprioception for the control of tools, we hypothesis that tool-use would affect proprioception of the limb that used it and not the stationary one, and that this effect will be specific to the tool-use session. Then, we wanted to relate our results concerning the acuity changes to the changes in the body schema following tool-use by using a tactile localization task, a paradigm known to reflect the plasticity of arm representation length after tool-use. Therefore, we investigated whether this change in proprioception coexist with an increase arm representation after tool-use. Given the importance of proprioceptive information for the body schema, we expected changes in acuity should accompany changes in the length of the arm representation.

The last experimental chapter investigated the role of vision on body schema plasticity in blind population. We tested congenitally and late blind groups by analyzing their kinematic profiles of free-hand reach-to-grasp movement toward an object before and after tool-use session, in order to determine whether having experienced vision during childhood is an absolute requirement for body representation plasticity to occur. We hypothesize that loosing vision early in life or during development would affect the ability of the body schema to be updated and that vision is a fundamental element for the plasticity phenomena.

EXPERIMENTAL PART

CHAPTER 4: ONLINE PROPRIOCEPTION FEEDS
PLASTICITY OF ARM REPRESENTATION FOLLOWING
TOOL-USE IN HEALTHY AGING

Online proprioception feeds plasticity of arm representation following tool-use in healthy aging

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ABSTRACT

Following tool-use, the kinematics of free-hand movements are altered. This modified kinematic pattern has been taken as a behavioral hallmark of the modification induced by tool-use on the effector representation. Proprioceptive inputs appear central in updating the estimated effector state. Here we questioned whether online proprioceptive modality that is accessed in real time, or offline, memory-based, proprioception is responsible for this update. Since normal aging affects offline proprioception only, we examined a group of 60 year-old adults for proprioceptive acuity and movement's kinematics when grasping an object before and after tool-use. As a control, participants performed the same movements with a weight - equivalent to the tool-weight- attached to their wrist. Despite hampered offline proprioceptive acuity, 60 year-old participants exhibited the typical kinematic signature of tool incorporation: Namely, the latency of transport components peaks was longer and their amplitude reduced after tool-use. Instead, we observed no kinematic modifications in the control condition. In addition, online proprioception acuity correlated with tool incorporation, as indexed by the amount of kinematics changes observed after tool-use. Altogether, these findings point to the prominent role played by online proprioception in updating the body estimate for the motor control of tools.

INTRODUCTION

Adapting the environment to our needs often requires the use of tools. Whether for leisure or for work, tools are present in many aspects of our life, but their skillful control represents a challenge for our sensorimotor system. Imagine a surgeon using tools with different sizes. The control exerted over the tip of different tools ought to be accurately adapted. To achieve this flexible control, the state of the effector (e.g., its position, dimensions, etc.) needs to be continuously monitored. Such body estimate (or schema) is a critical element of motor control: it provides the internal model with the information needed to execute actions correctly ^{1,2}. Furthermore, it can update this information if rapid changes of the effector occur, as when grabbing objects with tools that temporarily increase the size of the effector (i.e., arm + tool length). It is indeed well-established that using arm-elongating tools induces a temporary increase of the arm-length representation, as indexed by changes in movement kinematics and tactile perception ³⁻⁹.

In the last decade, tool-use has emerged as a valuable paradigm to investigate plasticity of the body representation for action ^{6,10-12}. In a typical pre/post tool-use paradigm, participants are required to reach and grasp objects with their hand, before and after using a mechanical grabber that elongates their arm's reaching capabilities. The pre-post tool-use comparison has consistently outlined a pattern of kinematics changes in the transport phase of the ensuing movements (noteworthy, without the tool), displaying smaller peaks (of acceleration, velocity and deceleration) and longer latencies (of the same peaks). This pattern has been taken as the kinematic signature of the so-called tool incorporation into the body state estimate. Indeed, movements performed after tool-use are akin to those observed when reaching with a naturally longer arm ^{6,13}. Not least, the kinematic pattern generalizes to free hand movements that were not specifically exposed to tool-use (e.g., pointing instead of grasping ⁶), as well as to positions not exposed to tool-use (e.g., orthogonal to tool-use ¹³).

Recent studies showed that both vision and proprioception contribute to updating the arm estimate following tool-use ^{8,13}. Most importantly, proprioception is both sufficient and necessary to trigger such a plasticity, as proprioceptive deafferentation prevents updating the metrics of the arm estimate guiding our action ¹⁴. Overall, these findings point toward a critical role played by proprioception in lengthening the estimated metrics of the arm, which would thus influence subsequent movements execution, when the tool is no longer held ¹¹.

This raises the question of whether online, or memory-based proprioception is responsible for the changes in free hand kinematics following tool-use. While the need for a constant monitoring of the effector state would favor the online access hypothesis, an alternative possibility is that stored information is used, as tool-use effects are observable while the tool is no longer held. Proprioceptive information may indeed be accessed in real time (online) or, conversely, stored in order to be accessed later on (memory-based). This is reflected in different tasks for testing position sense. In the contralateral matching task, a joint displacement is experienced and the participant has to reproduce the joint angle with his/her opposite arm. In the ipsilateral matching task, the participant experiences the joint displacement only for a few seconds, then his/her arm is put back in the starting position and he/she has to reproduce the joint angle with the same arm. While the contralateral task typically taxes the online access to proprioceptive information, the ipsilateral task taxes the offline access to proprioception¹⁵. Interestingly, normal aging is known to affect proprioception^{15,16}, but it does not affect it evenly. Old adults are reported with a deficit regarding mostly the offline, as compared to the online access to proprioceptive inputs^{17,18}.

Here we leveraged this dissociation to test whether tool-use effects on kinematics are mediated by online or offline proprioception processes. To this aim, we first assessed upper limb proprioceptive sensitivity in young adults (average 25 y-old), as well as in group of old adults (average 60 y-old) with both ipsilateral and contralateral matching tasks. Several factors are at play in position matching tasks, as people may code for both joint position and kinaesthetic amplitude of the movements (see¹⁹). For the sake of comparison, here we leveraged tasks that already documented the off-line/online dissociation in old adults^{17,18}. Based on previous work¹⁷ we predicted that old participants would report less accurate proprioception in the ipsilateral, but not in the contralateral matching task. Then, we assessed the same group of old participants for the emergence of the changes in movement's kinematics that have been typically reported after tool-use¹¹. In line with the hypothesis that efficient motor control requires online monitoring of the effector state estimate, we predicted that typical kinematic signature of tool-use should be observed in old adults with impaired offline, but spared online access to proprioception.

METHODS

Participants

Twenty participants (six males and fourteen females, mean age = 60.1 ± 5.05 , range 51-69) took part in this study. Three participants were left-handed as assessed through the Edinburgh Handedness Inventory ²⁰. None of the participants reported neurological or psychiatric disorders nor peripheral vascular disease or peripheral neuropathy. All participants had a normal or corrected-to-normal vision and audition and a normal range of upper limb movements. Participants provided written informed consent prior taking part in the study, which was approved by the French ethics committee (Comité de Protection des Personnes Sud-Est IV). All experimental procedures conformed to the Helsinki declaration ²¹.

Experimental design

The experiment consisted of two sessions run over two consecutive days. A cognitive and proprioceptive assessment were performed on the first day, together with the first experimental session that could be the tool-use session or the weighted-wrist session. The second day was an experimental session only (tool-use or weighted-wrist), the order of sessions being counterbalanced across participants. As in previous work using this paradigm ⁶, the weighted-wrist session served as a within-subject control condition aimed at ruling out any unspecific fatigue effects due to the weight of the tool, or test-retest effects, on arm representation. For this reason, the weight attached to the wrist in the weighted-wrist session equaled the weight of the tool. If fatigue or repeated testing affects arm kinematics, this would be captured by this control session.

Cognitive and proprioceptive assessment

We assessed participants global cognitive function by administering the Mini Mental State Examination (MMSE) test ²². The mean score value was 27.5, ranging from 24 to 30, thus highlighting no cognitive impairment in any of our old adult participants. In addition, a selection of five subtests of the Rivermead Assessment of Somatosensory Performance (RASP) ²³ was used to exclude any obvious somatosensory impairment. The mean score value was 98.3 %, ranging from 87.5 % to 100 % of correct answers, confirming the absence of pathological impairment.

Further, we assessed online and offline proprioception through the *joint position matching task* performed in remembered and concurrent tasks ²⁴. As there is no standardized scale, or cut-off to define proprioceptive impairment, we additionally enrolled and tested both offline and online

proprioception in a group of 20 young healthy adults (ten males and ten females, mean age = 25.4 ± 3.2 , range 21-35). Young participants completed the proprioceptive assessment only. This allowed us to assess whether our old participants' population was indeed impaired as compared to young participants. They also provided written informed consent prior taking part in the study, which was approved by the French ethics committee (Comité de Protection des Personnes Sud-Est IV), and all experimental procedures conformed to the Helsinki declaration. We used a custom made apparatus similar to the one of Allen et al ²⁵. In this setup, participants are blindfolded and their forearms are strapped to lightweight paddles aligned with the elbow joint. An inclinometer attached to each paddle directly displayed the value of the angular flexion of the elbow (precision value = 0.1°).

In the ipsilateral remembered matching task, an experimenter raised the paddle supporting the participant's forearm to a target angle (20° or 40° elbow flexion from the initial position) in the sagittal plane, maintained this position for 5 seconds as assessed by a stopwatch, and returned the arm to its initial position. The participant was then required to reproduce the position with the same forearm, with the use of proprioceptive memory. The experimenter maintained a steady pace for each trial. This task was done similarly for both arms: Ipsilateral Remembered Right (IRR) and Ipsilateral Remembered Left (IRL).

In the Contralateral Concurrent Matching task (CCM), a similar procedure was undertaken involving the passive displacement of the right forearm to a target angle (as before 20° and 40° elbow flexion from the initial position). In this task, the dominant forearm was set and maintained in the target position while the participant performed the matching with his/her non-dominant forearm.

In all tasks alike, each target angle was administered 6 times in a randomized order for a total of 12 trials per task. We used the absolute matching error value, as a measurement of proprioceptive acuity to compare both groups ¹⁶. For the three tasks, the absolute error value on every trial was computed as the unsigned difference between the reproduced/matched angular position and the reference one ($20^\circ/40^\circ$). The error values units were in angular degrees.

Tool-use and weighted-wrist sessions

The two sessions each consisted in three phases: a pre- and post- phase separated by a tool-use or a weighted-wrist phase, all performed in a dimly illuminated and sound-attenuated room. Participants were comfortably seated in front of a table, on an adjustable chair, their dominant hand closed in a pinch-shaped grip on a starting switch. They had to reach and grasp a wooden block (10 * 2.5 * 5cm, weighing 96g) placed on the table at a distance of 35 cm along the sagittal axis, in line with participants' right shoulder (or left shoulder for left-handed participants). Importantly, as in previous studies using the same paradigm^{4,6,13,26,27}, the object was always located inside the arm's reaching space, thus preventing potential confounding effects of tool-use on space representation.

Pre and post phases

In the pre and post phases, participants performed two tasks: a free-hand reach-to-grasp task and a forearm length estimation task. While the former informs about unconscious changes in arm body estimate via kinematics, the latter informs about subjective, conscious changes in arm length representation¹³. Free-hand reaching movements and forearm estimation tasks were proposed in a counterbalanced order across participants (*Figure 1*).

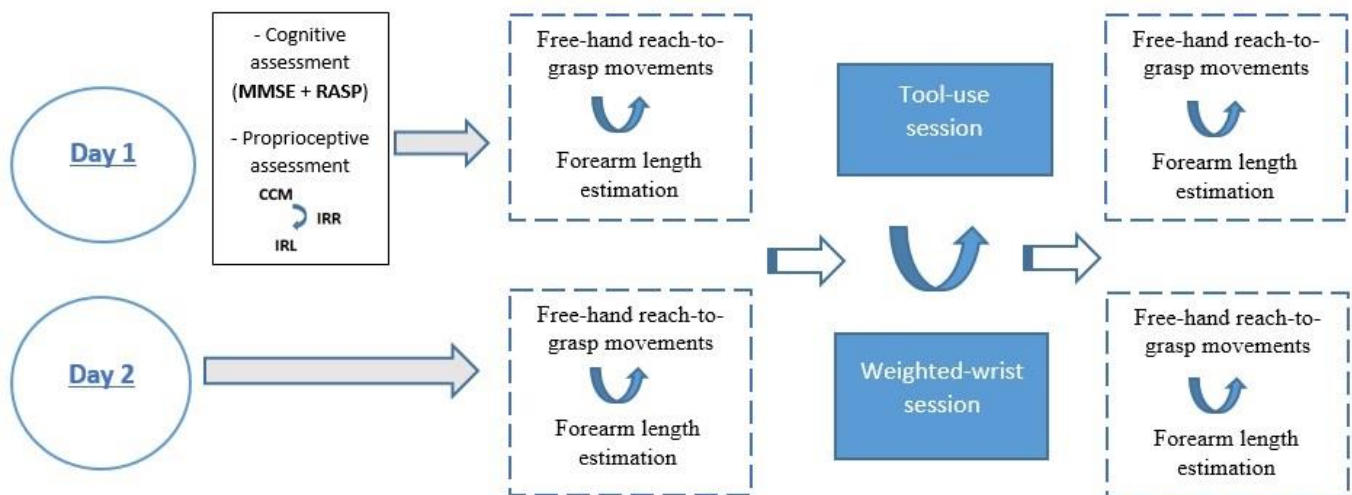


Figure 1. Within subject design run over two consecutive days: the first day consisted of cognitive and proprioceptive assessments followed by either a tool-use session or a weighted-wrist session. Curved blue arrows indicate the counterbalancing of session (tool-use and weighted-wrist) and the counterbalancing of pre-post tasks (free-hand reach-to-grasp movements and forearm length estimation) between subjects.

In the free-hand reach-to-grasp task, participants had to reach, grasp, and lift the object with their dominant hand for 18 trials. At the beginning of a trial, participants were asked to keep their dominant hand in the starting pinch-grip position, i.e. the tips of the thumb and the index in contact, pressing down the starting switch located in the proximal edge of the table, facing the object. After a random delay (ranging between 1 and 2 seconds), an auditory ‘go’ signal was produced and subjects had to reach, grasp and then raise the object keeping it between their thumb and index fingers. Then they had to put the object back on the table and return to their starting position.

In the forearm length estimation task (18 trials), blindfolded participants were asked to estimate the length of their dominant forearm from the elbow to the wrist. To that aim, starting from the switch, upon the auditory ‘go’ signal they had to slide their dominant index finger horizontally on the table (following a fronto-parallel axis) for a distance corresponding to the estimation of their forearm length.

To remind participants of the forearm distance to reproduce, the experimenter named and delivered a tactile stimulation on her dominant wrist and elbow before the first trial. Once a trial performed, participants had to return to the starting position and wait to perform the next trial.

Tool-use phase

The tool-use phase consisted of four blocks of 12 reach-to-grasp movements using a tool (48 trials). Participants were instructed to place the tips of the tool prongs (pinch grip) on the starting switch at the beginning of each trial and wait for an acoustic go signal to reach and grasp the object using the tool. The tool was the same used in several previous studies and consisted in an ergonomic handle (10 cm-long), a 30 cm-long rigid shaft and an articulated “hand” composed by two curved prongs with rubber allowing a stable grasp. The tool was controlled by squeezing the handle with the whole hand: closing the hand would close the tip of the prongs while opening the hand would release the grip (*Figure 2*). Participants were not allowed to train with the tool, and had never used it or seen it before the trial day.

Weighted-wrist phase

In the weighted-wrist phase, participants had to reach and grasp for the same object with their dominant hand equipped with a weight wrapped around the wrist. This task also consisted of four blocks of 12 trials each. The weight was a commercial gym wrist weight modified to equate

the tool weight (300gr). As in the previous tasks, participants maintained a pinch grip position on the starting switch and waited for the acoustic go signal.

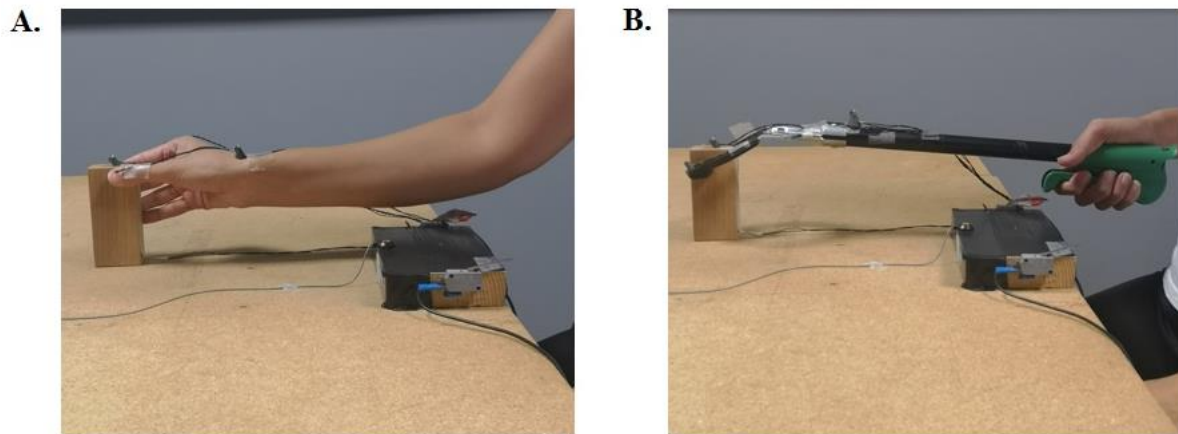


Figure 2. Final grasping position of a free-hand (A) and tool-use (B) reach-to-grasp movement. The tool consisted in an ergonomic handle (10 cm-long), a 30 cm-long rigid shaft and an articulated “hand” composed by two curved prongs.

Kinematic recordings and analysis

Three infrared light emitting diodes were taped on kinematic relevant locations on participant’s dominant hand, namely on the thumb (inside corner of the fingernail), index finger (external corner of the nail), and wrist (the skin proximal to the styloid process of the radius). The reaching component of the movement was characterized by the kinematic parameters of the wrist marker, while the grip component was characterized by the distance between the thumb and index. Three additional markers were placed on the tool in a similar functional arrangement: two on the extremities of the mechanical “fingers” and one in the distal part of the shaft “wrist”. Spatial positions of the markers were recorded with an Optotrak system (Optotrak 3020, Northern Digital Inc) placed perpendicularly over the table, with a sampling rate of 200 Hz (0.01 mm 3D resolution at 2.25 m distance). Kinematics analysis of 3D movements were performed offline to obtain for each trial the amplitude and latency of four parameters: the peaks of wrist acceleration, velocity and deceleration (transport component), as well as for the peak of grip aperture (grip component). In addition, we measured the duration of the movement.

STATISTICS

Proprioception

A repeated measure ANOVA was done with Group (Young/Old adults) as a between subject factor, and proprioceptive test Task (IRR/IRL/CCM) and Angle (20°/40°) as a within subject factor in order to compare the proprioceptive acuity between young and old adults.

Kinematics

To account for the interdependency of the kinematics parameters and movement components, a full factorial design permutation analysis was applied to free-hand movements, using the flip package on R^{28,29}. The factors were Session (Tool-use and Weighted-wrist) and Time (Pre- vs Post-) and their interaction to evaluate the impact of tool-use on the kinematics of movements performed before and after tool-use. Similar analyses were performed with the factors Session (Tool-use and Weighted-wrist) and Block (1st/4th) to evaluate potential learning effects of tool-use practicing. Importantly, the permutation analysis was designed for a multivariate framework. This allows to combine the significance of the kinematic parameters for the transport phase (amplitudes and latencies of peaks the wrist acceleration, velocity and deceleration) and those for the grasping phase (amplitudes and latencies of the grip aperture), to obtain one global p-value for each component. The global p-value is obtained via Nonparametric Combination (NPC³⁰) of partial p-values testing the single parameters. In keeping with previous work on the same paradigm and factors^{5,13}, this methodology accounts for dependence among tests through a nonparametric approach based on the joint (i.e. multivariate) permutation distribution^{28,29}.

Length Estimation

Because the forearm length estimation task involved only one parameter, a repeated measure ANOVA was performed on these data, with factors Session (Tool-use; Weighted-wrist) and Time (Pre- vs Post-session).

Correlations

Finally, for old participants, we performed Pearson correlations analysis between the proprioceptive tests and the delta of the kinematic changes between pre and post tool-use. The rationale for this approach was to identify whether proprioceptive acuity might be linked to the ability to incorporate the tool, as assessed through kinematic changes after tool-use session.

RESULTS

Online proprioception is spared in old adults

First, we compared the proprioceptive acuity between young and old adults to ascertain whether our sample of old adults displayed the expected decline in the offline (IRR/IRL) as compared to online proprioception (CCM). Noteworthy, all participants overshoot the reproduced or matched target position compared to the initial reference position. The repeated measures ANOVA performed on the proprioceptive assessment revealed a significant interaction between Group and proprioceptive Task ($F(1,37) = 3.575, p < .033$). Post hoc t-tests confirmed the expected significant difference between groups for the IRR and IRL Task (*IRR error for old adults* = 5.34° vs *for young adults* = $3.18^\circ, p < .001$; *IRL for old adults* = 5.62° vs *for young adults* = $3.37^\circ, p < .001$) and the non-significant difference for the CCM Task (*CCM error for old adults* = 6.28° vs *for young adults* = $5.34^\circ, p > .19$). This pattern of results confirms the findings reported in the literature on presbypropria¹⁵, an alteration of older adult's proprioception, affecting mostly the offline access to proprioceptive information¹⁷. Noteworthy, no significant difference was found when assessing the dominant vs non-dominant hand concerning the IR tasks (*IR for dominant hand error* = 5.57° vs *for non-dominant hand error* = $5.39^\circ, p = .49$) in old adults.

Tool-use changes movements kinematics

The full factorial design permutation analysis revealed that the factors Session (Tool-use and Weighted-wrist) and Time (Pre- vs Post-session) interacted significantly for the transport component (*Fisher combination*; $K = 29.84, p = .0007$) and the grip component ($K = 5.95, p < .03$). The combined p-value assessed for the tool-use session confirmed an effect of Time on the transport ($K = 31.16, p < .0004$) and grip component ($K = 8.14, p < .0058$). Figure 3 shows permutations analysis performed on each parameter, which highlighted a decreased acceleration ($t = -2.11, p < .04$) and a delayed velocity ($t = 4.46, p < .0001$) and deceleration ($t = 4.08, p < .0001$) peaks, as well as a trend to a delayed acceleration peak and decreased velocity and deceleration peaks (p values $< .068, .069, .057$ respectively) after the use of the tool. In addition, the latency of the maximum grip aperture (pre = 622.65 ms vs post = 707.43 ms; $t = 3.76, p < .0005$), as well as the movement duration (pre = 922.96 ms vs post = 1036.68 ms; $t = 3.43, p < .0008$), were longer after the tool-use session. In sharp contrast, the analyses performed for the weighted-wrist control session yielded no significant effect of Time either on the Transport component, or on the Grip component (*both* $p \geq .1$).

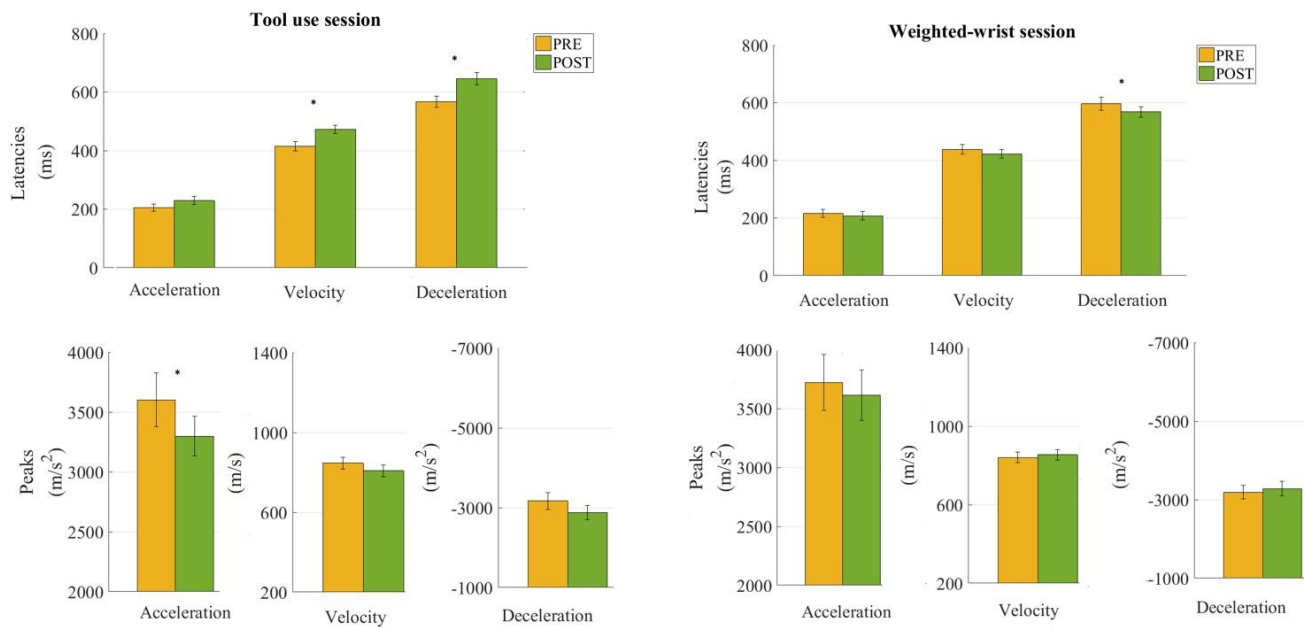


Figure 3. Free-hand movement kinematics modifications after tool-use (left panel) and weighted-wrist session (right panel). Bar graphs illustrate the S.E.M. Asterisks denote significant differences between pre (yellow) and post (green).

The forearm length estimation, as assessed via the explicit length reproduction task, was not affected by the factors Session (*Tool-use and Weighted-wrist*, $F(1,19) = .002$, $p = .961$) and Time (*Pre- vs Post-*, $F(1,19) = .908$, $p = .353$), nor by their interactions (*average pre-tool session = 105.48 % vs average post-tool session = 108.77 % and average pre-weight session = 106.45 vs average post-weight session = 108.76 %*, $F(1,19) = .151$, $p = .702$).

Kinematics does not change throughout the course of tool-use

The full factorial design permutation analysis with factors Block (1st/4th) * Session (Tool-use and Weighted-wrist) revealed neither significant main effects nor interaction on the transport component (*Fisher combination*; $K = 7.15$, $p < .28$) or the grip component ($K = 3.46$, $p < .15$), ruling out any gross learning effect during sessions for this component. The grip component was affected during the use of the tool ($k = 5.11$, $p < .02$), as the maximum grip aperture decreased significantly from the first to the fourth block of trials (*pre = 114.58 mm vs post = 106.71 mm*; $t = -2.69$; $p < .006$).

Online proprioceptive acuity is correlated with kinematic changes

To examine the potential link between proprioception acuity and the pattern of kinematic modifications observed after tool-use, we performed in our old population a series of Pearson correlations between the absolute errors participants made in the proprioceptive tests and the kinematic changes after tool-use (post-pre difference for each parameter). There was a highly significant correlation between the online proprioceptive acuity, as measured by the CCM task, and the difference between post minus pre tool-use on most of the kinematic parameters: *acceleration: $r = 0.802$, $p < .001$; velocity: $r = 0.769$, $p < .00012$; deceleration: $r = 0.766$, $p < .00013$; latency of velocity: $r = -0.707$, $p < .00071$; latency of deceleration: $r = -0.665$, $p < .0019$; movement time: $r = -0.770$, $p < .00012$; latency of maximum grip aperture: $r = -0.742$, $p < .00065$ (all p values are Bonferroni corrected). As shown in Figure 4, the better acuity in online proprioception, the larger the changes in kinematics parameters after tool-use. In striking contrast, there was no significant correlation between offline proprioceptive Task (IRR and IRL) and the pattern of kinematic changes after tool-use (all p -values $> .12$).*

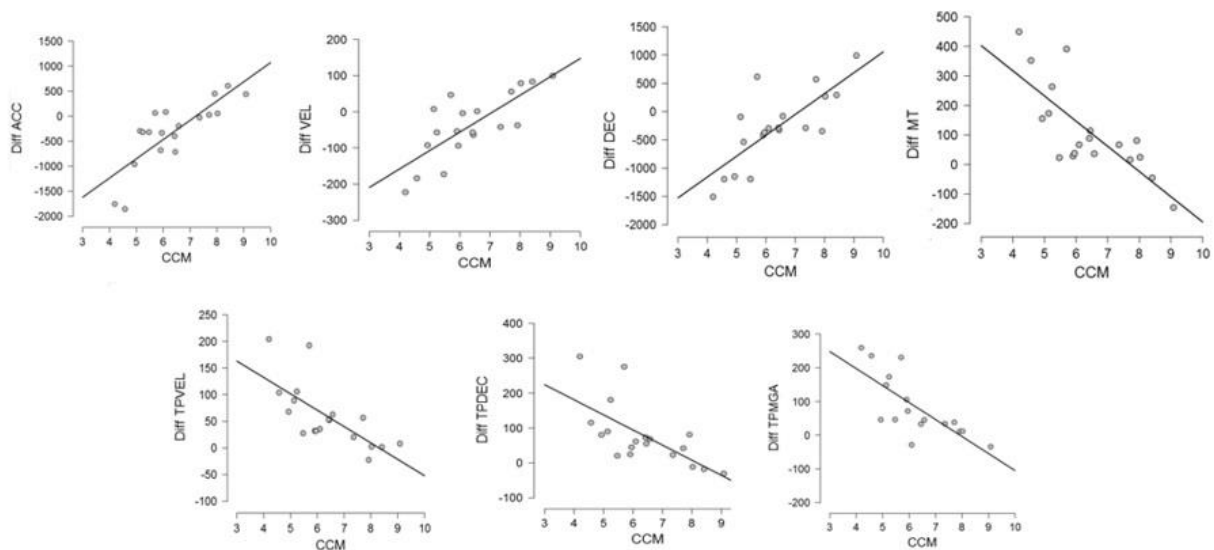


Figure 4. Correlation plots between error in CCM (Contralateral concurrent matching task) and the changes in kinematics induced by the tool-use session. Post minus pre difference in the tool-use session (Diff) are presented for each significant parameter (after Bonferroni correction). TP indicates the latencies to peaks. ACC, VEL and DEC denote the acceleration, velocity and deceleration peaks, respectively. MT denotes the total movement time and MGA the maximum grip aperture.

Discussion

In the present study, we sought to disentangle whether online or offline access to proprioception updates the body estimate for movement execution following tool-use. To this aim, we first identified a group of ‘old’ healthy adults (60 y-o) showing declined offline, but preserved online proprioception. We then assessed them for the emergence of the pattern of kinematic changes that has been previously reported following tool-use in young adults (average 25 years-old in 7 previous studies). The results showed that relatively old participants display the typical (i.e., previously reported in young adults) kinematic signature of tool incorporation. After tool-use, the kinematics of their free-hand reaching movement’s changes, showing delayed latencies and lowered peaks amplitudes. This finding extends to the beginning of the old age the notion that tool-use modifies the unconscious estimate of the bodily effector used to control motor actions. Instead, tool-use does not modify the conscious perception of old peoples’ body, again in keeping with what known from the young population¹³. Most importantly, we found that online (but not offline) proprioceptive acuity correlated with the amount of the kinematics changes observed after tool-use, thus establishing for the first time a tight link between tool-use incorporation and real-time proprioceptive body state estimate. Altogether, these findings point to the prominent role played by online proprioception in updating the body estimate for the motor control of tools in old participants.

Previous work on the assessment of proprioception acuity mainly relied on tasks that vary in terms of either memory requirements (offline) or interhemispheric transfer (online)¹⁷. Our findings confirm the presence of a specific offline impairment in the old adult population, indexed by the ipsilateral matching task, as well as a preservation of online proprioceptive acuity, derived from concurrent contralateral matching task. The presence (and the nature) of proprioceptive decline with age is still debated, as is its potential contribution to motor control³¹. Its presence may vary depending on what variables are measured and which tasks are used, as is typically not observed when assessed by visual to proprioceptive matching tasks³². Yet, proprioceptive decline with age has been consistently reported when testing proprioceptive memory: the pattern we report here conforms to previous findings on the decline of the offline component of proprioception in healthy ageing^{15,17,32}. By using the same offline/online testing procedures employed by Adamo et al.¹⁷, here we actually extend their results to the very beginning of the old age. While Adamo et al.’s study observed significant decline in offline proprioception in adults aged 75/76 on average^{17,33}, here we report that significant decline in offline proprioception can be detected in adults aged 60 on average.

Most interesting for the scope of our study, following tool-use, old participants exhibited the typical kinematic signatures so far reported in young adults only. After tool-use, free hand reaching movements displayed protracted and lowered transport component parameters (three out of six parameters were significantly altered). Importantly, and also in line with previous work, these effects emerged specifically following tool-use. The weighted-wrist control session did not trigger any of such effects on movement's kinematics. These tool specific kinematic modifications have been interpreted as a kinematic signature of tool incorporation in the effector representation, which would be represented as longer after tool-use^{6,11}. Indeed, similar kinematics characteristics (longer latencies, reduced amplitudes) are also observable in participants having a naturally longer arm when compared to shorter-armed participants' movements^{6,13}. Finally, tool-use did not influence the conscious arm representation of old adults, as evaluated through the forearm length estimation task, as it was not affected by tool-use. Here, we further confirm that the explicit, verbal and conscious representation of the body, referred as the Body Image^{34,35}, is immune to factors affecting the body representation for action^{13,27}. In agreement with our predictions, these findings clearly indicate that offline proprioception is not crucial to motor control plasticity following tool-use. Would that be the case, we should expect old participants with impaired offline proprioception not to display significant changes in their movement kinematics, or displaying changes that differ from the pattern repeatedly reported in young adults. Instead, their presence and the fact that both peak amplitudes and latencies were qualitatively affected in the same directions as in the young population, suggest that preserved online proprioception plays a critical role in updating our body state estimate.

Among the first conceptualizations of unconscious body representations devoted to action control, originally called body schema, stemmed from neuropsychological observations of patients with various somatosensory diseases³⁶. Since then, proprioception has been considered among the main inputs feeding this implicit body representation³⁷⁻⁴⁰. In previous work, we reported that proprioceptive deafferentation may still allow fairly accurate touch localization on a tool⁴¹, but prevents tool-use from affecting the subsequent kinematics¹⁴. This inability to incorporate a tool at motor level, at odds with what typically shown by young and now old healthy participants, attests to the crucial role of proprioceptive inputs in building an updated representation of the motor effector. Martel and coworkers¹³, by observing the same kinematic signature of tool incorporation in healthy blindfolded participants, further showed that proprioception is not only necessary, but also sufficient to trigger tool incorporation. The

present results allow to step further and reveal the correlation existing between online proprioceptive acuity and the kinematics signature of the tool incorporation: the better proprioceptive acuity, the larger the extent of kinematic changes following tool-use. While these findings are in keeping with the role of proprioception in updating body representation^{37,42,43}, they concur in indicating this body representation feeds internal models of motor control^{1,13,14}. Our findings refine current models by suggesting that the state estimation of the body relies heavily on online proprioceptive inputs to monitor and update the represented metric of effectors. While the neural correlates of this update remain to be elucidated, the sensorimotor regions, as well as more posterior parietal cortices, could be likely candidates. Previous neuroimaging work indeed pointed to the intraparietal sulcus and the premotor cortex as neural correlate of the body estimate, and have more recently underlined the role of the somatosensory cortices in the coding of proprioception^{44,45} and position sense^{46,47}.

Here we report for the first time that having used a tool that lengthens participants' arm affects the arm length representation in the old population. The presence of these plastic changes in old adults is in keeping with the suggestion that motor control may remain relatively preserved with age, as long as it concerns relatively simple movements (see, for review⁴⁸). Noteworthy, when comparing the kinematics during the tool-use sessions across blocks, we did not observe evidence of tool learning on the transport component. Transport parameters were comparable between the first and last blocks of trials. Importantly, this absence of gross learning effects has also been reported in previous studies^{4,6,13,26}. Here however, one kinematic parameter displayed signs of tool learning, namely the tool grip aperture, whose maximum was reduced in the last compared to the first block of trials. This effect is compatible with a reduced safety margin⁴⁹ while grasping the object as participants got used to the tool. Importantly though, after tool-use the hand maximum grip aperture did not differ from that observed before tool-use. Thus, the plastic mechanisms of tool incorporation that affect the transport component are likely independent from the processes of learning to control the tool grip aperture during tool-use. To conclude, here we show that 60 years-old participants display plastic changes in movement kinematics of their arm following tool-use, akin to those known in young adults. As suggested elsewhere^{13,14} these changes may reflect the update of 'state of affairs' of the body, in particular of the effector used. Our findings clearly indicate that in old participants, the online readout of proprioceptive information provides a major contribution to this update. In addition, online proprioceptive acuity predicts the extent to which tool-use will impact subsequent freehand

kinematics, corroborating the notion that tool incorporation relies heavily on ongoing processing of position sense.

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Author Contributions S.B., A.F., and A.C.R. designed the experiment. S.B., conducted the experiment. S.B., and L.E.M., analyzed the data. All authors discussed the results and wrote the paper

Competing Interests: The authors declare no competing interests.

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**CHAPTER 5: TOOL-USE MODULATES PROPRIOCEPTIVE
ACUITY AND REPRESENTED ARM LENGTH**

TOOL-USE MODULATES PROPRIOCEPTIVE ACUITY AND REPRESENTED ARM LENGTH

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1. INTRODUCTION

Successfully acting on the environment requires a representation of our body and its parts. The brain thus needs to encode and update the characteristics of the effectors that are relevant for performing actions, including its posture and metrics (De Vignemont, 2010; Gallagher, 1986). This allows to compute a body state estimation (Martel et al., 2019; Shadmehr & Krakauer, 2008; also referred to as body schema), which is fundamental for an accurate action planning and execution.

Tool-use has become a well-established paradigm for uncovering this update of the effector state (see, for review, Martel et al., 2016). Several studies confirmed that the use of a tool that functionally extends the arm or fingers (Maravita & Iriki, 2004; Cardinali et al., 2009; Cardinali et al., 2016) modulates the effector representation. Different behavioral signatures witnessed the modification of the effector representation. For example, a few minutes of tool-use are sufficient to induce modifications in the arm perceived midpoint (Garbarini et al., 2015; Romano et al., 2018; Sposito et al., 2012). In addition, touch localization or tactile length perception may differ after tool-use (Canzoneri et al., 2013; Cardinali et al., 2011, Miller, Cawley-Bennett, Longo, & Saygin, 2017; Miller, Longo, & Saygin, 2014, 2017) and participants localize touches on their arm as farther apart after using a tool elongating their arm (Cardinali et al., 2009, 2011). Finally, after tool-use bare hand prehension movements exhibit a kinematic pattern that matches that characterizing participants having long(er) arms by nature: reaches display protracted latencies and reduced peak amplitudes. This kinematic signature of body representation plasticity following tool-use had been found consistently across several studies (Baccarini et al., 2014; Bahmad et al., 2020; Cardinali et al., 2009, 2012; Martel et al., 2019).

Since its seminal conceptualization (Head & Holmes, 1911), this plastic capability has been thought to be fed mainly by proprioceptive signals, a notion supported by convergent series of findings. In a recent single case study of a deafferented patient, some of us reported that proprioception plays indeed a critical role in plasticity following tool-use. Though the patient after several sessions was able to use the tool, the kinematic signature of tool-induced plasticity typically observed in healthy subjects was altered (Cardinali, Brozzoli, Luauté, Roy, & Farnè, 2016). On the one hand, tool-use affected kinematics both on the reaching and the grasping components of her movements, while healthy participants displayed alterations selectively on the reaching component (Cardinali et al., 2009, 2012). On the other hand, kinematics modifications were found on prehension movements (trained with the tool), but did not

generalize to (untrained) pointing movements. In sharp contrast, healthy participants show kinematics modifications over tool-untrained movements and irrespective of their movement direction (Cardinali et al., 2009, 2012; Martel et al., 2019), as one would expect if they were performing actions with a longer arm. Proprioception is not only necessary but also sufficient for plastic tool incorporation, as its typical kinematic signatures can be observed when movements are performed without visual feedback (Martel et al., 2019). In particular, online proprioceptive inputs are thought to provide the major contribution to update the body state estimation, as the degree of proprioceptive acuity correlates with the amount of kinematics changes following tool-use (Bahmad et al., 2020). Despite multiple converging evidence indicating the key role of proprioception in the plastic update of the body estimate, whether tool-use modulate proprioceptive acuity remains unknown.

Here, we thus attempt to delineate the involvement of proprioception in updating the effector state. To this aim, we assessed whether tool-use induces changes in proprioception in two experiments. In Experiment 1, we investigated whether elbow proprioceptive acuity, measured before and after tool-use, is modified after tool-use. In particular, would proprioception contribute updating the body estimate of the effector handling the tool, we should expect proprioception to be modified in the arm using the tool, but not in the contralateral arm. In Experiment 2, besides repeating the same design to provide internal replication of the results, we additionally assessed the change induced by tool-use on the represented arm length through a tactile localization task. We anticipated both changes in proprioceptive acuity and represented arm length.

Experiment 1

2. METHODS

2.1. Participants

Thirty subjects (thirteen male and seventeen female, mean age = 24.9 ± 3.6 , range 21-34) took part in the study. All subjects were right-handed as assessed through the Edinburgh Handedness Inventor (Oldfield, 1971). None of the subjects reported neurological or psychiatric disorders. All of the subjects had normal or corrected-to-normal vision. Participants, received a monetary compensation for their participation and provided written informed consent prior taking part in the study, which was approved by the French ethics committee (Comité de Protection des Personnes Sud-Est IV). All experimental procedures conformed to the Helsinki declaration (World Medical Association, 2013).

2.2. Apparatus

2.2.1. Assessment

The proprioceptive assessment of the elbow was done using the joint position sense test (JPS) performed in remembered and concurrent tasks. We used a custom made apparatus similar to the one of Allen & Proske (Allen et al., 2010). Subjects were blindfolded and had their forearms strapped with Velcro onto two lightweight paddles aligned with the elbow joint. Digital LCD inclinometers were fixed on the paddles providing a voltage signal proportional to elbow angle with a resolution of 0.1 deg.

2.3. Experimental protocol

Subjects performed two sessions done over two consecutive days: In the tool session, proprioception was assessed before and after a brief tool-use session. In the control session, proprioception was assessed before and after a weighted-wrist session. The weight fixed to the wrist equaled the weight of the tool. This session was performed to control for unspecific fatigue effects of the weight of the tool, or for test-retest effects on proprioceptive assessment. The order of the sessions was counterbalanced across the participants (*Figure 1*). The order of the three proprioceptive assessment tasks (see below) was counterbalanced across the participants, but remained consistent across sessions.

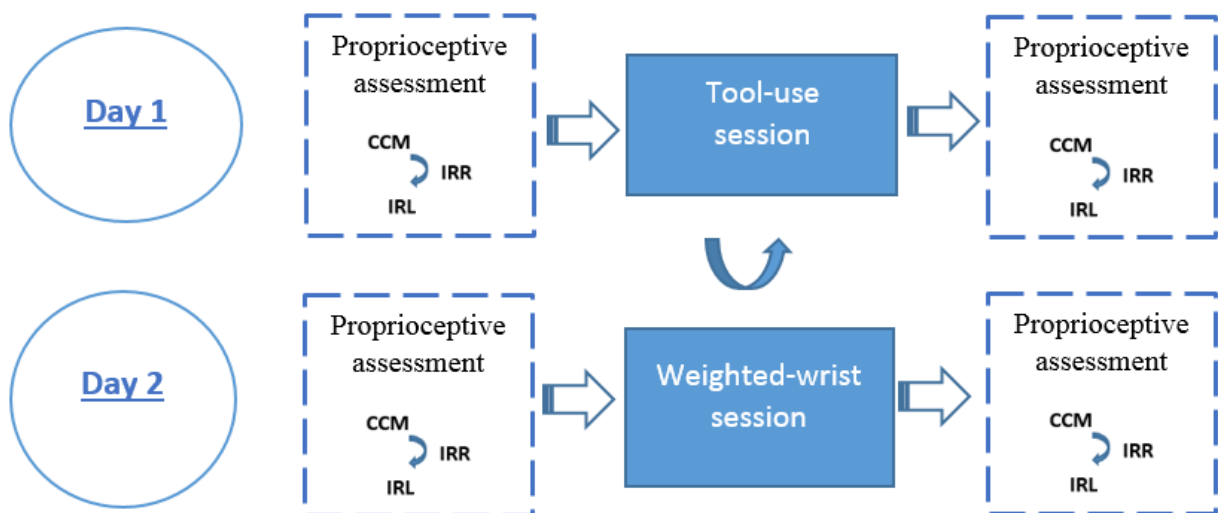


Figure 1. Within subject design experiment done over two consecutive days; one consisting on a tool-use session and the other a weighted-wrist session separated by a proprioceptive assessment done before and after the sessions. Curved blue arrow indicate the counterbalancing of sessions (tool-use and weighted-wrist).

2.3.1. Proprioceptive assessments

Participants were blindfolded and the order of the three tasks was counterbalanced across participants. The starting position for all tests was standardized for the shoulder (30 degree flexion), elbow (30 degree flexion), and wrist (neutral) joints across participants.

Ipsilateral Remembered matching task (IR): On each trial, the experimenter passively moved the participant's forearm around the elbow to a predetermined target joint position (20° or 40° from the starting position) for five seconds as measured by a stopwatch; the joint was then returned to its initial position by the experimenter. Participants were then required to actively reproduce the previously experienced arm position with the same limb. This task was ran for the dominant right hand (IRR) and non-dominant left hand (IRL). The order of the target angles was pseudo-randomized. There were five trials for each of the two angles, corresponding to 10 trials in total. The experimenter maintained a steady pace for each trial.

Contralateral Concurrent Matching task (CCM): The procedure of this task was identical to the IR with one major difference: On each trial, the joint of right elbow was moved to the target position and remained there. The participant's task was then to match its current position using their left arm.

We computed the absolute matching error value, as a measure of proprioceptive acuity. For the three tasks, the absolute error value on every trial was calculated in angular degrees as the unsigned difference between the reproduced/matched angular position and the reference one (20°/40°).

2.3.2. Tool-use session

The tool-use session consisted of four blocks of twelve reach-to-grasp movements using a tool (48 trials in total). At the beginning of each trial, participants were instructed to place the tip of the tool on the same starting position used in the pre and post tool-use phases and wait for the auditory "go" signal. Upon which they used the tool to reach and grasp an object that was positioned in front of them, aligned with their shoulder, 35 cm from the starting point. The tool was identical to that used in several previous studies (some refs) and consisted of an ergonomic handle (10 cm-long), a 30 cm-long rigid shaft, and an articulated "hand" composed by two curved prongs allowing a stable grasping movement. The tool was controlled by squeezing the handle with the right hand and digits: closing the hand in a fist-like posture would bring the tip of the prongs to contact while opening the hand would release the grip. Participants were not allowed any previous practice with the tool, and had never used it before the day of testing. The non-dominant left hand was kept still on the table during tool-use.

2.3.3. Weighted-wrist session

The weighted-wrist session consisted of four blocks of twelve reach-to-grasp movements, identical to those performed in the tool-use session, but with a weight identical to the weight of the tool (300gr) wrapped around participant's wrist. The weight is a commercial gym wrist weight that was modified to equate the tool's weight. As in the tool-use session, participants maintained a pinch grip position on the starting switch and waited for the auditory go signal.

3. STATISTICS

Consistent with prior studies (Adamo et al., 2007; Goble, 2010), we analyzed the absolute error in the position matching via repeated measures ANOVAs. We performed an omnibus 2 (Session: tool-use, weighted-wrist) x 2 (Time: pre, post) x 3 (Proprioceptive tasks: IRR, IRL, CCM) x 2 (Angles: 20°, 40°) repeated measures ANOVA. Bonferroni post-hoc tests were used to test interactions terms.

4. RESULTS

The omnibus ANOVA revealed a three-way interaction between Session, Time, and Proprioceptive task ($F(1,29) = 7.44, p < .001$). Bonferroni post-hoc tests revealed that the absolute error in the IRR task decreased after the tool-use session ($pre = 4.00 \pm 0.36$ vs $post = 3.22 \pm 0.31, p \text{ value} < .04$), but not after the weighted-wrist session ($pre = 3.92 \pm 0.29$ vs $post = 4.20 \pm 0.29, p > .9$). The same pattern of error decrease after tool-use was observed for CCM task (tool-use session $pre = 5.16 \pm 0.46$ vs $post = 3.51 \pm 0.37, p \text{ value} < .001$; weighted-wrist $pre = 5.33 \pm 0.50$ vs $post = 5.22 \pm 0.50, p > .9$). In contrast, the error values in the IRL did not change, whatever the session considered (tool-use session $pre = 3.59 \pm 0.27$ vs $post = 3.86 \pm 0.30, p \text{ value} > .9$; weighted-wrist session $pre = 3.58 \pm 0.29$ vs $post = 4.23 \pm 0.33, p \text{ value} > .9$), indicating the absence of proprioceptive modulation on the left arm, which did not use the tool (Figure 2).

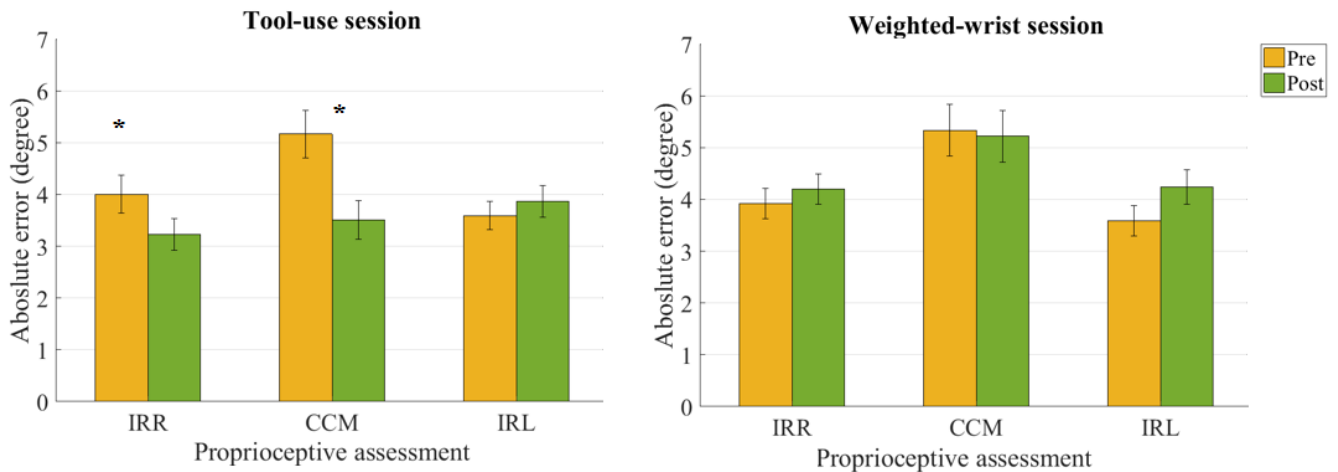


Figure 2. Proprioceptive errors before and after sessions; grasping an object with a tool (left panel) led to a reduction in the absolute error in the IRR (Ipsilateral Remembered Right arm task) and CCM (Contralateral Concurrent Matching task) but not for the task assessing the left hand (IRL), which did not use the tool. This pattern differed for the control session (right panel; weighted-wrist session); Absolute errors for either task were not reduced after grasping the same object with a weight attached to the wrist. Bar graphs illustrate the S.E.M. Asterisks denote significant differences between pre and post session condition. Orange corresponds to the pre-session error values and green to the post-session error values.

5. INTERIM DISCUSSION

The results of Experiment 1 report the first evidence that using the mechanical grabber increases proprioceptive acuity, selectively for the arm that manipulated this tool. No change was found in the proprioceptive acuity of the opposite arm. These effects were specific for tool-use as the control session, where the grasping movement were performed having a tool-equivalent weight wrapped around the wrist, did not modulate proprioceptive acuity. This finding allows to rule out any unspecific effect of fatigue, or a general test-retest effect. These findings are thus specific in two respects: tool-use (but not acting with a weight) improves proprioceptive acuity of the arm, which used to tool (but not the opposite one).

As recalled in the Introduction, previous work reported that using this kind of tools affects the represented length of the arm (Cardinali et al., 2009, 2012; Martel et al., 2019; Miller, Cawley-Bennett, et al., 2017; Miller et al., 2014; Miller, Longo, et al., 2017, 2017; Romano et al., 2018; Sposito et al., 2012). The arm metrics update has been observed in tactile localization tasks in which touches delivered on the elbow and middle fingertip of the arm are localized farther apart after tool-use (Cardinali et al., 2009). To ascertain whether tool-induced proprioceptive

improvements accompany the update of the effector state, and assessing the potential relationships between proprioceptive and representational changes, we performed a second experiment in which we administered again the three proprioceptive tasks and added a tactile localization task. As in Experiment 1, the tasks were administered before and after a tool session and a weighted-wrist session.

Experiment 2

1. METHODS

1.1. Participants

Thirty neurologically healthy participants (sixteen male and fourteen female, mean age = 28.86 ± 3.99, range 19-34) took part in the study; none of them took part in experiment 1. All participants were right-handed as assessed through the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision. Participants received a monetary compensation for their participation and provided written informed consent prior taking part in the study, which was approved by the French ethics committee (Comité de Protection des Personnes Sud-Est IV). All experimental procedures conformed to the Helsinki declaration (World Medical Association, 2013). The results of one participant were removed from analysis because she didn't comply with instructions in the tactile localization task.

1.2. Apparatus and experimental protocol

Proprioceptive assessments: The apparatus and procedure were the same as for Experiment 1; the three tasks (IRR; IRL; CCM) were counterbalanced between participants and the order of tasks was maintained across pre and post-sessions.

Tactile localization task: Blindfolded participants were seated at a table, a touch screen was placed parallel to their sagittal axis near their right dominant forearm, facing their non-dominant arm (see Figure 3). The right forearm of the participants was placed on a lightweight paddle equipped with the inclinometers, used for the proprioceptive assessment. The left hand was kept on a foam support, the index fingertip in contact with a starting pad (Black Square in Figure 3). The experimenter delivered single touches (~ 1s) with a von Frey monofilament, on one of two points located on the right forearm of the participant: close to the elbow (5 cm proximal to the midline of the forearm-arm articulation) or close to the wrist (5 cm proximal to the midline of the forearm-wrist articulation). After each tactile stimulation, participants had to indicate with

their left index finger the location corresponding to the felt tactile stimulation by pointing on the touch screen. Each point was stimulated 10 times, with the right arm positioned in three angular positions, corresponding to the elbow flexions of 0, 20 and 40 degrees.

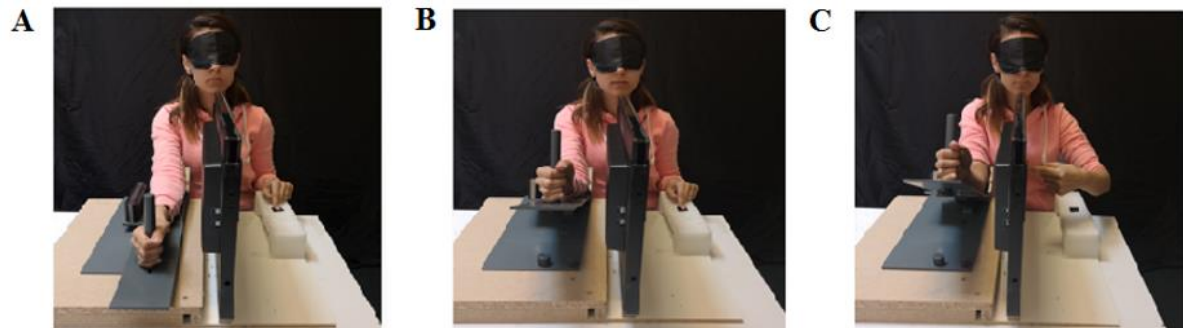


Figure 3. Illustration of a single trial of the tactile localization task. **(A)** At the beginning of the trial, the left index finger of the blindfolded participant is set in a starting position (raised Styrofoam). **(B)** The experimenter then sets the angular position of the right elbow, here displayed at 20 degrees flexion. A tactile stimulus is then delivered to one of two points on the participant's right forearm. **(C)** The participant then points with their left index to the corresponding position on the screen.

The experimental protocol, schematized in Figure 4, consisted of a proprioceptive assessment identical to Experiment 1 and a tactile localization task, conducted before and after either the tool-use or the control weighted-wrist session. Sessions were proposed in counterbalanced order across participants. Pre and post sessions were also counterbalanced, half of the participants completed the proprioceptive assessment first and then the tactile localization task; vice versa for the other half of the participants. The order of the tasks was the same for both the pre and post session. Apparatus and procedures for tool-use and weighted-wrist sessions were identical to those performed in Experiment 1.

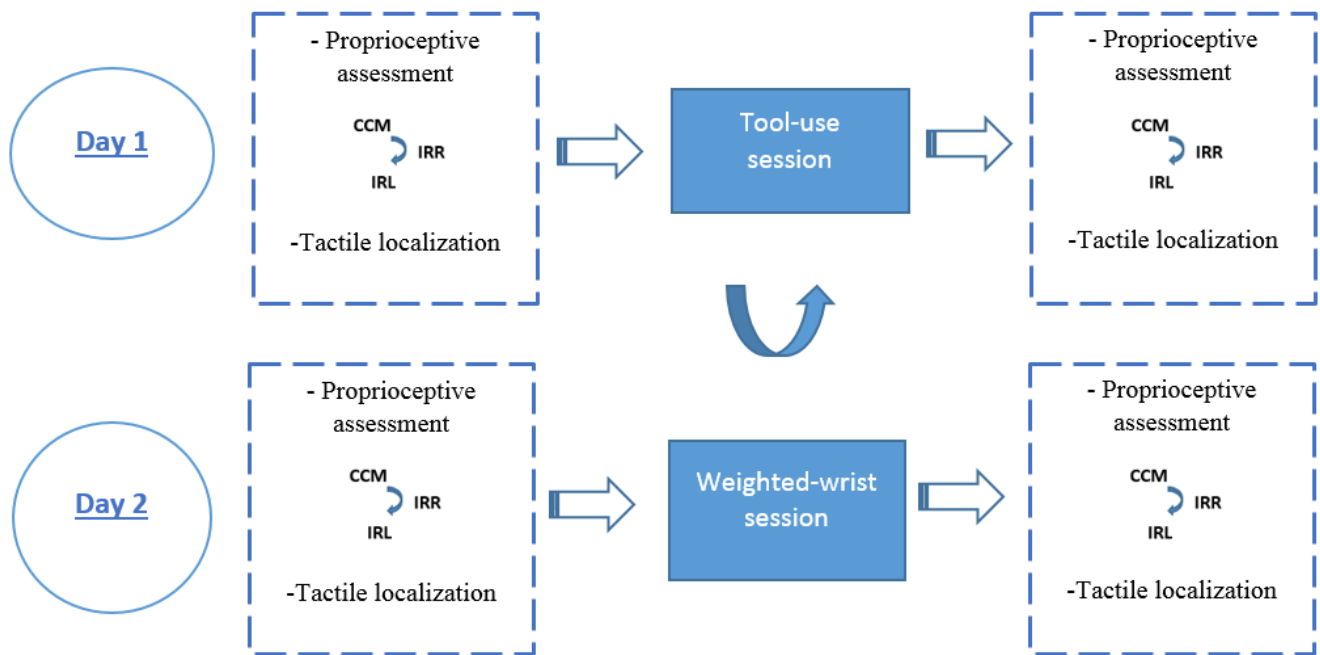


Figure 4. Within subject design experiment, ran over two consecutive days and consisting on a tool-use session and a weighted-wrist session (control). The proprioceptive assessment and the tactile localization task were performed pre and post sessions. Curved blue arrows indicate the counterbalancing of session (tool-use and weighted-wrist) and the counterbalancing of pre-post tasks (proprioceptive assessment and tactile localization) across participants.

2. Statistics

To assess changes in proprioceptive acuity, we performed the same statistical analysis as described above for Experiment 1. We thus ran an omnibus 2 (Session: tool-use, weighted-wrist) x 2 (Time: pre, post) x 3 (Proprioceptive tasks: IRR, IRL, CCM) x 2 (Angles: 20°, 40°) repeated measures ANOVA. Bonferroni post-hoc tests were used to test interactions.

To assess changes in the tactile localization task, we first used polar coordinates to calculate the distance between the mean judged locations of the two tactile points. Specifically, we calculated the distance between the two touched points as $L = \sqrt{(\Delta x)^2 + (\Delta y)^2}$, with $\Delta x = x_2 - x_1$ and $\Delta y = y_2 - y_1$, with point 1 (x_1, y_1 ; close to the elbow) and point 2 (x_2, y_2 ; close to the wrist) (Figure 5). Then the mean distance was calculated in pre and post-sessions. We performed an omnibus 2 (Session: tool-use, weighted-wrist) x 2 (Time: pre, post) x 3 (Angles: 0°, 20°, 40°) repeated measures ANOVA. Greenhouse-Geisser correction was applied whenever necessary.

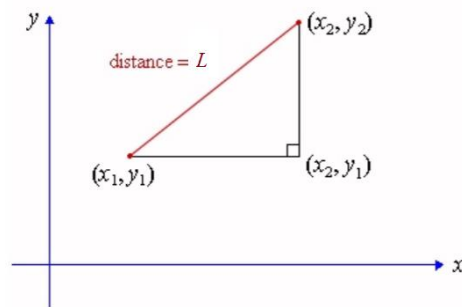


Figure 5. Polar coordinates used to calculate distance between two points pre and post-sessions.

Finally, we performed Pearson correlations between the changes in proprioceptive acuity and localization to ascertain whether increase in proprioceptive acuity could be directly linked to modifications of the tactile localization of touches.

3. Results

3.1. Proprioceptive assessment

The results on proprioceptive modulation induced by tool-use fully replicated those obtained in Experiment 1. The ANOVA revealed a significant interaction between Session * Time * Proprioceptive tasks ($F(1,29) = 5.105, p < .009$, Greenhouse-Geisser corrected). Bonferroni post-hoc tests highlighted a decrease in the absolute error in the IRR task after tool-use ($pre = 3.61 \pm 0.22$ vs $post = 2.62 \pm 0.19, p \text{ value} < .001$), but not after the weighted-wrist session ($pre = 3.41 \pm 0.18$ vs $post = 3.46 \pm 0.19, p > .9$). As in experiment 1, the same pattern of error decrease appeared in the CCM task after the tool-use session ($pre = 4.72 \pm 0.32$ vs $post = 3.56 \pm 0.30, p \text{ value} < .001$), but not after the weighted-wrist session ($pre = 4.63 \pm 0.35$ vs $post = 4.47 \pm 0.34, p > .9$). Finally, error amplitude in the IRL did not vary in either session (Tool-use session: $pre = 3.20 \pm 0.23$ vs $post = 3.23 \pm 0.24, p \text{ value} > .9$; weighted-wrist session: $pre = 3.06 \pm 0.23$ vs $post = 3.44 \pm 0.23, p \text{ value} > .11$), indicating that there was no proprioceptive change affecting the left arm, which did not use the tool (Figure 6).

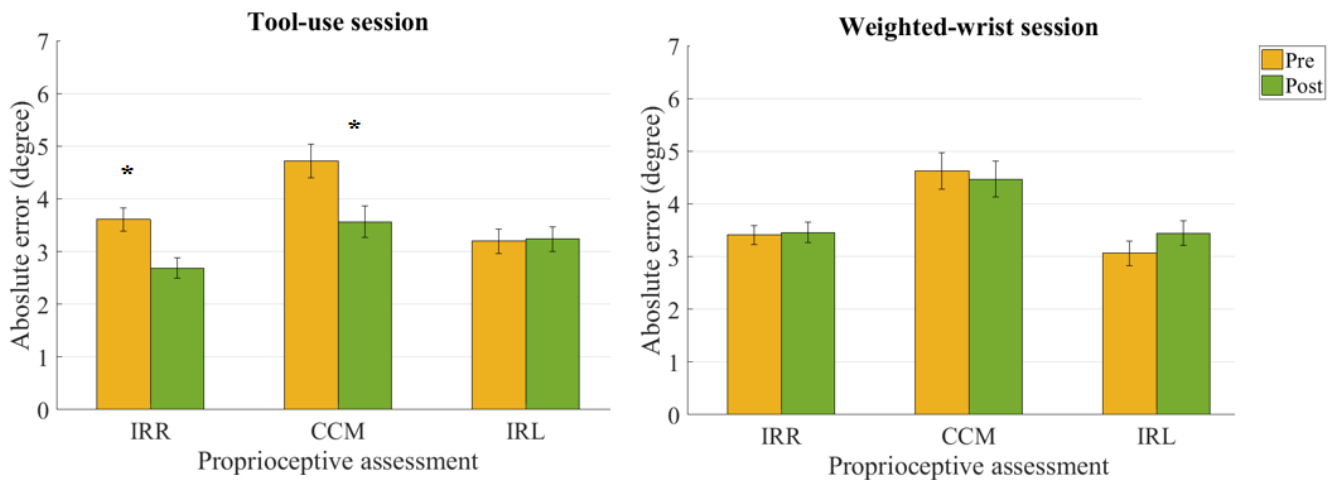


Figure 6. Decrease of proprioceptive errors after tool-use sessions. Results replicated those of Experiment 1; improvement of proprioceptive acuity is specific to the tool-use session and to the arm using the tool. Bar graphs illustrate the S.E.M. Asterisks denote significant differences in the post session condition (Orange color illustrates the pre-session error values and green color illustrates the post-session error values).

3.2. Tactile localization task

The repeated measures ANOVA for the tactile distance analysis revealed a significant Session*Time interaction ($F(1,28) = 18.36, p < .001$) indicating that the distance between the two points changed depending upon the type of session. Paired samples t-test revealed that participants localized the two points as farther apart from each other after tool-use session only (*Tool-use session: length pre = 16.13 ± 0.70 vs post = $18.75 \pm 0.77, t(28) = -4.51, p < .001, d_z = -0.84$; Weighted-wrist session: length pre = 15.34 ± 0.60 vs post = $15.47 \pm 0.68, t(28) = -0.32, p > .75, d_z = -0.06$; Figure 7).*

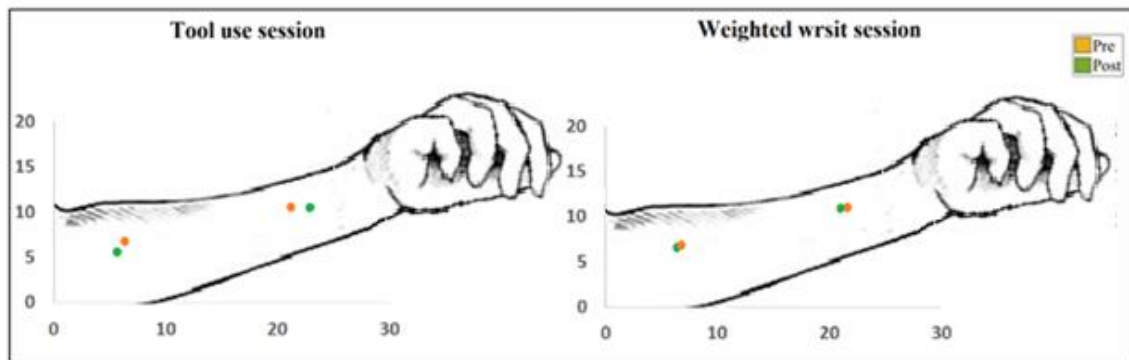


Figure 7. Average localization of both points (close to the elbow and the wrist) as a function of session (tool-use, weighted-wrist) and time (pre, post). Orange dots illustrate the pre-session localization and green dots illustrates the post-session localization.

3.3. Relationship between changes in localization and proprioceptive acuity

The analysis of the potential relationship between the tool induced changes in proprioceptive acuity and tactile localization did not reveal any significant correlation between proprioceptive changes after tool-use and represented length arm changes ($r = .180, p > .36$) as revealed by the Pearson correlation.

General discussion

In the present study, we sought to investigate the modifications of proprioception following tool-use. To this aim, we assessed proprioceptive acuity of participants' elbow before and after tool-use and contrasted the results with those of a weighted-wrist control condition. Our findings reveal that tool-use improves the proprioceptive acuity in the arm that used the tool. In a second experiment, through a tactile localization task, we demonstrate that an increase in the represented arm length parallels the proprioceptive improvement following tool-use. These findings provide the first, internally replicated evidence that the tool-use induces a consistent improvement in proprioceptive acuity, thus confirming long-standing hypothesis about the role of proprioception in updating the body state estimation following tool-use.

Importantly, here we report that proprioceptive acuity was improved by tool-use. Fatigue following extended periods of exercise modulates proprioceptive acuity in the opposite direction. Shoulder exercise lasting at least 20 minutes have been reported to decrease proprioceptive acuity at the level of the hand (Sadler & Cressman, 2019). This opposite effect direction, together with the absence of improvement in the control weighted-wrist session, firmly rule out the possibility that fatigue may explain the observed increase in proprioceptive acuity. These results are in keeping with previous work that addressed the role of proprioception in body representation plasticity by measuring the arm representation through the kinematics of reach-to-grasp movement. For example, proprioceptive deafferentation has been shown to prevent tool-use from affecting the subsequent arm kinematics (Cardinali et al., 2016). In the same vein, the kinematic signatures of tool incorporation were present in healthy blindfolded participants, thus suggesting that proprioception is not only necessary but also sufficient for tool incorporation (Martel et al., 2019). In addition, old participants display a correlation between their on-line proprioceptive acuity and their kinematic integration of the tool in the effector state estimate: the better the proprioceptive acuity, the larger the extent of kinematics changes following tool-use (Bahmad et al., 2020). Here we provide an important step forward, by showing that tool-use sharpens the proprioceptive acuity. Although no linear relationships was observed between the changes induced by tool-use concurrently on proprioception and tactile localization, these findings offer the first demonstration that proprioception is indeed modified by tool-use.

When considering the motor control domain, modified limb position sense has been reported in participants being exposed to a force field (Ostry et al., 2010). As shown by Martel and colleagues, kinematics modifications of arm movements following tool-use ought not to be considered as a mere consequence kind of proprioceptive enhancement. Indeed, these changes in kinematics are not spatially selective for the region where the tool is used (Martel et al., 2019), while changes in position sense are selective (Ostry et al., 2010). Wong and colleagues also reported an enhanced proprioceptive acuity in participants trained to grasp the handle of a robotic arm to guide a cursor to a series visual targets (Wong et al., 2011). They concluded that sensory changes parallel changes to motor commands. Our results complement those of Wong and colleagues, ascribing to proprioceptive signals the possibility to update the effector metrics and thus ensure an accurate motor control.

In addition to the enhanced proprioceptive acuity, here we report that participants pointed to an elongated representation of their arm. A modified proprioceptive percepts and an elongated representation of a touched body part has also been reported by de Vignemont and colleagues. In their paradigm the proprioceptive modification was not induced by the use of a tool but by a vibration applied to the biceps muscle tendons (de Vignemont et al., 2005, see Longo et al., 2009 for a shrank arm representation following proprioceptive illusion). The authors pointed to the fact that proprioceptive manipulations of the body representation affects tactile perception (de Vignemont et al., 2005). As tactile distances felt larger when the touched body part felt elongated after the proprioceptive illusions. Tactile localization has been previously used as an estimate of the tool-effector representation update (Cardinali et al., 2009; Miller, Cawley-Bennett, et al., 2017) highlighting the privileged access of touch to the body representation (Cardinali et al., 2011). Here we replicate and extend this notion by showing that tactile perception trustfully witnesses the modifications of body representation following tool-use irrespectively of the arm position in space. Interestingly, although coexisting the proprioceptive and tactile modifications induced by tool-use did not correlate significantly. This lack of a direct link between touch localization and proprioception actually converge with recent findings from a proprioceptively deafferented patient: able to localize touches applied on a tool fairly accurately (Miller et al., 2019), she nevertheless lacked the typical kinematic signatures of tool incorporation (Cardinali et al., 2016).

While the newly reported findings that tool-use actually improves proprioceptive acuity add importantly to the significance of proprioception for the body state estimation, they also make

clear that further studies are needed to precisely identify the mechanisms through which higher proprioception may update arm length representation.

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CHAPTER 6: BLINDNESS ALTERS ARM REPRESENTATION
PLASTICITY FOLLOWING TOOL-USE

Blindness alters arm representation plasticity following tool-use

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Introduction

To accurately control grasping movements, the brain needs to monitor two main elements: the state of the environment, including the object's characteristics, and the state of the body, that is an estimate of the posture and metrics of the effector used to reach and grasp the object (Shadmehr & Krakauer, 2008). When grabbing the same object with a tool, the body estimate or schema (Maravita & Iriki, 2004) must account for the suddenly longer effector: the brain has to somehow incorporate the tool in the arm's movement plan (see, for review, Martel et al., 2016). While the online effects of tool-use on body representations remain debated (Bongers, 2010; Ganesh et al., 2014), the kinematic signatures of tool incorporation observed after using a mechanical grabber are well-established: free-hand movements performed after tool-use display longer latencies and smaller peaks amplitudes (Baccarini et al., 2014; Cardinali et al., 2009, 2012; Martel et al., 2019). This kinematic pattern corresponds to that typically observed in long-armed participants, as compared to short-armed participants (Cardinali et al., 2009; Martel et al., 2019). It has therefore been attributed to a longer arm representation induced by the use of the tool (see, for tactile signatures of tool incorporation, Cardinali et al., 2011; Farnè et al., 2007; Miller et al., 2014, 2017; Sposito et al., 2012).

Proprioception is crucial for changes in the effector estimate to occur. Since seminal observations of the last century (Head & Holmes, 1911), its involvement in the building of the body schema has been largely confirmed by neuropsychological (Dijkerman & de Haan, 2007; Medina & Coslett, 2016; Shenton et al., 2004), neuroimaging studies (Corradi-Dell'Acqua et al., 2009) and developmental studies (Cignetti et al., 2013, 2017). Behaviorally, the pathological loss of proprioception abolishes the typical kinematic signatures of tool incorporation (Cardinali, Brozzoli, Luauté, et al., 2016). Importantly, proprioceptive acuity correlates positively with the incorporation of the tool, as indexed by kinematics (Bahmad et al., 2020, Experimental contribution 1). In addition, proprioceptive inputs are not only necessary, but also sufficient to trigger the typical kinematic pattern of tool-use. Consistent with the findings observed for movements executed under visual guidance (Cardinali et al., 2009), blindfolded participants display longer latencies and smaller peaks amplitudes after using a tool they never saw, nor used before (Martel et al., 2019). Altogether, these findings stress the crucial role of proprioceptive inputs in updating the body estimate.

Yet, vision is critical to maintain a coherent sense of the body (de Vignemont, 2014) and impacts our control of action. When shown with a hand larger than their own, participants reduce their maximum grip aperture while grasping an object (Marino et al., 2010). Akin to the kinematic effects observed when the tool is no longer held, this modified grasp kinematics is observed also when the enlarged hand is no longer visible, thus suggesting that visual inputs contribute to update the effector state estimate (Bernardi et al., 2013). In the same vein, Miller and collaborators observed typical (tactile) signatures of tool incorporation on a stationary arm, which was merely seen to use a tool-via mirror reflection of the opposite arm (Miller et al., 2017). Ganesh and colleagues proposed that vision would be particularly important when using a new tool, for which no sensorimotor associations have yet been built (Ganesh et al., 2014). Observing online kinematic changes, i.e., during tool-use, they suggested that arm-length representation is initially shortened and subsequently elongated. This contraction-elongation pattern corresponds to that we recently observed in a developmental population of children and adolescents (Martel et al., 2020, under revision). Consistent with the weak reliance on proprioception at early developmental stages (Assaiante et al., 2014), the monitoring and update of the children's body estimate would particularly rely on vision (Cignetti et al., 2013). These findings thus raise the question of whether vision would actually contribute to updating of the body estimate for motor control, particularly in the early stages of life.

Here we thus tested the hypothesis that the availability of vision is important for the development of plastic representation of the arm. Accordingly, we searched for the presence of kinematic signatures of tool incorporation (i.e., after a short period of tool-use) in two blind populations consisting of congenitally impaired participants (early blind group) and participants whose visual impairment emerged after their fifth year of life (late blind group). Based on findings from the developmental population showing initial reliance on vision for motor control (Assaiante et al., 2014; Martel et al., 2020, under revision), we hypothesized that the lack of visual inputs during development would hamper the ability to update the body state estimate. Hence, we expected absent or reduced kinematics modifications following tool-use in congenitally blind participants. By comparing performance in early and late blinds, we further aimed at determining whether having experienced vision during infancy and childhood is sufficient for body representation plasticity to occur.

METHODS

Participants

Two groups of blind individuals (early and late blind) participated in the study. The early blind group (EB) was composed of 20 adults (9 females; 4 left-handed; mean age \pm SD: 20.39 ± 3.11 ; range: 18–31 years). The late blind group (LB) was composed of 16 adults (8 females; 1 left-handed; mean age \pm SD: 22.34 ± 5.59 ; range: 18–37 years). The EB group was constituted by congenitally blind individuals. The mean age of blindness onset (first symptoms) in the LB group was 10.59 years (range: 5–23 years) and the mean duration of blindness before participating in the study was 11.75 years (range: 4–28 years). In all cases, blindness was attributed to peripheral deficits with no additional neurological problems (see Table 1 for details). To prevent any confound from residual vision, all participants were blindfolded during the experiment. They all gave audio-recorded informed consent prior to their enrollment into the study, which was approved by the French ethics committee (Comité de Protection des Personnes Sud-Est IV) and received a monetary compensation for their participation.

Table 1. Demographic and clinical characteristics of early and late blind groups

Subjects	Age	Sex	Handedness	Cause of blindness	Onset	Visual deficit duration
Early Blind (EB)						
EB1	18.9	F	R	Albinism, nystagmus	0	18.9
EB2	31.3	F	R	Oculocutaneous albinism	0	31.3
EB3	19.6	M	R	Genetic: X-linked juvenile retinoschisis	0	19.6
EB4	18.6	M	R	Nystagmus, hypermetropic astigmatism	0	18.6
EB5	19.2	M	L	Congenital Anomalies of the Optic Nerve	0	19.2
EB6	22.0	F	R	Microphthalmia, nystagmus, coloboma	0	22.0
EB7	18.7	F	R	Myelin optic nerve malformation	0	18.7
EB8	26.7	M	R	Congenital myopia and cataract, retinal detachment right	0	26.7
EB9	19.6	M	R	eye	0	19.6
EB10	19.0	M	R	Genetic: Retinitis pigmentosa	0	19.0
EB11	19.4	M	L	Genetic	0	19.4
EB12	20.0	F	R	Genetic: Retinitis pigmentosa	0	20.0
EB13	20.0	F	L	Congenital Amaurosis of Leber	0	20.0
EB14	20.0	M	R	Cerebral haemorrhage at birth	0	20.0
EB15	19.0	M	R	Nystagmus, hypermetropic astigmatism	0	19.0
EB16	19.0	F	R	Congenital Amaurosis of Leber	0	19.0

EB17	19.0	M	R	Congenital malformation of the eye and glaucoma	0	19.0
EB18	19.0	F	L	Congenital Amaurosis of Leber	0	19.0
EB19	20.0	F	R	Aniridia	0	20.0
EB20	19.0	M	R	Cataract Juvenile retinoschisis	0	19.0
Late Blind (LB)						
LB1	26.0	F	R	Stargardt disease	5	21.0
LB2	18.7	F	R	Accident, opaque crystalline	6	12.7
LB3	34.2	F	R	Glaucoma	6	28.2
LB4	18.3	M	R	Hereditary, Retinitis pigmentosa	6	12.3
LB5	18.5	M	R	Genetic	7	11.5
LB6	19.8	F	R	Wolfram Syndrome	8.5	11.3
LB7	21.1	M	R	Meningitis	9	12.1
LB8	19.1	M	R	Leber's hereditary optic neuropathy	10	9.1
LB9	19.5	F	R	Optic chiasmal cancer, left hemianopia	14	5.5
LB10	21.3	M	R	Leber's hereditary optic neuropathy	14	7.3
LB11	19.0	M	L	Genetic : Stargardt disease	15	4.0
LB12	20.1	M	R	Compression of the optic nerve at the level of the	16	4.1
LB13	19.0	F	R	chiasma	6	13.0
LB14	24.0	F	R	Retinitis pigmentosa	10	14.0

LB15	22.0	F	R	Retinitis pigmentosa	14	8.0
LB16	37.0	M	R	Usher syndrome	23	14.0
				Usher syndrome		

Apparatus

Three infrared light emitting diodes (IREDs) were placed on kinematically relevant locations on the dominant hand of the participant: on the medial lower corner of the thumb nail, on the lateral lower corner of the index finger nail and on the skin proximal to the styloid process of the radius at the wrist level. Three more IREDs were located on the tool: on its “fingers” and on the distal part of the shaft (“wrist”). The transport component of the movement was characterized by the kinematic parameters of the wrist marker, while the grasping component was characterized by the thumb and index displacement derived from the thumb and index finger markers. Spatial localization of the markers was recorded with an Optotrak 3020 (Northern Digital Inc, Ontario, Canada; sampling rate: 200Hz; 3D resolution: 0.01mm at 2.25m distance). For each free-hand reach-to-grasp movement, we extracted and analyzed off-line (with a Matlab custom program) the following parameters: latencies and amplitudes of the wrist acceleration, velocity and deceleration peaks (transport component), and latency and amplitude of the maximum thumb-index distance (Maximum Grip Aperture) (grasping component). For each movement we measured the overall movement time as the time between the beginning of the movement and stabilized grasp on the object (before object lifting). If participants accidentally missed the object in free-hand reaches, we repeated the trial at the end of the session. For the arm length estimation task (see Procedure), we computed the distance between the starting switch and the end point of the index finger displacement using the IRED marker on the index finger. We measured the actual length of the participants’ dominant forearm (from the wrist to the elbow) for comparing it to the estimated length.

Procedure

Procedure was similar to what reported by Martel and collaborators (Martel et al., 2019). In detail, all participants were first blindfolded and then, with the help of the experimenter, entered the experimental room. They were comfortably seated in front of a table, with their dominant hand in a pinch-shaped posture (thumb and index fingertips touching) on a start-switch. Their non-dominant hand was positioned to contact the lower corners of the target object, constituted by a wooden block (10 * 2.5 * 5cm, 96g) and located at 35 cm from the start-switch. The object was placed by the experimenter between the thumb and index fingertips of the participants, who were instructed to keep their non-dominant hand flat, palm down on the table and keep gentle contact with the objet.

Participants performed three sessions: a pre and a post session, separated by a tool-use session (see Figure 1). The pre and post tool-use sessions were identical and included a free-hand reach-to-grasp movements task and a forearm length estimation task. Order of free-hand reach-to-grasp movements and forearm length estimation tasks was counterbalanced across the participants.

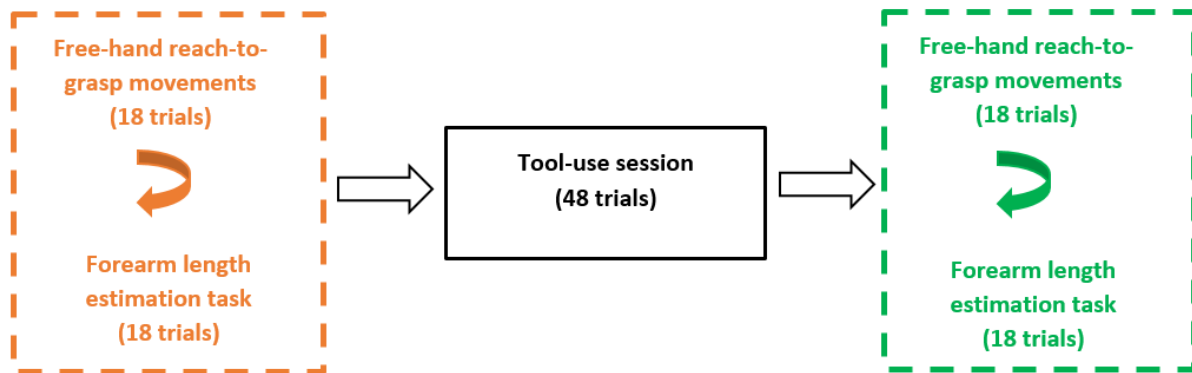


Figure 1. Experimental protocol. The two pre- and post-tool-use tasks were proposed in a counterbalanced order across participants.

Free-hand reach-to-grasp movements

Participants performed eighteen trials of free-hand reach-to-grasp movements with their dominant hand. They started in a pinch-grip position, i.e. the tips of the thumb and the index in contact, pressing down the starting switch. After a random delay (range 1000–2000 ms), an auditory ‘go’ signal was presented and participants had to reach and grasp the object between thumb and index finger of their dominant hand, lift it then place it on the table and go back to their starting position.

Forearm length estimation task

Participants performed eighteen trials to estimate the length of their forearm by sliding their dominant index fingertip horizontally, along the proximal edge of the table, from the start-switch till the point they judged to cover a distance matching the one between their elbow and wrist. To make sure all participants estimated the correct body part, participants were touched only once, at the beginning of each forearm length estimation task (pre and post), on the elbow and wrist of their dominant arm, recalling them what was the anatomical distance to be

estimated. Once a trial was performed, participants got back to the starting position and waited for an acoustical ‘go’ signal to perform the next trial. Notably, this task involves no pointing or implicit knowledge of the body posture such as in the forearm bisection task (Garbarini et al., 2014; Sposito et al., 2012), typically used to investigate the body schema, but rather investigates the explicit knowledge of arm length. Estimated length was derived from the coordinates of the starting position point and the end point of the index finger displacement. The actual forearm length measurement was done at the end of the experiment.

Tool-use session

The tool-use condition consisted of four blocks of twelve reach-to-grasp movements using a tool (48 trials in total). At the beginning of each trial, participants were instructed to place the tip of the tool, kept in a pinch-grip posture as for the hand, on the same starting switch used in the pre- and post-tool-use phases and wait for an acoustic go signal. Then they had to reach, grasp, and lift the same target object used in the free-hand reach-to-grasp task, but with the tool. The tool consisted in an ergonomic handle (10 cm-long), a 30 cm-long rigid shaft and an articulated “hand” composed by two curved prongs allowing a stable grasping movement. The tool was controlled by squeezing the handle with the entire hand and digits: closing the hand in a fist-like posture would bring the tip of the prongs to contact while opening the hand would release the grasping. Participants were not allowed any previous practice with the tool and had never used it before. Participants were however allowed to explore it haptically before the beginning of the session to understand how it operated.

Statistical analysis

One participant of late blind group, did not correctly understand the length estimation task instructions, hence their data for this task have been discarded from the analysis of the forearm length estimation task only. And so, analysis were conducted on data from 15 participants from the LB group (7 females; 1 left-handed; mean age \pm SD: 21.55 ± 4.79 years; range from 18.33 to 37).

As in previous studies with free-hand reach-to-grasp movements, given the interdependency of the kinematics parameters and movement components (Bahmad et al., 2020; Cardinali et al., 2016; Martel et al., 2019), we performed a full factorial design permutation analysis (Basso & Finos, 2012; Finos & Basso, 2014) using the flip package on R (Finos, 2015; R Core Team, 2018). The full factorial design was with Group (EB/LB) as a between-subject factor and Session (Pre/Post) as a within-subject factor to evaluate the effect of tool-use session across groups. Although similar to an ANOVA, the interaction test in this permutation analysis differs in the calculation as it is the comparison of the differences between pre- and post- among the independent groups. Importantly, this is designed for a multivariate framework; it allows to combine the significance of the kinematic parameters for the entire movements, for the transport phase (amplitudes and latencies of peaks the wrist acceleration, velocity and deceleration) and those for the grasping phase (amplitudes and latencies of Maximum Grip Aperture), to obtain one global p-value for the movement, or for the transport and the grasping component separately. These global p-values are obtained via Nonparametric Combination (NPC; Pesarin, 2001) of partial p-values testing the single parameters. The global p-value shows significance when half of parameters are significant or borderline significant, which attests of the consistency and robustness of the effects. The methodology accounts for dependence among tests through a nonparametric approach based on the joint (i.e. multivariate) permutation distribution. The analysis of the forearm length estimation task was done with a paired-samples T-test to determine whether this task is modified after tool-use.

The lack kinematics signatures of tool incorporation in the post-tool-use free-hand reach-to-grasp movements in the blind would stress the importance of vision during development to scaffold the body metrics plasticity. A difference between the early (kinematics changes absent) and late blind group (kinematics changes present) would inform about the importance of early availability of visual inputs for the acquisition of the ability to incorporate tools in the body representation.

Results

Tool-use does not modify free-hand reach-to-grasp movements in blind participants

The permutation analysis revealed no significant interaction between Group (EB/LB) * Session (Pre/Post) when the entire movement was considered (*Fisher combination*; $K = 9.03$, $p = .37$). The transport component did not show either any significant interaction (*Fisher combination*; $K = 3.46$, $p = .9$). Finally, the grasping component was differently affected by Session in the two Groups (*Fisher combination*; $K = 4.51$, $p = .047$), however neither group significantly modulated the grasping component (EB: $t = -1.30$, $p = .207$; LB: $t = 1.85$, $p = .087$; figures 2&3).

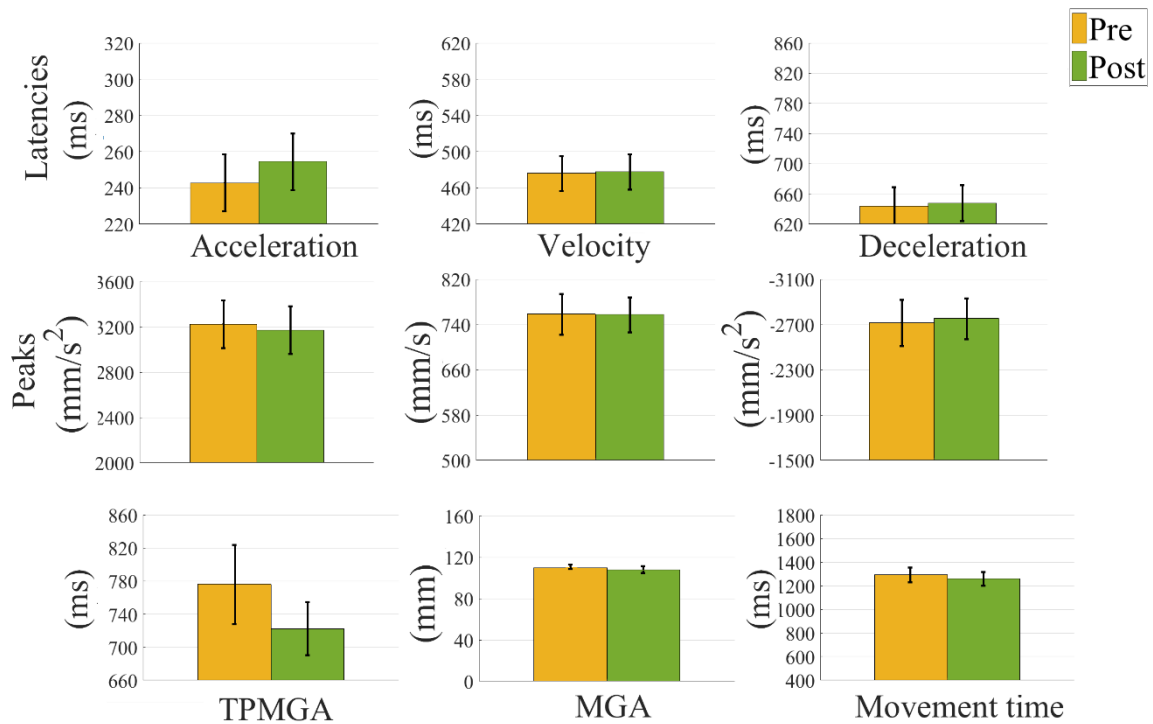


Figure 2. Kinematics of free-hand reach-to-grasp movement were not affected by the tool-use session in the Early Blind group (p values between .28 for TPMGA and .97 for the amplitude of the wrist velocity). Error bars indicate SEM. MGA stands for Maximum Grip Aperture.

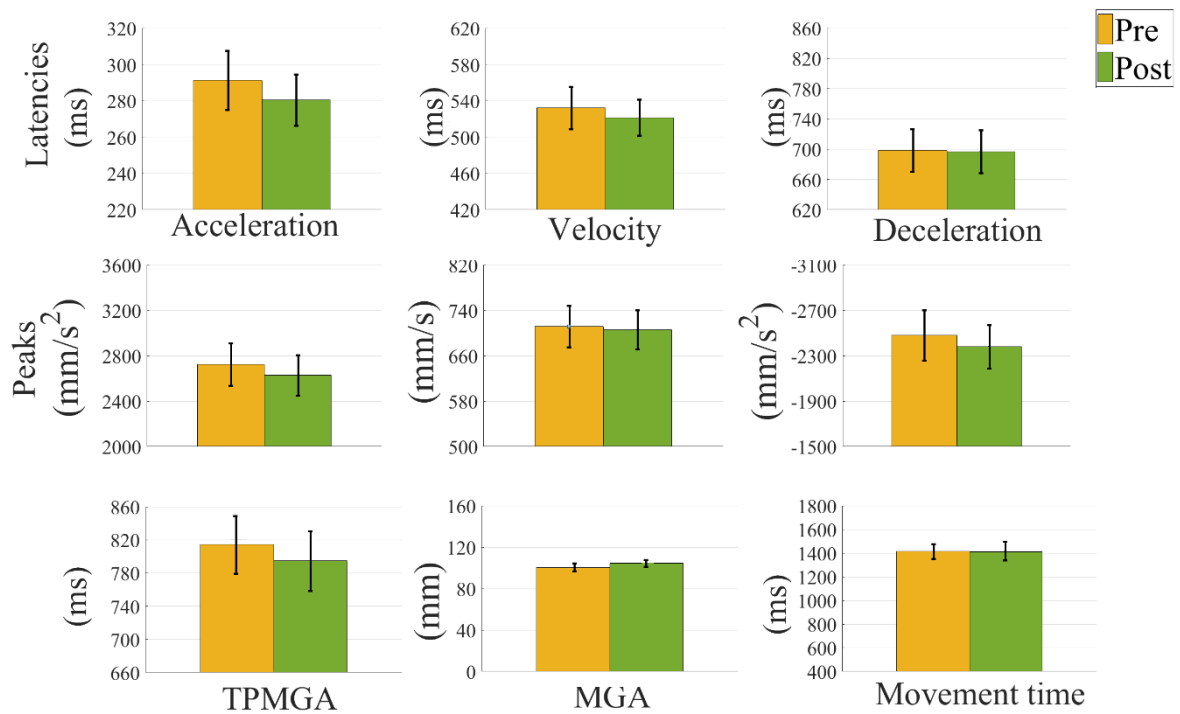


Figure 3. Kinematics of free-hand reach-to-grasp movement were not affected by the tool-use session in the Late Blind group (p values between .10 for MGA and .97 for the movement time). Error bars indicate SEM. MGA stands for Maximum Grip Aperture.

Tool-use decreases forearm length estimation in early blind participants

When comparing the forearm length estimation before and after tool-use, paired samples T-Test revealed that the estimated length decreased after tool-use in the EB group only (*pre*: $297.1 \text{ mm} \pm 17.81$ vs. *post*: $272.3 \text{ mm} \pm 15.72$; $t(1,19) = 2.51$, $p = .022$, $d_z = .58$). Participants forearm estimation corresponded to 113% and 103.7% of their actual forearm length before and after tool-use, respectively ($t = -2.51$, $p = .019$; *figure 4*). On the contrary, forearm estimated length was not significantly modulated in the Late Blind group (*pre*: $256.2 \text{ mm} \pm 11.03$ vs. *post*: $249.8 \text{ mm} \pm 11.93$; $t(1,14) = 0.99$, $p = .34$, $d_z = .25$).

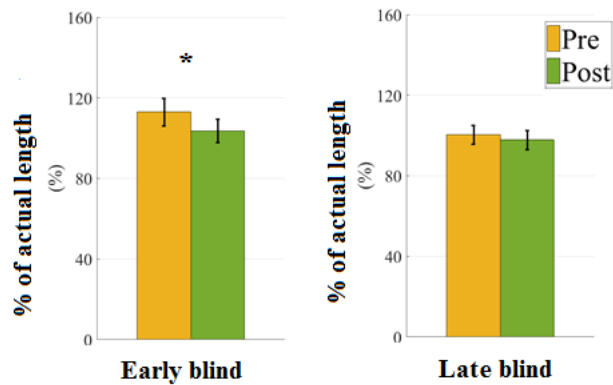


Figure 4. Forearm length estimation decrease in the Early Blind group only. *Bars indicate S.E.M. Asterisks denote significant differences in pre/post.*

DISCUSSION

Does visual experience contribute to the plastic incorporation of tools into body representation? To answer this question, we investigated two groups of participants that differed regarding their early (congenital) or late onset of blindness (> 5 years). Would vision be ancillary to proprioception, early and - even more so - late blind people should display the pattern of kinematic changes typically observed after tool-use in sighted individuals: free-hand reach-to-grasp movements would feature longer latencies and smaller peak amplitudes. This well-established pattern has indeed been reported when sighted adults perform actions both under visual (Cardinali et al., 2009, 2012) and proprioceptive guidance (Martel et al., 2019), and has been proposed to represent the hallmark of implicit tool incorporation in the body state estimate (also referred to as body schema, see for review Martel et al., 2016). Contrary to this possibility, neither the early, nor the late blind participants displayed such kinematics signatures. Interestingly, early (but not late) blind participants did show sensitivity to tools use effects in another task: namely, the explicit forearm length estimation. So far reported to be immune to the effects of tool-use in sighted individuals, (Bahmad et al., 2020; Martel et al., 2019) the latter task is thought to reflect a different, conscious body representation (typically referred to as the body image). These findings provide compelling evidence that vision not only does indeed contribute to, but also appears critical for the plastic ability to incorporate tools to develop.

After a short period of tool-use, blind participants did not show any change in their free-hand movement kinematics. This is contrary to what has been consistently reported in sighted participants (Baccarini et al., 2014; Cardinali et al., 2009, 2012; Miller et al., 2014, 2017; Sposito et al., 2012; Bruno et al., 2019), even when blindfolded and, as here, allowed with only haptic information about the novel tool to use (Martel et al., 2019). Most interestingly, blind participants did not update their effector metrics following tool-use irrespective of whether vision was available in their childhood. This would imply that having daily visual experience since early in life –and for a relatively prolonged period - is mandatory to allow body representation plasticity following tool-use to emerge.

The role played by vision in scaffolding this ability could be relatively direct, contributing a high-resolution metric of the bodily effectors to nourish the state estimate of the body (Camponogara & Volcic, 2019; Shadmehr & Krakauer, 2008). Given its superior spatial precision (van Beers et al., 2002) vision may add relevant information to proprioception to achieve flexible motor control (Bozzacchi et al., 2018; Juravle et al., 2018; Reichenbach et al., 2009). This would be particularly important during development, when (sighted) children rely heavily on vision compared to their poor proprioception, requiring a relatively long time to develop fully (Assaiante et al., 2000, 2014). Lack of vision during development may thus impact directly the building and updating of body state estimates relative to motor effectors.

One may also consider that lack of vision during development might alter this ability more indirectly, for example by hampering proprioceptive tuning. In this respect, the available findings are quite inconsistent. Congenitally blind individuals tend to have lower performance when discriminating the spatial direction of reaching movements via kinesthesia (Fiehler et al., 2009), although functional imaging did not reveal any difference in activation patterns between congenitally blind and sighted participants (Fiehler & Rösler, 2010). Cappagli and collaborators (Cappagli et al., 2017) observed larger movement reproduction errors, thus impairments in spatial representations in the early blind, but no impairment in late blind participants. On the contrary, using a similar task early and late blind were reported to outperform sighted controls (Gaunet & Rossetti, 2006). Thus, while some have suggested that congenital blinds were impaired when the tasks required a metric representation of space (Cappagli et al., 2017; Gori et al., 2014), opposite evidence is gathered both in audition (Battal et al., 2019; Mattioni et al., 2018, 2020) and somatosensation (Grant et al., 2000; Van Boven et al., 2000), whereby early visual deprivation may trigger an enhancement of spatial abilities. In

addition, and most important in relation to the present work, congenitally blind individuals are known to behave as sighted ones in motor adaptation tasks where only proprioception is at stake (DiZio & Lackner, 2000; Miall et al., 2018; Sarlegna & Mutha, 2015). Thus, although future studies are needed to fully assessing the proprioceptive abilities of blind people, we consider very unlikely that the lack of kinematics effects reported here may be explained by poor proprioception. Indeed, even participants with late blindness onset (> 10 years on average), for who proprioception is reported being as good as in sighted (Cappagli et al., 2017), did not show any kinematic modifications. These findings further suggest that, once vision is lost, the visual experience during life before the onset of deficiency is not sufficient for the body representation to be updated by tool-use.

In sharp contrast with the lack of kinematics changes, as an implicit test of body representation plasticity following tool-use, our findings reveal that the early - but not late - lack of vision makes the explicit, conscious representation of one's arm length sensitive to the same tool-use activity. To date, neurotypical (blindfolded) adults have shown to be immune to changes in the so called body image representation, as measured by the explicit length estimation task (Martel et al., 2019). In keeping with these findings, here LB individuals were comparably accurate when estimating their arm length before and after tool-use. Instead, EB participants reported their forearm as being shorter after tool-use. Interestingly, a reduction of the explicit arm length representations has also been recently observed in adolescents, on the same tool-use paradigm, but under visual guidance (Martel et al., 2020, Under revision). This reinforces the dissociation between tool effects on implicit and explicit body representations (for review, see Martel et al., 2016). A classical way to study body representations, and especially the conscious Body Image, has been the Rubber Hand Illusion (RHI; see for review Kilteni et al., 2015; Martel et al., 2016; Tsakiris, 2010). In this illusion, stroking a rubber hand congruently with someone's real hand leads to a feeling of ownership of the rubber hand, and a drift of the position of the real hand toward the rubber hand. While blindfolded healthy and late blind participants experience the spatial recalibration of their hand's location, congenitally blind do not (Ehrsson et al., 2005; Nava et al., 2014; Petkova et al., 2012). This difference has been attributed to the fact that early vision allows the development of the default use of an external frame for multisensory action control (Röder et al., 2004, 2007, 2008). As they lack early vision, congenital blinds would thus not experience the RHI (Nava et al., 2014), or crossing effects when judging which of two stimulus came first with crossed arms (Crollen, Albouy, et al., 2017; Crollen, Lazzouni, et al., 2017; Röder et al., 2008) as they do not automatically externally remap the sensory inputs when

they do not need it (Dolk et al., 2013). This might suggest a link between the effect of tool-use on the explicit arm representation, and the ability to automatically code stimuli in an external reference of frame and deserves more investigation.

Recently we proposed that the processes involved in the plasticity of body representations imply the state estimation as one needs to update the length of the effector by comparing measured and predicted feedback (Cardinali et al, 2016; Martel et al., 2017, 2019). Sensorimotor processing with a tool is thought to repurpose mechanisms devoted to sensorimotor processing of the actual body (Miller et al., 2018) and involve both primary sensory and integrative areas of the brain such as the posterior parietal cortex (Gallivan et al., 2013; Jacobs et al., 2010; Johnson-Frey et al., 2005; Miller, Fabio, et al., 2019; Miller, Longo, et al., 2019; Valyear et al., 2007). This is in keeping with recent views proposing the main role of PPC is the state estimator (Medendorp & Heed, 2019) with a rostral (anterior) body-related pole, which estimates the state of the body, and a caudal (posterior) limb-unspecific environment-related one. Higher activity is observed in the posterior part of the PPC in congenital blind, as compared to sighted individuals during proprioceptively guided transport (Lingnau et al., 2014); this was interpreted as a change in the weight attributed to proprioceptive and visual inputs, as congenitally blind people do not automatically use external reference frames (Gaunet & Rossetti, 2006; Röder et al., 2004, 2007, 2008). One could thus speculate that blind individuals may rely on different processes for body state estimation, preventing the update of their represented limb length during tool-use. Overall, these considerations converge towards the need of refining the current models of motor control (Shadmehr & Krakauer, 2008) to better account for the body, and the weighting of different modalities in developing or pathological populations.

To conclude, our results show that blind individuals do not display the plastic body representation that are typical after tool-use and indicate that vision provides a major contribution to the ability to incorporate tools during development.

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GENERAL DISCUSSION

This thesis investigated the role played by sensory modalities, in particular vision and proprioception in the context of body representation's plasticity following tool-use. On the one hand, we focused on the contribution of both proprioceptive submodalities in the tool-induced body representations' plasticity. We particularly assessed proprioception in an old adults' population as an example of an unbalance between online submodality, thought to be accessed in real time and the off-line submodality (memory-based), thought to be stored in order to be accessed later on. Then, in the same population, we investigated the free-hand kinematics following tool-use, or conversely following a weighted-wrist control session. As a further aim, and in the same context of proprioceptive contribution in body representation's plasticity, we questioned whether the proprioception of the forearm would be affected after tool-use in young healthy adults. We investigated both the existence of these changes in acuity and the possibility they relate to the changes in the body schema that is updated following tool-use, with a focus on the changes in the represented arm length. Finally, to unveil the role of visual experience in these plastic phenomena we investigated whether blindness affects the ability of the brain to update the body representation following tool-use. After a brief summary of the results, we will turn discussing the overall findings in the context of the contribution and balancing between visual and proprioceptive modalities in the tool-induced body representation's plasticity phenomena.

1. Insights into the role of proprioception and body representation's plasticity

Main results

In the first chapter of experimental studies, we questioned the contribution of both proprioceptive submodalities in the plasticity of body representation induced by the classical tool-use paradigm. Healthy old adults were tested as a model of an asymmetry between submodalities; the off-line submodality being affected by age while the on-line modality is preserved (Bullock-Saxton et al., 2001). Participants were required to perform free-hand reach-to-grasp movements before and after a session of reaching and grasping with a tool that

elongated the length of their arm. Despite an altered off-line proprioceptive submodality, the old population displayed the typical, previously identified pattern of kinematic changes following tool-use (Cardinali, Brozzoli, Finos, et al., 2016; Cardinali et al., 2009, 2011, 2012; Miller et al., 2014; Miller, Longo, et al., 2017); that is, longer latencies and smaller peaks for most of the transport component parameters of free-hand reach-to-grasp movements. The important point to shed the light on is the correlation found between these kinematic changes induced by the use of the tool and the online proprioceptive acuity of this population: the best proprioceptive acuity is, the most the kinematic parameters changes after tool-use. Thus, even if proprioception in general is affected by age, the ability of the brain to incorporate the tool into the body representation is preserved, as long as online proprioception is preserved. Now, if we look at the tool incorporation phenomena in the framework of motor control, the online modality as the main proprioceptive input is in accordance with the need for a constant monitoring of the effector state estimate needed for tool incorporation. This finding extends to the healthy brain the observation made by Cardinali and colleagues on a single-case study of a deafferented patient (Cardinali, Brozzoli, Luauté, et al., 2016), reporting that tool incorporation is not possible in the complete absence of proprioception. Our findings go further by stressing the importance of online proprioception and by establishing for the first time a direct link between its acuity and the amount of kinematics incorporation of the tool in the control of movements.

Proprioception and the update of the body estimate for the motor control of tools

In order to execute an appropriate movement, one has to build a motor program through the inverse model that, in turn, is updated on the basis of sensory signals. As underlined in the introduction section, to avoid the delay of sensory signals, the sensory consequences of the movement are predicted in the forward model, thus enabling a better tuning of the action. Hence, body schema is suggested to be operationalized into a specific state estimate of the body (Martel et al., 2019). Tang and collaborators (Tang et al., 2016) proposed that reaching with a tool would not share a common motor program as when reaching with the arm, instead change in the state of the body would tune the inverse model. Accordingly, reaching with a tool would imply an update of the state of the arm in the internal model, adjusting the length parameter of the arm. In other words, the metric of the arm state estimate would be extended in order to (at least partially) include the tool. State estimation is thought to be a bridge between the (predicted) sensory signals and the update of the inverse models (Shadmehr & Krakauer, 2008). Yet, arm representation's plasticity following tool-use could originate from both asserted and

predicted feedbacks, depending on the current availability of the sensory information and the task's specific constraints. Thus, as a richer sensory information becomes available it is supposed to lead to a better-tuned model, and hence a better tool incorporation. This is well illustrated in the first experimental chapter of my dissertation that concerns the old adult's participants. The online readout of proprioceptive information not only provides a major contribution to the update of the state estimate, but also its acuity predicts the extent to which tool-use will impact subsequent freehand kinematics. Our results corroborate the notion that tool incorporation relies heavily on ongoing processing of position sense, and so the better the available acuity of the online proprioception, the better the incorporation phenomenon is observed, as indexed by the impact on subsequent free-hand kinematics.

Proprioception is crucial for the online control of tools. It allows us to manipulate and control the tip of the tool properly, in particular by localizing and orienting it in space. Hence, proprioception is tuned during a manipulation with tools, possibly allowing for a coherent yet helpful movement. Indeed, the second experimental part of my dissertation revealed that tool-use induced an improvement in proprioceptive acuity specific to the hand that used it.

Thus, tool incorporation phenomena induce at the same time a proprioceptive improvement for the arm that manipulates the tool and an elongated representation of the arm into the state of the body, and this would depend, at least in the aging population, on the available intact acuity of the online proprioception.

2. Insights into the role of vision and body representation plasticity

Main results

Through the third chapter of my experimental section, we tested the importance of visual experience on the body representation update following tool-use. Using the same tool-use paradigm, we tested two groups of blind participants that differs in term of visual experience during growth, and compared their kinematics after tool-use session. All the participants were blindfolded through all the experiment duration, and had never used the tool before. At the beginning of the experimental session, they were allowed to haptically explore the workspace and the tool. Then, they were asked to reach for an object with their dominant hand, before and after reaching it with a long mechanical grabber. They could localize the object relying on their proprioception, thanks to their non-dominant hand placed at the bottom of the target object. We

reported that the two blind groups did not show any significant modification of their kinematics after using the tool while, as reported previously, healthy participants do update their implicit body representation after tool-use based on somatosensory inputs (Martel et al., 2019). Irrespectively of the onset of blindness, somatosensation was not sufficient for the blind groups to update their implicit body representation (see *figure 7*). Correlations failed to show any link between visual experience during growth and the ability to incorporate tool into the body schema and thus update the representation of the arm.

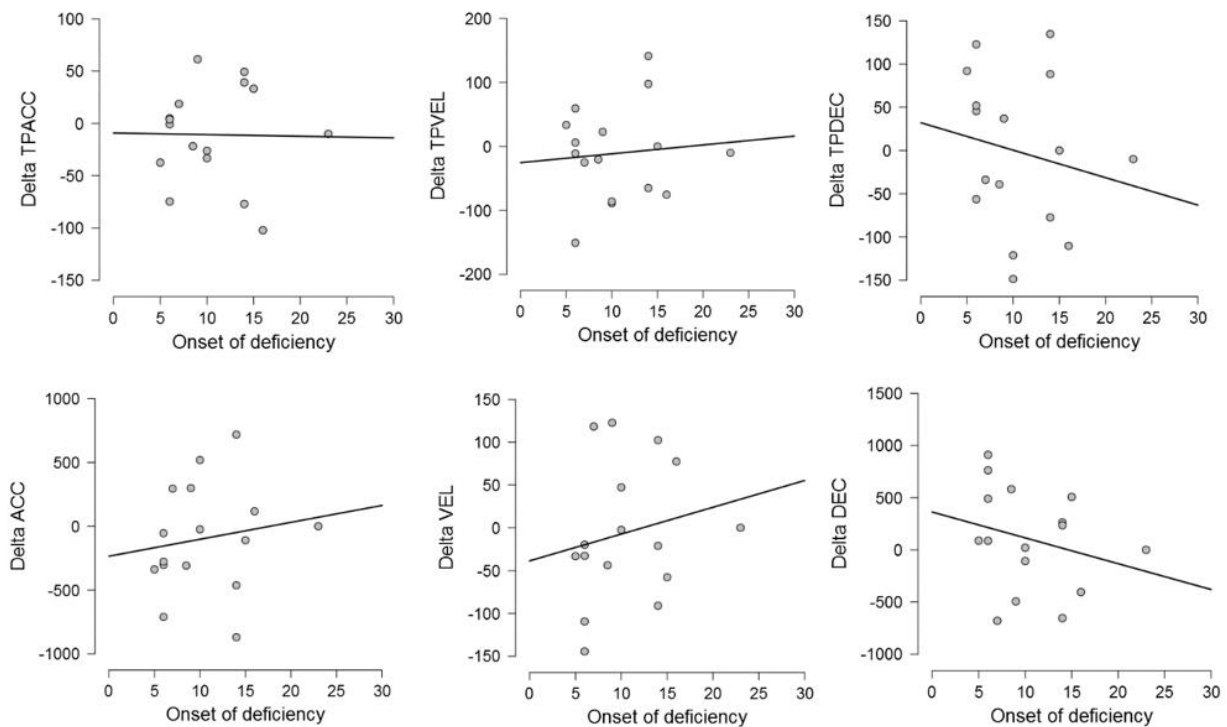


Figure 7. Correlation plots between the onset of visual deficiency and the kinematic changes induced by tool-use. Post minus pre difference in the tool-use session (Delta) are presented for each parameter (after Bonferroni correction). TP indicates the latencies to peaks. ACC, VEL and DEC denote the acceleration, velocity and deceleration, respectively.

Visual experience up to 10 y-o seems a determinant for the plasticity phenomena to occur. This could either mean that, having a daily visual experience shapes body representation in a way that allows plasticity, or that blind participants do not have typical somatosensation, or both. In the first view, vision would be primordial in allowing tool-induced body representation plasticity to occur; conversely lost early in life or during development, the update of the body representation would be impaired. Ganesh and colleagues have proposed that vision would be particularly important when using a new tool for which no sensorimotor associations have yet

been built (Ganesh et al., 2014). The authors reported first a shorter arm representation that was followed by the expected arm elongation. They explained this subsequent increase in body representation dimension as a result of the construction of new sensorimotor associations. And conversely, the immediate reduction in arm length representation would follow from the need of using a new tool, for which no sensorimotor association has yet been built. The control over this new tool would entail a safety margin, enabling to perform the reach under visual feedback guidance solely. Accordingly, the decrease in arm representation would depend on the use of visual feedback. Most recently, Martel and colleagues have proposed, on the basis of their findings in a population of children and adolescents, that the effector estimate update may particularly rely on vision (Martel et al, under revision). Indeed, before the growth spurt (before puberty and hence stability of body size), they observed a kinematic movement profile following tool use that was opposite to that repeatedly observed in adults, thus suggestive of a shortening rather than an elongation of the arm representation. Their findings revealed the complex dynamics of tool incorporation across development, possibly indexing the transition from a vision-based to a proprioception-based body representation plasticity. As long as adulthood is not reached, tool-use behavior would rather rely on vision alone, inducing a representational shrinking of the arm after tool-use. As they grow up, adolescents would progressively rely on proprioception, before being able to incorporate tools as adults do. In this case, the lack of vision from birth or till relatively late in life (i.e., till puberty is complete, Martel et al., 2020, Under review) would prevent vision from providing the necessary information for the body state estimate processes to develop normally. Hence the lack of kinematics signatures of tool incorporation in both congenital and late blind people;

According to an alternative view, the impact of the lack of vision may be more indirect, affecting proprioception. Cardinali and collaborators showed that somatosensation is indeed an important element allowing plasticity of body schema to occur (Cardinali, Brozzoli, Luauté, et al., 2016). In their longitudinal study on a deafferented patient, the authors observed that tool incorporation was not immediate in this patient and that, instead, she needed to build a new motor program to control the tool. First, the effect they noticed after tool session was not limited to the transport phase but affected the grip phase as well, while it is usually (Cardinali, Brozzoli, Finos, et al., 2016; Jovanov et al., 2015) specifically dependent upon the function and morphology of the tool used (Cardinali, Brozzoli, Finos, et al., 2016; Miller et al., 2014; Sposito et al., 2012). Also, the effect of tool-use was not generalized to pointing movement (Cardinali, Brozzoli, Luauté, et al., 2016), while in the typical tool incorporation paradigm, the lengthening

of the arm representation operates whatever the movement performed after tool-use (Cardinali et al., 2009; Martel et al., 2019). Further investigation of proprioception in the blind population would tease apart these two alternative explanations, although some considerations seem to suggest that the direct effect of the lack of vision may be better supported. On the one hand, Fiehler and collaborators found that untrained, congenitally blind individuals tend to have lower proprioception compared to healthy control group, and they suggested that this could be explained by the important role of integrating visual feedback in developing a good sense of proprioception to begin with. However, if blind individuals undergo orientation and mobility training early in life, they perform on par with sighted individuals (Fiehler et al., 2009; Fiehler & Rösler, 2010). Congenitally blind individuals who received training later (after the age of 12) did poorly (Fiehler et al., 2009). On the other hand, people who became blind later in life don't seem to have significantly different proprioception (Cappagli et al., 2017). This was explained by a “calibration” phenomena that blind had the chance to undergo early in life. Rather, several studies pointed to a somatosensory and proprioceptive superiority in the blind (add here the ref of the paper). The absence of any kinematic effects even in the late blind group, who was the most likely to have preserved proprioception, is a clear cue suggesting that the inability for blind people to update their body estimate may be due to a lack a vision during a relatively long and critical period of development.

3. Balancing/calibration between visual and proprioceptive information to induce the plasticity phenomena

As mentioned before, body representation's plasticity that allowed the incorporation of the tool into the state of the arm, could originate from both measured and predicted feedbacks, depending on the current availability of the sensory information and the task's specific constraints. Richer sensory information would lead to a better-tuned model, and hence a better tool incorporation. From this point of view, and after the three experimental chapters presented in my dissertation, we suppose that body representation plasticity phenomena following tool-use are the result of a balance between sensory modalities, accordingly both vision and proprioception would be fundamental for this phenomena to occur.

Indeed, vision alone is not sufficient to induce tool incorporation into the body representation, as evidenced by the case of a deafferented patient who did not show the kinematic signature of tool incorporation phenomena, thus underlying the central role of proprioception in this (Cardinali, Brozzoli, Luauté, et al., 2016). Our results indicate that a preserved online

proprioceptive modality can overcome the impairment of the offline modality and contribute to the update of body representation. When looking at the results of our old adults group and the one of healthy young adults (Cardinali et al., 2009), we can see that after tool-use session, free-hand reaching movements displayed protracted and lowered transport component parameters in five out of six parameters were significantly altered in the adults group, while three out of six parameters were significantly altered in the old adults group (see figure 8). Hence, the global pattern of body representation's plasticity following tool-use is still present in our population even if less pronounced compared to healthy adults. Our results showed that their online proprioceptive acuity predicts the extent to which tool-use will impact subsequent free-hand kinematics, corroborating the notion that tool incorporation relies heavily on ongoing processing of position sense. Using a tool not only calibrates the proprioception of the arm that used it, as shown in the second experimental chapter of the dissertation, but it also updates its representation as evidenced by the kinematic signature of tool-use.

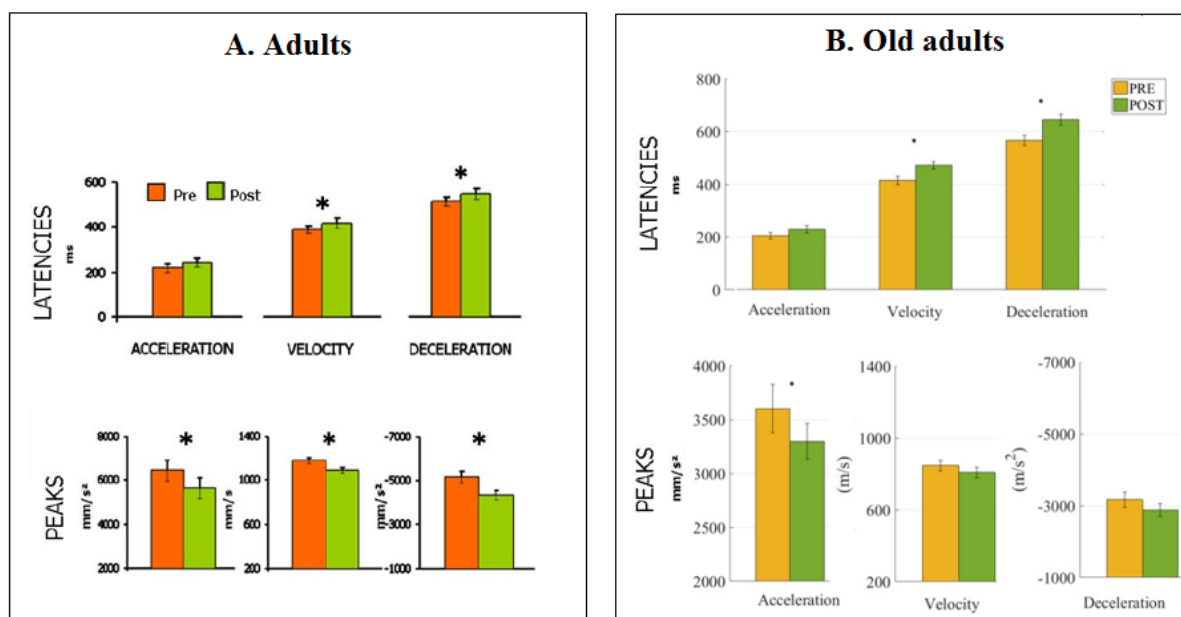


Figure 8. Free-hand movement kinematics modifications after tool-use in adults group (A) and old adults one (B). Bar graphs illustrate the S.E.M. Asterisks denote significant differences between pre (yellow) and post (green).

Proprioception alone is also not sufficient to induce the plasticity phenomena in blind participants, independently of their initial visual experience (at least up to 10 years on average), as presented in the third experimental chapter of my dissertation: Proprioception alone could not compensate for the lack of visual feedback in the induction of tool incorporation effects. This suggests that growing with visual inputs is crucial for allowing a tool-induced body

representation plasticity to emerge. If lost early in life or during development, the absence of vision definitively impairs the ability to update the body representation used to perform actions.

To conclude, body representation plasticity following tool-use is a phenomenon that relies on both proprioceptive and visual feedbacks. If one of them is totally lost during life it dramatically hampers the ability of the brain to update the body representation used to perform actions. While intact online proprioceptive can compensate for the offline proprioceptive deficits due to aging and maintain the ability to update body representation following tool-use, nothing could compensate for the early (and late) lack of vision: when lost, this plasticity would result impossible.

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