Perception and motor control in healthy and brain damaged patients

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Chapter 1

Introduction

1.1 Theories of motor control and the degrees of freedom problem

The complexity of common and well-practiced motor acts is often underestimated by the naïve observer, but even reaching for a cookie inside a jar and bringing it to our mouth is not a trivial task. It is composed of different stages and requires solving different problems, such as getting the spatial coordinates of the jar, planning a movement that will bring our hand inside the jar closing the grip only when we can actually hold the cookie (but not with excessive force, to avoid facing the risk of crumbling it), and coordinating hand and mouth movements.

Understanding how humans control motor tasks is a scientific endeavor that started before the scientific era: Meijer (2001) traces an history of the study of human movement, from Plato and Aristotle and up to the present days, but the most influential author in the field is probably Nikolai Bernstein, whose work was translated in English only after his death (Bernshteĭn, 1967). Among his other contributions, Bernstein is remembered for what has been called the *degrees of freedom problem*: the motor system is composed by a great number of parts that can move – too many, Bernstein holds, to be consciously controlled independently. Indeed, there are countlessly many ways to perform even the most simple of tasks. For example, Rosenbaum (2009) mentions touching the tip of the nose and argues that this movement can be executed in a great number of ways (with different fingers, with the palm of the hands, etcetera) many of which are not commonly adopted. In his overview of the motor control literature, Rosenbaum (2009) identified three more problems that have been the subject of scientific investigation:

- sequencing and timing, or how does the motor system choose the right order of actions to reach a goal and decide the speed and timing of execution
- perceptual-motor integration, or how perception and motor control are combined
- learning, or how we acquire new motor skills and become more proficient in using them

Most of the papers published in the field of motor control address one or more of these questions. To solve the degrees of freedom problem, Bernstein (1967) proposed that the relationship between the different components of the musculoskeletal system is based upon reciprocal interactions or, in its words, *synergies*. This approach can solve, at least partially, the degrees of freedom problem by introducing a fixed relationship (a synergy) between two (or more) components of a system to reduce its degrees of freedom.

Taking an example from geometry, a system consisting of two points in the Cartesian plane has four degrees of freedom - the x and y coordinates of each point. However, if we introduce a relationship between the points (i.e. by fixing the distance between them), we reduce by the number of free parameters of the system (see figure 1), as once we set the coordinates of the first point and one of the coordinates of the second point there is only one possible value for the last coordinate – *we cannot freely change it* without violating the relationship we established.
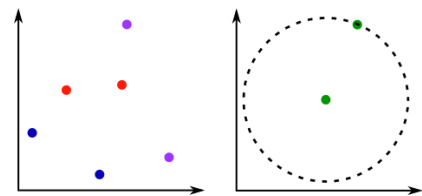

Figure 1.1 - <u>Left</u>: as there is no relationship between the points composing each couple (different colors), both the x and the y coordinate of each point can be freely set. <u>Right</u>: the relationship between the dots takes away one free parameter: the second dot must lay on a circle centered on the first one.

The concept of muscular synergies has recently resurfaced in terms of a neural mechanism of motor control. For instance, Ting and McKay (2007) define a synergy as "a vector specifying a pattern of *relative* levels of muscle activation" (p. 622), which is then modulated by a single neural signal. While the overall activation (and therefore speed, force or extent of a single movement) is determined by the central nervous system, the details regarding the activation of each single muscle are not – the brain "chooses" one of the available motor solutions. Synergies have been studied as a mechanism for obtaining postural control (Ting and McKay, 2007; Torres-Oviedo and Ting, 2010), but also as dynamic patterns of muscle activation. For instance, Ivanenko, Poppele, and Lacquaniti, (2004) found that five component factors (as identified by a principal component analysis) could explain about 90% of the variance in the electromyography data collected from limb and trunk muscles during walking at different speeds as well as during walking with bodily weight partly supported, but warn that the EMG factors only represent the temporal structure of muscle activity, and not spinal synergies as the ones proposed by Bizzi (D'Avella, Saltiel, and Bizzi, 2003).

While the concept of synergy has experimental data supporting it and provides an elegant answer to the degrees of freedom problem, Tresch and Jarc (2009) pointed out that there are arguments both in favor and against the role of muscle synergies as atomic components of movement . For instance, the authors cited Kutch and coll.'s (2008) work, in which they recorded

EMG data from several finger muscles and the forces expressed by the index finger of the participants as they pressed with it against three sensors placed in a rigid tube. By analyzing he variability in the forces produced by the participants the authors were able to examine the properties of muscle recruitment, finding that in their task muscles are recruited flexibly and independently rather than in stereotypical activation patterns that could have been explained as a result of the activation of synergies.

Another argument limiting the role played by muscular synergies is that motor tasks are often subjected to constraints that limit the number of viable ways in which they can be successfully executed. The *uncontrolled manifold* (UCM) *hypothesis* (Kang et. al, 2004; Scholz and Schöner, 1999) has been used as framework to investigate the role of muscle synergies. Plainly stated, the UCM hypothesis proposes that we can distinguish between variability in execution of a movement that does not impact negatively the accuracy ('good' variability) and variability that could lead to deviations from the intended result ('bad variability'). In a given task, variables that only give rise to 'bad' variability are controlled, while the ones that produce 'good' variability are not. For instance, in a task requiring participants to stand up from a sitting position (Scholz and Schöner, 1999) it was found that the horizontal position of the center of mass of the participants was controlled, as if the center of mass falls outside of the "base" of the standing person, he or she would lose balance (and therefore this is an example of bad variability), while the vertical position expressed a much greater variability, as it did not entail a similar risk for the stability of the participants (thus, this is an example of good variability). While some authors (Kang et al., 2004; Krishnamoorthy et. al, 2004) suggested that muscle synergies are required in the UCM hypothesis, and Latash (2008) even proposes that the UCM can be used as a computational tool to identify the synergies in different motor tasks, in Tresch and Jarc (2009) the authors argue that when referring to the UCM, the term *synergy* does not refer to the grouping of muscle activations as described before, but rather to the control of execution variables to regulate the variability that is relevant to the task.

Muscle synergies are not, however, the only way in which constraints are added to models of motor system with the goal of reducing the number of degrees of freedom. Another way of achieving this goal is to introduce a *minimum principle*: under this assumption, of all the possible movements that will produce the same trajectory in space, the central nervous system will select the one that minimizes some cost function. Amongst the theories following this approach are the **Minimum Jerk Model (MJM)**, put forward by Flash and Hogan (1985) and the **minimum torque-change theory** (Kawato, Maeda, Uno, and Suzuki, 1990; Wada and Kawato, 1995).

In the MJ the cost function that is minimized is the derivative, or rate of change, of acceleration (this is the definition of *jerk*). Movements that obey to this rule tend to be smooth and graceful, two characteristics common in movements executed by living beings. On the other side, the minimum torque-change theory postulates that the variable to be minimized is the total change over time of the torque (the tendency of a force to rotate an object around an axis or a fulcrum) exerted by the muscles at the joints. Besides jerk and torque-change, other studies proposed alternative minimum principles, like the minimization of energy (Nelson, 1983), of acceleration or of jolt (Dingwell, Mah, and Mussa-Ivaldi, 2004; Richardson and Flash, 2002; Stein, Oguztoreli, and Capaday, 1986).

While the MJM and the minimum torque-change model both showed good agreement with experimental data, it is interesting to note that some of the variables proposed as the target of the minimization (such as energy or torque-change) are physical quantities that depend on the dynamic of the musculoskeletal system, while velocity and its derivatives (acceleration and so on) are solely dependent on the kinematics of movement. This implies that it is computationally and analytically easier to compute the ideal trajectories when using models belonging to the latter group than to the former. However, it is worth noting that the minimum torque-change theory finds biological grounding on the fact that it implies reducing the wear and tear on the joints and articular cartilages (Ben-Itzhak and Karniel, 2008).

Of the aforementioned theories probably the most influential one is the minimum jerk model. This model was proposed to model planar multi-joint arm movements (Flash and Hogan, 1985) and was initially used to describe two phenomena: unconstrained (straight) point-to point hand movements and curved point-to-point movements. The authors proposed that the 'task' that is being accomplished when executing a straight movement can be described as "Generate the smoothest motion to bring the hand from the initial position to the final position in a given time." (*ibidem*, p. 1689), while curved trajectories can be obtained by adding a constraint in the form of a via-point that the trajectory must cross before reaching the final target. It is worth noting that in this model time is not a free parameter but must be fixed in advance, otherwise it would tend to infinity (since jerk is the rate of change of acceleration over time, increasing the time would, ceteris paribus, decrease the jerk), and that the movements were modeled as starting and ending with zero speed and acceleration (that is, in a resting state)

The model proved to be successful not only because of its ability to fit behavioral data, but also because it could describe both straight and curved paths using a single optimization principle and predicted a number of features of human movements: invariance under translation and rotation

of the workspace, scaling of trajectories with time and amplitude, the coupling between curvature and speed and the isochrony principle (Flash and Hogan, 1985). The model was confirmed by several subsequent studies and expanded to describe a wider range of movements (Paolo Viviani and Flash, 1995), most notably by introducing a way to concatenate multiple submovements abiding to the minimum jerk principle.

I will refer globally to these characteristic of human movements (smoothness or minimum jerk, isochrony and coupling between speed and curvature) as 'motor laws', a term in which I will also include Fitts' law (Fitts, 1954), as it was the first one of the first mathematical expressions of motor control principle and describes a now widely-known phenomenon, the tradeoff between speed and accuracy in the execution of movements.

1.2 Motor Laws and kinematic aspects of human movement

Human movement is characterized by some distinguishing features, which have often been described in mathematical terms. The first that has been stated is Fitts' Law, which links the speed of a pointing movement to both the distance between the starting point and the target, and the size of the target itself . This law has been formulated in several different ways, amongst which the so-called 'Shannon form' is:

$$T = a + b_{log2}(1 + \frac{D}{W})$$

in which *T* is the average movement time, *a* is the start time of the movement (the intercept of the function), *b* is a parameter that represents the speed of the movement, *D* is the distance from the start of the movement to the end and *W* is the width of the target. It is thus easy to see that this equation expresses an inverse relationship between speed and accuracy: when the target is narrower movement must be more accurate, thus the average movement speed decreases. On the other hand, a larger target allows for a less accurate, but faster, movement. Fitts' law has been investigated by psychologists, who found that it correctly describes reaching movements executed with different limbs (Errol, 1991) , that it is valid for both physical movement and mental imagery (Sirigu et al., 1996) and that also holds for action perception (Grosjean et al., 2007). Fitts' law also received attention from computer scientists studying human-computer interfaces (see Soukoreff and MacKenzie, 2004), who applied successfully Fitts' law to movements performed with pointing devices and applied the principle to the design of user interfaces.

Another well-known mathematical formula describing an aspect of human movement is the so-called **2/3 power law**, first proposed by Lacquaniti, Terzuolo, and Viviani (1983). This law, which was firstly found in drawing and scribbling movements links a geometrical aspect of the movement path (curvature) with a kinematic feature (instantaneous velocity). This can be equivalently expressed in a number of mathematical formulations, amongst which

$$V = kR^{1/3}$$

where *V* is the tangential velocity of the movement and *R* is the radius of curvature (the reciprocal of curvature, or of the how much the path deviates from being a straight line) while *k* is a velocity gain factor that can be held to be piecewise constant. In fact, this law states that velocity has an inverse relationship with curvature and thus human movements are characterized by higher speed on straightaways and slowing down on curves. Figure 1 shows the relationship between speed (v) and curvature (k) in a movement obeying to the 2/3 power law. As the law predicts, high curvature

parts of the path (marked in the figure with black crosses) are the ones where the movement slows down the most.
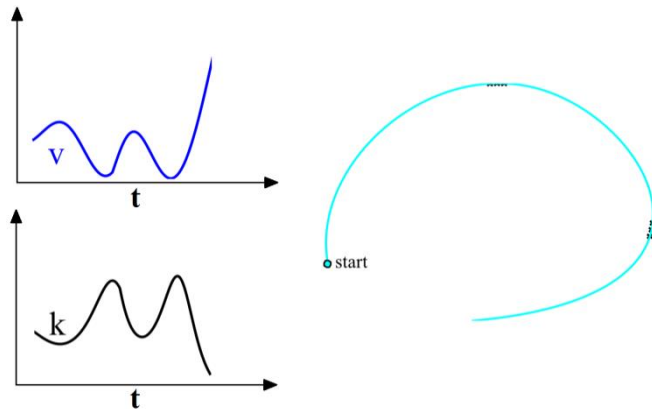

Figure 1.2 - Relationship between speed and curvature in an hypothetical movement following the 2/3 PL. Velocity (v) is plotted on the top left, curvature (k) on the bottom left and the path of the movement on the right

This law has been verified in perception (see section 2.2) , in drawing (Lacquaniti et al, 1983), in the motion of the eyes during smooth pursuit tasks (De' Sperati and Viviani 1997) and in human locomotion (Ivanenko et. al, 2002; Vieilledent et al., 2001). However, some of the strongest evidence in support of the hypothesis that the 2/3 power law is actually coded in neural circuits and does not simply arise from the characteristics of the musculoskeletal system comes from the results of Schwartz and Moran (1999), who found that the 2/3 power law can be extrapolated from the cortical activity in motor areas during drawing movements performed by monkeys.

While the two-thirds power law has been experimentally proven for movements in two dimensions, its original formulation has been modified and generalized to 3D movements (Maoz, Berthoz and Flash, 2009). The resulting formula is known as the one-sixth power law:

$$V = kR^{1/3}|\tau|^{-1/6}$$

where k and R are, as before, the velocity gain factor (or speed gain factor), and the radius of curvature, and τ is the torsion, or a measure of how sharply the curve is twisting in the space. Other mathematical models (summarized in Table 1) have been proposed to describe the relationship between velocity, curvature and torsion.

Set exponent power laws		Free exponent power laws	
Two-thirds power law	$V = \alpha \varkappa^{-1/3}$	Curvature power law	$V = \alpha \kappa^{\beta}$
One-sixth power law	$V = \alpha \varkappa^{-1/3} \tau^{-1/6}$	Curvature-torsion power law	$V = \alpha \kappa^{\beta} \tau^{\gamma}$
One-third total-curvature power law	$V = \alpha(\sqrt{k^2 + \tau^2})^{-1/3}$	Constrained curvature-torsion power law	$V = \alpha(\kappa \sqrt{\|\tau\|})^{\beta}$
		Total-curvature power law	$V = \alpha(\sqrt{k^2 + \tau^2})^{\beta}$

The laws summarized in Table 1 can be divided in two groups: *free* and *fixed* exponent. The difference between the two groups is that in the fixed exponent laws the strength of the relationship between curvature and speed is fixed and given by the exponents themselves, while in free exponent power laws the exponent is another free parameter of the model. The exponents have been shown to be dependent both on the nature of the movement being analyzed (such as walking or drawing) and on the shape of the movement itself (Hicheur et al., 2005), and therefore free exponent power laws can describe a wider range of movements. Furthermore, when considering long and continuous movements, it is often found that different parts of the movement are characterized by different velocity gain factor (α), a phenomenon that has been regarded as evidence for motor segmentation (Viviani and Cenzato, 1985).

It should be noted that the two-thirds power law and the one-sixth power law are in fact both incarnations of the same geometrical principle: constant equi-affine speed (Flash and Handzel, 2007). This result gave rise to the hypothesis that the brain could use geometries different from the Euclidean one when planning or executing the movement, or even a mixture of different geometries, depending on the nature of the task and on the shape of the paths themselves (Bennequin et al., 2009)

Building on these results, Polyakov et al. (2009) found that for some geometrical shapes (namely, parabolas), movements that abide to the 2/3 power law (or, equivalently, constant equi-affine speed) also satisfy the constraint of minimum jerk. Furthermore, in this study the authors found that movements performed by monkeys could be accurately described as sequence of parabolic segments. Therefore, not only this result provides further evidence in support of the convergence of the 2/3 power law and minimum jerk model, but also proposes a working hypothesis for identifying the single segments that compose complex movements.

Another feature of human movements that has long been known is the **isochrony** (Viviani and Schneider, 1991). This notion refers to the experimental finding that, for biological movements, movement speed increases with the length of the movement itself: for instance, analyzing motor data recorded from subjects that were asked to draw ellipses of different sizes and eccentricities it has been shown (Bennequin et al., 2009) that the mean speed when drawing bigger ellipses was higher than with smaller ones. In human movements, isochrony can be expressed in two different ways: global and local. While *global isochrony* refers to the phenomenon just mentioned, *local isochrony* refers to the structure of a single movement that can be decomposed in smaller parts and postulates that the average speed is higher when tracing a long segment than when tracing a short one.

Isochrony, minimum jerk and the two thirds power law are not necessarily alternative descriptions of biological motor act: as stated before, MJM predicts local isochrony and the inverse relationship between speed and curvature (Viviani and Flash, 1995), and for some classes (Polyakov et al., 2009) of movements the MJM and the two thirds power law are equivalent. It is therefore probable that these features are not dependent on different factors, but rather represent deeply interlinked aspects of biological motion.

1.3 Kinematics of reaching and grasping

Reaching and prehension are amongst the most common and motor tasks and have been the focus of much scientific investigation. Scholars investigated these arguments mainly with two different approaches: analysis of the hand's trajectory (Kaminski, Bock, and Gentile, 1995; Lacquaniti and Soechting, 1982) and analysis of the joints configuration (Lacquaniti and Soechting, 1982; Soechting and Lacquaniti, 1981).

Early studies investigating point to point hand trajectories, as in reaching movements, showed that movements are almost straight and exhibit a bell shaped speed profile (Abend, Bizzi, Morasso, and others, 1982; Abend et al., 1982; Georgopoulos, Kalaska, and Massey, 1981) which remains consistent regardless of movement execution times. These features of human movements are also present in some models of prehension. In fact, the first model of human prehension movements has been formulated by Jeannerod (1981), who modeled it as a motor act composed of two components acting independently: the *transport* of the hand towards the object to be grasped and the *grasp*, or the gradual opening and closing of the fingers needed to take hold of the object. We could in fact say that in this model, prehension equates to reaching and grasping. Jeannerod proposed that each component constituting the act of grasping composes an identifiable system with its own input and output and distinct visuomotor channels (see Figure 4) as the neural substrates of each component. In particular, for reaching he proposed a pathway comprising the parietal operculum (PO), projecting to both the medial intraparietal area (MIP) and the medial dorsal parietal

Figure 1.3 - Anatomy of visuomotor channels involved in grasping.A represents the reaching pathway, B the grasping one (taken from Jeannerod, 1997).

area (MDP), which are connected to the dorsal premotor cortex and then to the primary motor area (pathway A in Figure 4). For grasping the areas involved are dorsal ES, anterior intraparietal area (AIP) and ventral premotor cortex (PMv) (pathway B in Figure 4). Subsequent studies supported the idea of two distinct neural pathways by providing examples of selective impairment of the reaching or of the
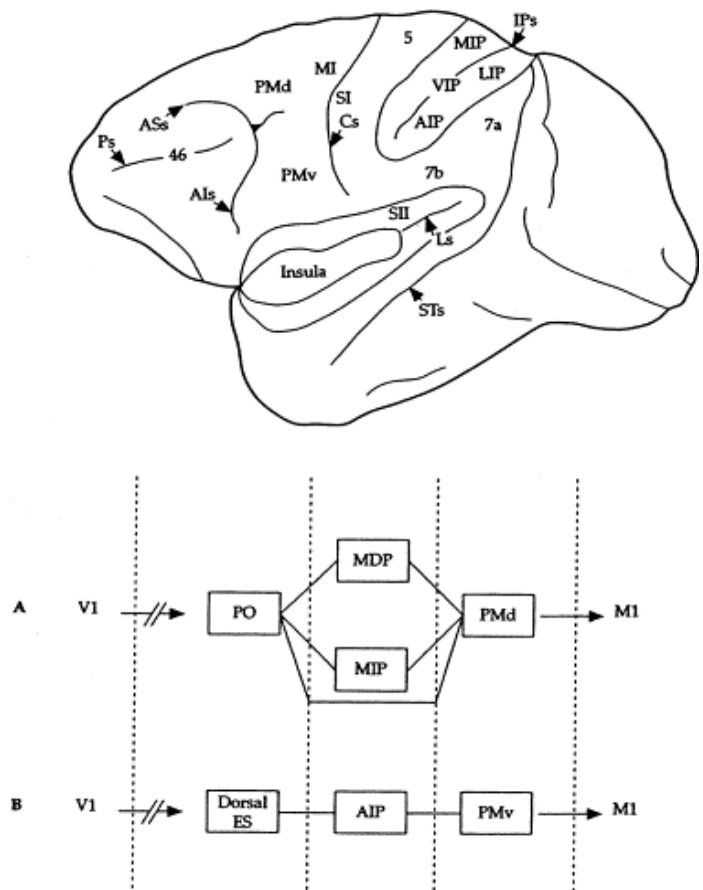
grasping components (see Jeannerod, 1999, for a short review): for instance, a study by Gallese et al. (1994) showed that farmacological inactivation of area AIP produced grasping errors without affecting the reach component, and a similar dissociation (impairment of the grasp component but not of the reach) was shown in a patient with bilateral posterior parietal lesion (Jeannerod, 1994). While a more recent study (Gréa et al., 2002), did not found impairment of the grasp component in a patient with posterior parietal lesion, this result is not necessarily in opposition with Jeannerod's, as in Gréa study the lesion spared the anterior portion of the intraparietal sulcus, an area that was found to be activated in grasping movements performed by healthy participants.

More recently, an alternative account of human prehension movements has been proposed by Smeets and Brenner (1999, 2001). In this view, grasping emerges from the trajectories of the individual fingers involved in the task: therefore, grasping could be thought as a 'double pointing' task. Rather than hypothesizing a distinct elaboration of the grasping and reaching parameters, in their first model (Smeets and Brenner, 1999), the authors proposed that the brain computed the trajectory of each finger such that the grip would be oriented orthogonally to the surface of the object being grasped, while the movement of the finger themselves would have been computed by the brain using as predicted by the minimum jerk model. However, Smeets and Brenner model has been criticized on theoretical (Marteniuk and Bertram, 1999) and experimental (Van de Kamp and Zaal, 2007) grounds.

In Jeannerod's model, grasping movements are commonly described by a set of kinematic parameters: movement time, maximum grip aperture, time needed to reach maximum grip aperture (time to maximum grip), peak velocity, maximum acceleration/deceleration and duration of the acceleration phase. Maximum grip aperture and the time needed to reach it are considered as *grasping* parameters, while the other ones describe the *reaching*. The characteristics of the object that is been grasped have been shown to influence both grasping and reaching parameters. In particular, it was originally proposed that the reaching channel only used the information related to the position of the object in the space (distance and direction), called *extrinsic*, while the grasping channel would elaborate the information relative to the object itself (size, roughness, fragility, shape, weight and so on), called *intrinsic* characteristics. However, Fitts' law predicts that reaching movements towards small targets are slower than movements towards bigger ones. Some studies (Marteniuk et al,. 1990; Paulignan et al., 1991b) manipulated the diameter of cylindrical objects used as the target of grasping movements and found that such manipulation has also an influence on movement times, violating the assumption of independence between the reach and the grasp channels, while a study by Gentilucci et al. (1991) found that the kind of grasp (precision grip versus power grasp) used did not significantly affect movement times of a prehension movements, but only once the accuracy requirements determined by the different sizes of the objects (as revealed by a subsequent pointing tasks) were taken into account.

It therefore seems that grasp and prehension component are not completely independent. Actually, in his 1999 paper, Jeannerod suggests that the covariations between transport and grip components could be seen as evidence of crosstalk between the two components and in particular on the nature of the coordination of transport and grip or, alternatively, as an effect of top-down regulatory mechanisms affecting different aspects of the same action.

A more recent review of the effect of the characteristics of the object to be grasped on the grasping parameters can be found in Smeets and Brenner (1998). In this study the authors reviewed the factors affecting grasp parameters, using experimental data gathered from 35 previous studies. The results showed (i) a linear relationship between object size and maximum grip size (with an average slope of 0.8); (ii) an increase of the relative time needed to reach maximum grip as the object size increased, but (iii) no net effect of the object size or of the time to maximum hand velocity on the average movement time for movements performed with similar precision requirements, no effect of the weight of the object on the grasp aperture and that some characteristics such as slipperiness influenced both transport (longer movement times for slippery objects) and grasping (earlier reaching of maximum grip aperture) parameters.

Other questions that have been the object of investigation in the literature regarding human prehension are the coordination between the two components of Jeannerods' model (grasping and reaching) and the role of the task (or of the final goal of the manipulation of the object). The first question, that is the relationship between grip formation and hand transport, is still open. Jeannerod initially proposed (1984) that the time of maximum grip aperture would coincide with the time of maximum hand deceleration, but other theories have been put forward: for instance, Rand and Stelmach (2005) proposed that the time of maximum grip aperture could be dependent on the distance between the hand and the object, while Zaal and Bootsma (2004) proposed the time to contact with the target as the relevant factor to determine the time of maximum aperture.

The role of the goal of a task involving grasping an object has been investigated from multiple points of view. The *end-state comfort effect* (see Rosenbaum et al., 2006, for a review) is the tendency of people to grasp object in an uncomfortable (or awkward) way if this allows for a more comfortable position while during the task or at the end of the movement, but the role of goal has been demonstrated in other aspects: a study by Marteniuk (1987) showed that the accuracy constraints imposed by the final goal (i.e.: throwing an object in a bin rather than carefully placing it) influenced also the prehension of the object itself: for instance, movement were slower and exhibited longer deceleration phases (a behavior linked with higher control on the movement) when the participants were requested to accurately place the object.

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To summarize, the body of work on grasping and reaching suggest that, far from being a trivial motor act, prehension is a task that requires fine coordination between multiple components and flexibility, as not only the motor plan is adapted to external circumstances such as the distance from the object or the roughness, but also to future events such as the action that is to be taken after having grasped the object.

1.4 Perception of biological and non-biological movement

The ability of distinguishing a moving animal from a moving object in a fraction of second must have been of the uttermost importance for our progenitors, and still it is so for human beings as for other animals. This section will briefly review the evidence in favor of different brain mechanisms and areas for processing biological compared to non-biological moving stimulus. The word 'biological' is used in the literature with at least two different meanings:

i. Having human appearance, as opposed to robots or other inanimate objects.
ii. Exhibiting dynamic and kinematic characteristics typical of biological movement.

One of the perhaps most amazing visual phenomena, which consists in recognizing human motion in animated *point-lights displays* (Figure 3), belongs to the second category. Using only the data extracted by a small set of points on a contrasting background, we can recognize an human figure walking or performing other actions – going so far as deducing the gender of the moving person or the emotional state (Barclay et al.,1978; Kozlowski and Cutting, 1978; Dittrich et al., 1996; Brownlowet al., 1997).
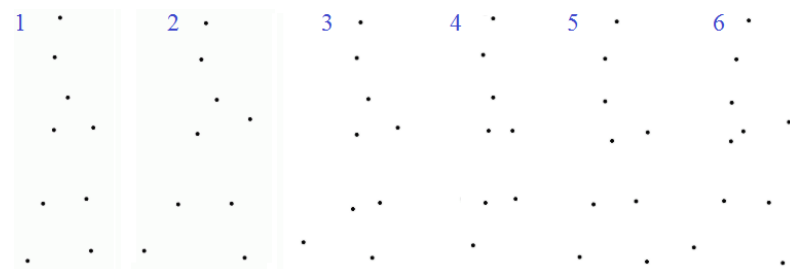
Figure 1.4 - classical point lights display - walking man

The neural substrate for this ability has been identified in specialized areas in temporal and occipital cortices (Grossman et al., 2000; Grossman and Blake, 2002). Evidence for this phenomenon has not only been found in newborn babies (Simion, Regolin, and Bulf, 2008), but even in newly hatched chicks (Vallortigara, Regolin, and Marconato, 2005), as they show a preference bias towards this kind of stimuli and can be imprinted by them more easily than by a point display moving in random motion.

Still, point light displays are not the only evidence of perceptual processes that are specifically activated by biological motion: it has been shown that the motion of a dot tracing an ellipse is perceived as moving uniformly when it is actually moving with a speed profile compatible with the 2/3 power law rather than at constant Euclidean speed (Viviani and Stucchi, 1992). Related to this phenomenon is the finding of another study: in a paper, Viviani and Stucchi (1989) showed that healthy subjects show large individual biases in estimating the aspect ratio (the relationship between the two axes of an ellipse) of the ellipses traced by a dot moving with constant Euclidean

velocity and that, likewise, modulating the velocity profile of the dot causes a change in the perception of the aspect ratio itself.

Recent studies tried to identify the neural substrates of this phenomena: in a paper by Dayan et al. (2007) it has been shown that while the motion of dots tracing an ellipse with kinematics compatible with the 2/3 power law activates more strongly motor areas such as the primary motor cortex, dorsal and ventral premotor cortices and supplementary motor area and the superior temporal sulcus, dots moving at constant Euclidean speed activated more strongly visual areas. The authors argued that while the response of visual systems for motion obeying to the two thirds power law could be explained with the sensitivity for biological stimuli or with the influence of motor processes in vision, there might be similarities in neural coding of biological movement in different part of the brain and the brain network dealing with movement could actually be distributed rather than be confined in specific areas.

A subsequent neuroimaging study (Casile et al., 2010) explored the effect on brain activation of watching a human model performing arm movements with biological or non-biological (distorted) kinematics, and found a greater activation for biological kinematics in a network of areas in left hemisphere (dorsal part of premotor cortex, middle and frontal gyri) and in the bilateral medial frontal cortex , although with a stronger response in the left hemisphere. The authors concluded that regions in the left dorsofrontal and premotor cortex that are critical for action recognition are selectively activated by biological kinematics, and that therefore the kinematics of a movement could be a factor taken into consideration while matching an observed movement with proprietary motor schemas.

Finally, a recent study (Dayan, Inzelberg and Flash, 2012) shed further light on the relationship between perception, motor system and biological movement by showing that patients with Parkinsons' disease do not perceive biological movement in the same way as healthy controls. Using an experimental setup similar to the one of Viviani and Stucchi (1992), participants could alter the relationship between speed and curvature of the movement of a dot moving along ellipses of different eccentricity, until the dot seemed to move at constant speed. Notably, the authors found that patients with Parkinsons' disease choose significantly different relationships between speed and curvature than the healthy controls, as patients with PD judged motions closer to uniform Euclidean speed to be more uniform, while controls choose movements with a speed profile similar to the one predicted by the 2/3 power law . The authors propose damage to the basal ganglia or impairment in motor production as possible reasons for such a finding, which is one of the few reported cases of modifications in neural representation of movement laws in patients with brain damage or dementia.

In short, there is evidence in the literature that the visual system processes in a different way (and possibly with the contribution of different brain areas) motion with biological kinematics than movement that do not follow motor laws such as the 2/3 power law, while the paper by Dayan et al (2012) shows a relationship between motor impairment and changes in sensory perception of motion, possibly linked by the role played by the basal ganglia in motor timing and in the neural representation of time. The distinction between biological and non-biological models has also been assessed in imitation tasks, which are briefly reviewed in the next section.

1.5. Motor Laws and kinematic in imitation

Imitation is a process that usually starts with the perception of a motor act performed by someone else. Therefore, a specific aspect of imitation is that the motor performance of the imitator is influenced by the characteristics of the model. For instance, it has been shown that imitation is modulated by whether the observed movement can be interpreted as biological, as when it is performed by a human actor, or not biological, such as when the movement is executed by a robotic arm, or represented by the motion of an inanimate object (Castiello et al., 2002; Press et al., 2005; Crescentini et al., 2011).

For instance, the work by Press and collaborators (2005) assessed the magnitude of the stimulus-response compatibility effect in an automatic imitation task, using both biological (human) and non-biological (robotic arms) stimuli. Participants were asked to close their hand upon presentation of the visual stimulus and were shown the picture of either an human or a robotic arm, represented in an open posture (incompatible) or closed (compatible). In this study, the authors showed that biological and non-biological stimuli are processed differently, as stimulus-response compatibility had a greater effect if the participants were imitating a human hand than when imitating a robotic one.

Neuroimaging studies suggested a possible neural substrate for this phenomenon: a study by Tai et al. (2004) showed that fronto-parietal areas considered to be part of the human mirror neuron system are more strongly activated when observing a biological model rather than with a non-human one. This result was corroborated by the fMRI study of Crescentini et al. (2011), who modified the paradigm used by Brass (2005) and asked participants to perform finger motions (tapping or lifting) after having observed the same (compatible) or the opposite (incompatible) movement performed by a biological (human hand) or non-biological (a white dot) model. Analyzing the reaction times the authors found a stronger compatibility effect when the stimulus displayed a human hand. Furthermore, neuroimaging data showed an enhanced activation of motor, premotor and parietal cortices when imitating the a biological model than a non-biological one.

While these studies explored the role of the nature of the stimulus, they did not specifically investigated the role of kinematic characteristics of the model to be imitated. However, other studies showed that kinematics of the gesture seem too to play an important during imitation.

A study by Kilner et al. (2007) investigated which aspects of biological (human) stimuli are responsible for the interference effect found in a previous study on imitation (Kilner et al., 2003). In the 2007 study, the authors asked participants to perform an arm movement while watching a video

showing a movement in the same (compatible condition) direction or in a different one (incompatible condition). The videos could show either biological (movements performed by human actors) or non-biological (the motion of a ball) stimuli, but the authors also added the kinematics of the movement as a factor: movements could have biological (defined as abiding to the minimum jerk criterion) or non-biological (constant Euclidean velocity) kinematics. Interestingly, the authors found the videos displaying the ball could generate the interference effect regardless of the kinematics of the motion, but no interference effect was found when the video displayed an human model moving with non-biological kinematics, highlighting therefore a possible difference in the elaboration of biological versus non biological stimuli.

Another result showing the importance of the kinematics of the model in imitation task comes from the study of Noy et al. (2009). In this study, participants were first asked to imitate the movement of a virtual hand (lifting of either index or middle finger). The hand itself could be presented in the 'common' posture or rotated by different angles. The authors found that rotating the hand caused the participants to respond more slowly (longer RTs) to the stimulus and, in a subsequent experiment, that the same effect could be replicated using non-biological stimuli (the motion of a sphere or an icosahedron). However, in another experiment participants were asked to respond verbally to the same stimuli as in the first experiment instead of imitating it, and in this task no effect of the rotation angle was found. The authors took this last finding as evidence of the absence of a mental rotation process, and concluded that the effect of the angle on the reaction times on the imitation tasks could be adequately explained by the kinematics of the movement, regardless of the nature (biological or not) of the stimulus, and that kinematics features could be enough to automatically map the perceived movements to actions.

Taken together, these evidences suggest that the nature of the effector of the movement (for instance, seeing a robotic pincher rather than a human hand) can modulate the imitative response, but also the kinematic characteristics of the gesture play an important role, in particular when the movement to be reproduced looks biological.

1.6 The influence of aging on motor control and kinematics of movement

More than reaching, grasping or the generation of arm movements, scientists working in the field of motor control and ergonomics studied the effect of aging on gait (Harada, Miyai, Suzuki, and Kubota, 2009; Kurz and Stergiou, 2003; Polcyn, Lipsitz, Kerrigan, and Collins, 1998), balance (Woollacott, Shumway-Cook and Nashner, 1896) and use of electronic devices (Smith, Sharit, and Czaja, 1999).

Salthouse (1985) was amongst the first to postulate a theory of generalized slowing with increased age, that was confirmed by subsequent studies: Welford (1988) shows that older adults have lengthened reaction times in a variety of tasks, while a longitudinal study by Fozard et al. (1994) showed that in a group of 1265 participants, tested for 28 year, there was a constant decrement in simple and disjunctive (go-no go task) reaction times, finding an average increase of 0.5 milliseconds per year for simple reaction times and of 1.6 milliseconds for the go-no go tasks. Other studies show that older participants make slower movements in tasks such as tracing lines on a graphical tablet (Goggin and Stelmach, 1990), point to point movements (Cole, Rotella and Harper, 1999) or grasping and reaching movement (Bennett and Castiello, 1994).

The differences in performance between old and young adults could be explained by a number of musculoskeletal changes related with the ageing process: in a review, Carmieli et al. (2003) listed some of the possible functional, morphological and pathological changes that could be held responsible for the slowing down of arm and hand movements in ageing. Among the others, the authors listed decreases in haptic sensitivity (especially in areas such as the palm or the fingertips), in the thickness of the skin, a loss of muscle mass, a decrease in tendon elasticity and tensile strength and pathologies such as arthritis or osteoarthritis.

Some studies, however, tried to assess the differences between young adults and older participants in activations of brain areas during motor tasks. Mattay et al. (2002) found no difference in accuracy between young and old subjects in a button pressing task, but the elderly showed an increase in response time and a greater extent of activation in broad cortical areas (sensorimotor cortex, lateral premotor area, supplementary) and in the ipsilateral cerebellum. Furthermore, older adults showed a specific activation in the putamen, contralateral cerebellum and ipsilateral sensorimotor cortex. The authors explain their findings as evidence of a compensatory mechanisms used to counteract the consequences of aging and brain changes, an interpretation already proposed by Hutchinson et al. (2002) to explain similar results. These findings are in partial disagreement with the study by Riecker et al. (2006): while in this paper the authors found the effect of ageing consisting in a increase of on reaction times during a tapping task and hyperactivation in the ipsilateral sensorimotor cortex, they did

not find a correlation this hyperactivation with age or with the frequency of tapping, concluding that over activation of motor areas is not necessarily related to the motor task, nor it does imply a compensatory mechanisms. However, all these studies point out an increase in reaction times for older subjects, which did not correspond with a decrease in accuracy, suggesting at least at a behavioral level, a slowing down but not deterioration of motor skills.

The hyperactivation of brain areas related to motor control during motor tasks could be part of a more general aspect of motor control in older adults: it has been observed that elderly people adopt strategies to minimize the number of motor errors and in general prefer a 'play it safe' strategy (Welsh et al., 2007). For instance, Cole (1991) observed that elderly participants used higher forces than young adults in a grasping task, and argued that could have done so partly in order to compensate for the increased slipperiness of their skin. Other studies examined the speed profiles of movements performed by young and elderly people: while straight movements performed by young ones tend to have a symmetrical, bell-shaped speed profile, often older adult exhibit an asymmetrical pattern, with shorter acceleration and longer deceleration phases in different tasks such as grasping (Bennet and Castiello, 1994; Cole et al., 1999) and line tracing (Goggin and Stelmach, 1990). Longer deceleration phases have been linked with an increased number of corrective submovements and with higher feedback processing (Warabi et al, 1986): therefore, older adults could be using a number of compensatory mechanisms that taken together contribute to minimize the errors, possibly sacrificing speed of execution.

It is however possible that elderly participants suffer from a degradation of motor schemas: a study from Skoura et al (2008) explored the differences between young and elderly participants in a task requiring either overt or simulated pointing towards target in space and found that in the overt motor task both groups modulated movement duration according to the size of targets. However, in the mental task young subject showed a relationship of similar strength between target size and movement duration, while the association was less strong in older participants, in particular in the simulation of the movement with the non-dominant hand. In addition, older participants showed a greater discrepancies between the timing of imaginary movements and overt ones, which suggested a decline in the capacity of predicting motor actions and not only of the motor performance.

It is worth noting that not all studies show a decrease in motor performance in older adults, and that familiarity with the task (or lack thereof) might explain the differences between young and elderly adults. For instance, Carnahan et al. (1998) found that elderly participants have lower variability, longer acceleration phases and shorter movement times than young participants, in disagreement with most of the literature briefly summarized in this section. The authors proposed that older adults might have a

more consistent but less flexible motor system, explaining both the reduced movement times and the reduced variability.

Finally, the hypothesis that the differences in motor performance linked to aging could be less evident in ecological as opposed to more experimental tasks was explored in some studies. For instance, Bennett and Castiello (1994) assessed the differences between young and elderly participants using an ecological task (grasping), and found between that elderly subjects showed slower movements with longer deceleration phases, but only subtle changes in the coordination of the transport and grip components and no impairment in the ability to modify the kinematics of the movement according to the grasp adopted: therefore, the authors concluded that the differences between young and elderly participants, while present, could be attributed to a strategy aimed at compensating deterioration in other systems.

On the other hand, Bock (2012) compared the performance of elderly and young adults in two tasks. The motor aspect was identical in the two tasks (moving the hand from a joystick to a lever and pressing the lever), but what changed was the final goal of the task: in one condition, described as repetitive, meaningless and external-triggered, the participants executed the movement when told to do so. In the other condition, which the author described as more ecological, participants executed the gesture as part of a movement required to play a computer game. Therefore, in this case the movements were self-initiated and had a specific goal (beating the game and winning a small monetary reward) . The author observed that elderly participants performance was deteriorated in different aspects, including reduced movement speed and increased variability and, most notably, that the difference between the groups actually *increased* in the more ecological task.

Even if it might be argued that the task used in the study by Bock was not really ecological, as elderly participants are unlikely to be as well practiced in playing computer games as young participants, the evidence found in the literature does not clearly support the hypothesis that the difference in motor performance between young and older adults can be completely ascribed to the nature of the experimental tasks and setting.

1.7 Alterations of kinematics characteristics of movement in apraxia

From the beginning of the twentieth century, when Liepmann (1900, 1905) formulated his model of apraxia, an enormous amount of effort has been dedicated to the exploration and to the explanation of this syndrome. However, the analysis of spatial and temporal features of movements

performed by apraxic patients only became possible with the availability of adequate instrumentation and computing power.

Since the mid-nineties, some studies tried to assess the kinematic abnormalities in patients apraxia: for instance, Poizner et al. (1994) describe the result of kinematic analyses on the 3D trajectories of movements performed by patients with left brain damage and limb apraxia. The movements were chosen from a set of skilled movements (more precisely from *transitive* movements, that is movements that require the limb to work in concert with a tool) and it was found that apraxic patients show impairments in three distinct aspects of movement: joint coordination, space-time relations and spatial orientation. For instance, the authors found that the relationship between speed and curvature (such as the one described 2/3 power law) was broken in apraxic subjects: while for healthy subjects there was a close temporal coupling between maxima in curvature and minima in speed, as the two were less than a millisecond apart, in apraxic patients this coupling was disrupted and the time interval between maxima in curvature and speed was found to be as high as 80 milliseconds. Furthermore, when performing another meaningful gesture (unlocking a door) apraxic patients showed a deficit in joint coordination: instead of generating the twisting motion distally from the elbow, as healthy controls, apraxic patient generated the motion from the shoulder, resulting in much higher displacement of the elbow. In fact, if for healthy controls the displacement of the hand was higher than the one of the elbow, for apraxic patients the opposite held true.

In a subsequent work by Haaland et al (1998), the authors assessed the motor performance of patients with left brain damage and limb apraxia or left brain damage without apraxia in a computer-administered reaching task. The authors found that both group of patients did not require more time than healthy controls to plan and initiate the movements, but that the implementation of movement in apraxic patients (but not of patients without apraxia) was heavily dependent on visual feedback: when feedback was withdrawn apraxic patients showed higher spatial errors than healthy controls and never accurately hit the target. However, even in the presence of spatial errors and longer secondary submovements, the temporal parameters of movements (velocity and movement time) were not impaired in apraxic patients, supporting the hypothesis of the decoupling of spatial and temporal representation of movement in apraxia.

While the previous two studies analyzed the kinematic aspect of motor performance of patients with limb apraxia either in meaningful gestures (Poizner, 1994) or in reaching tasks (Haaland, 1998), a study by Hermsdorfer et al. (1998) focused on the kinematical analysis of imitative performance. In this study, the authors assessed the difference in imitation of meaningless gestures between patients with left brain damage and apraxia, healthy control and patients with right brain damage. While patients with

right brain damage performed as well as control subjects, patients with left brain damages committed spatial errors and showed kinematics abnormalities. However, as in Haaland et al. work (1998), spatial errors in the single trials were dissociated from kinematic abnormalities: in some trials patients with left brain expressed a movement with multiple velocity peaks and correcting submovements (as opposed to the single-peaked velocity profile of normal controls), but correct final position; while in other the speed profile of apraxic patients was comparable to the one of healthy controls, but the final hand position was incorrect. The authors interpreted their results arguing that kinematic abnormalities do not derive from apraxia: rather, the deficit is to be found in the representation of the final target position: if patients are aware of the deficiency of their representation might choose to compensate it (resulting in a perturbed kinematic profile, but possibly correcting the spatial error) or not (giving rise to a normal kinematic profile, but the strong possibility of a final spatial error).

Even if apraxia is not due to elementary motor deficits, the results briefly summarized here show that limb apraxia can characterized by kinematics irregularities and impairment of joint coordination. However, while the results of Poizner et al. (1994) showed the disruption of motor laws and joint coordination, the other studies reviewed tend to agree on the fact that apraxic patients are highly dependent on visual feedback when performing movements. Apraxic patient might in fact be suffering from a diminished ability to represent the target position and the kinematic irregularities observed could result from corrective submovements and/or compensatory mechanisms aimed to reduce the final spatial error.

The present PhD thesis aims at exploring motor acts form different perspectives, ranging from the exploration of the possible connection between motor laws and perception in imitation to the influence of aging and brain damage on a series of ecological tasks (pointing, grasping and use of tools). The relationship between action and perception and the effect of the task will provide the common thread to all three experiments presented in this thesis:

On chapter two, analysis of eye and hand movements during imitation of stimuli moving with biological kinematics was used to investigate the representation of movement in sensory and motor systems and ascertain how the learning of the motor task influences the way we process visual stimuli.

On chapter three, I explored the effect of aging on a set of tasks of high ecological value: reaching, simple grasping, grasping to move and grasping to use common objects. In particular, the manipulation of one factor (peripheral/central presentation of the objects to be grasped) will be used to assess the interplay between perception and action in elderly and young adults and its relevance to motor control.

On chapter four, a slightly simplified version of the experimental paradigm used in chapter three was used to analyze from a kinematical point of view the differences between patients with left brain damage, patients with right brain damage and healthy controls.

Chapter 2

Changes in fixation pattern during an imitation task

2.1 Introduction

The way we explore the world and perceive events using our visual system reflects cognitive processes: despite the fact that in some cases bottom-up factors can be used to successfully predict the location of our gazes (Itti & Koch, 2001), it has been shown that top-down processes can control much of our oculomotor behavior (Henderson, 2003; Henderson et al., 2007). One of the top-down factors that can affect the way we look at the world with our eyes is expertise. For instance, it has been shown that experts and novice viewers have a different scanpath (that is, the sequence between saccades and fixations) depending on whether they are looking at a work of art (Humphrey & Underwood, 2009), they play chess (Reingold et al., 2001) or they have to predict the trajectory of a billiard shot (Crespi et al., 2012). Also short-term learning effects can have a similar influence: studies analyzing both arms and eye movements (Agam et al., 2010; Maryott et al., 2011) during a task requiring to reproduce a sequence of linear movements showed that the increase in the quality of smooth pursuit movements accompanied the increase in the quality of the reproduction of the movements.

It is therefore possible than when we watch a gesture to be imitated our scanpaths can be influenced by the motor task (Mataric & Pomplum, 1998) and by the characteristics of our motor system. Considering the geometrical characteristics of the path of the gestures, it is worth noting that extrema in curvature have been proposed as features of particular interest for both motor planning and shape perception. For instance, in the minimum jerk model proposed by Flash and Hogan (1985), simple curved trajectories as in obstacle-avoidance movements can be modeled with (i) a single via-point, located at the maximum curvature of the movement, (ii) zero velocity and acceleration at the start and endpoint. This allows obtaining predictions about hand movements which are in line with kinematic and temporal features of the human movement such as the relative isochrony (Viviani & Flash, 1995), or the scaling of the velocity profiles of the different subunits of a movement in a way that depends on their extent (longer segments have higher average speeds). In addition, the minimum jerk model was successfully used to generate different basic strokes used in handwriting (Edelman & Flash, 1987) by adding predetermined velocity constraints at the via-points. It is then possible to model a complex curved drawing (or handwriting) by a concatenation of segments all complying with the minimum jerk model. Using this approach, high curvature points of a shape would coincide with the

via-points required to trace it. Similarly, in the model proposed by Wada and Kawato (1995), complex curved paths (like hand-written letters) are represented as a sequence of via-points. The iterative algorithm proposed by the authors is composed by a module that computes the trajectory based on the minimum torque-change criterion and a module that extracts the appropriate via-point. A specific path is then generated by moving from the start to the end-point, passing through all via-points. Some of the via-points identified using this approach, named as 'kinematic feature points', are located at or closed to maximum curvature points of the trajectory.

As for the action literature, extrema in curvature have been shown to be relevant also for the visual system. Studies on the perception of silhouettes (Hoffman & Richards, 1984) have shown that points of maximum negative curvature are used for the segmentation of a shape into its component. In the authors' words, this "minima rule" for silhouettes '*divides a plane curve into parts at negative minima of curvature*'.This rule has been tested and expanded in subsequent studies (Singh, Seyranian, & Hoffman, 1999) to explore the best and most economic rule to segment a shape into different elements using the minima points. To the best of our knowledge, it is the minima in curvature rather than the maxima that appear to play a major role in perceptual segmentation of objects and silhouettes (Singh and Hoffman, 2001; Agam and Sekuler, 2008). However if a curve contains both points with positive and negative curvature, it should also contain points of inflection, i.e., points at which the curvature changes sign. While inflection points have not been specifically linked with perceptual segmentation of shapes, their characteristics make them good candidates for *motor* segmentation: for instance, they were proposed for this role in the original formulation of the 2/3 power law (Lacquaniti, Terzuolo, & Viviani, 1983), a model of human movement that captures the relationship between speed and curvature in biological motion: namely slowing down while tracing curved parts and speeding up on straight portions of movements.

While positive curvature extrema are not treated by the visual systems as minima in curvature, Reina and Schwartz (2003) showed that, during repeated tracing of an ellipse, monkeys fixated points of maximum local curvature, saccading from one such point to another during the movements. Since these saccades preceded the hand movement, it could be argued that high curvature parts of the ellipse were treated as intermediate points while continuously tracing the figure. Therefore, it can be speculated that maxima in curvature are selected by both the visual and motor systems as the next target, or via-point, in the execution of the movement.

In the present study, we used a simple asynchronous imitation paradigm to explore the interplay between perception and movement generation. Participants were presented with a movie of a dot moving along a simple geometrical shape path and were asked to reproduce that movement

immediately afterwards. Since points of maximum curvature are considered as good candidates at which to locate the via-points for the movements, we predicted that participants would fixate high-curvature points already during the first trial (see Land, Lee et al., 1994; Land & Tatler, 2001, Schwartz & Reina, 2003). Likewise, we predicted that high curvature points will be reproduced with less variability or with greater accuracy during the imitation of a movement or during any repeated gesture.

Given that learning to imitate a new movement could influence both the perceptual and motor systems, we also investigated the effect of learning by analyzing different features of the imitated movements: global similarity to the shape of the original stimuli, average speed during the execution of the gestures, size and orientation of the trajectory of the participants' gesture as compared to the original one.

We expected that participants would show an increased accuracy in reproducing the movement, i.e., an enhanced faithfulness of the produced gesture to the model as they repeat the same gesture. While we predicted that participants would look more at high curvature areas from the first trials (Reina & Schwartz, 2003), how practice and attentional effects can influence the visual processes by altering fixation pattern is a pending issue: while some studies (Agam et al., 2010; Maryott et al., 2011) showed an increase in the quality of smooth pursuit eye movements after repeated presentation of a motion sequence, in the present experiment we used different stimuli, presented in random order, to assess whether those learning effects can generalize and can be specifically related to kinematical or geometrical (instance.g., curvature) characteristics of the stimuli.

2.2 Methods and Materials

Participants. Thirteen participants (8 females), all right handed (mean age = 24.14±1.96; education = 15.34 ±1.47), with normal or corrected-to-normal vision took part in the present study. They were all tested at the Weizmann Institute of Science (Rehovot, Israel) and signed informed consent forms before starting the experiment in accordance with the Helsinki declaration and with the guidelines of the Ethics Committee of the Weizmann Institute of science.

Experimental task. Each trial was comprised of two parts: in the *perception phase*, participants were presented with a short movie of a dot moving along a path; in the *drawing phase,* they were asked to reproduce the movement of a dot on a graphic tablet using a stylus.
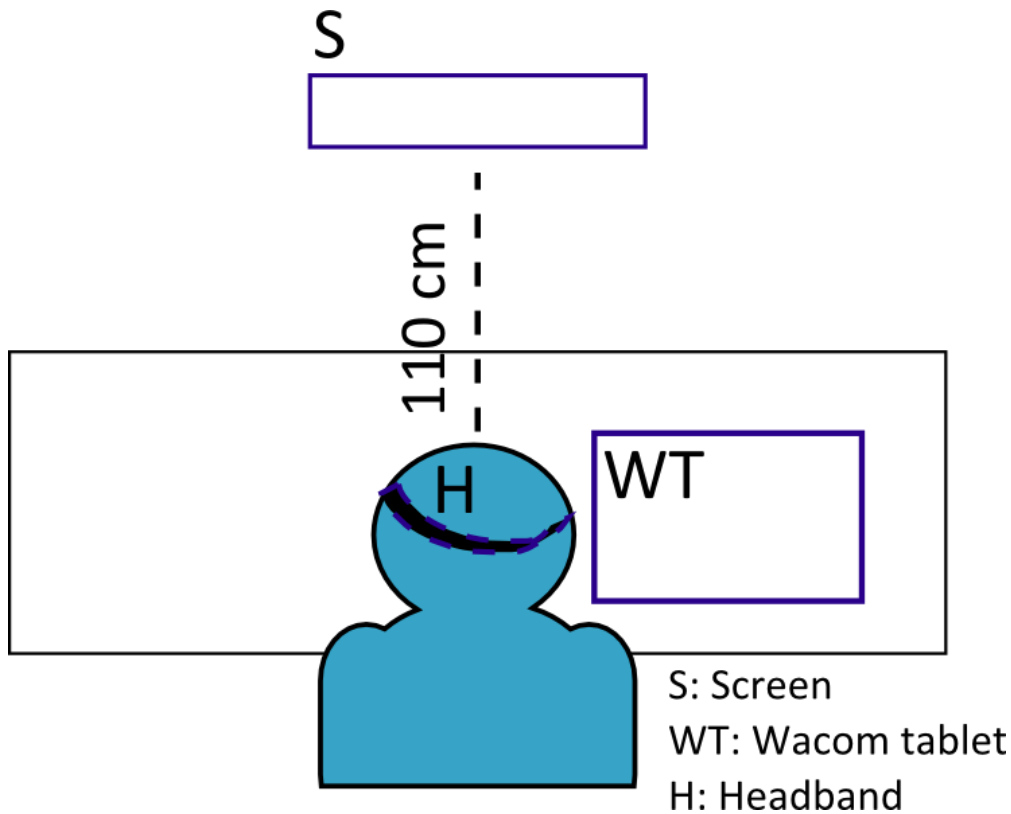
Figure 2.1 - Experimental setup

As shown in Figure 2.1, participants sat next to a table with their head fixed on a chinrest and were wearing the headband of an eye tracker (EyeLink II, operating at 250 Hz and recording both pupil position and corneal reflection).

They were asked to keep their right hand comfortably resting r on the table. A graphic tablet (Wacom Intuos 1, 12x18 inches) was also placed on the table, on the right of the chin rest. The movies were reproduced on a 21" PC monitor (Eizo Flexscan) placed on a shelf at a viewing distance of 110 cm, aligned with the participants' head and the chin rest. Each movie lasted for 3 seconds and showed a dark blue dot (RGB coordinates: 0 0 80), with a diameter of 0.65 degrees of visual angle, moving along a path of the same color, against a uniformly light grey background (RGB: 200 200 200). See Figure 2.2.

Figure 2.2 - Structure of experiments

Once the movie ended, participants were instructed to reproduce the movement while drawing on the digitizing tablet with their dominant hand. Participants were asked to reproduce the movement shown by the video, but no explicit time constraint about the initiation of the movement and no instructions about its duration were provided. Participants did not have a direct visual feedback of their hand movements, as they were asked to keep their head still on the chinrest and thus to abstain from looking at the table. On the other hand, continuous feedback of the drawing performance was provided as participants could watch the position of the tip of the stylus on the tablet as reported by a dot moving on the monitor in real-time, on a 1:1 scale. The position of the stylus on the tablet was recorded for the entire duration of the drawing phase of each trial; providing x and y coordinates sampled at 200 Hz. The drawing session started when participants placed the stylus on the active area of the tablet and ended when they lifted the stylus for more than a second. After the drawing phase ended the next trial started. The room was kept in the dark for the duration of the whole experiment with the monitor used being the only source of light in the room.
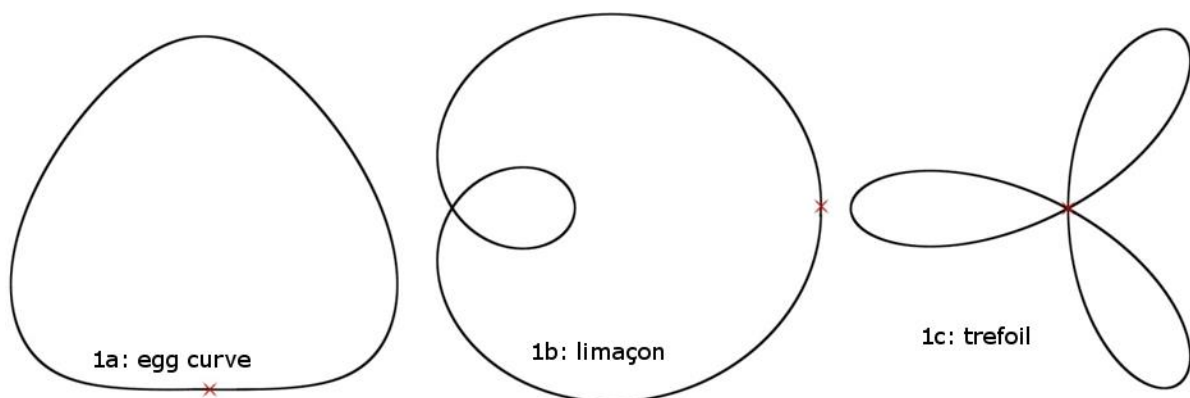
Figure 2.3 - Path of the stimulus used and starting point of the dot (marked by the red x)

The geometrical form of the path to be imitated and direction of the dot's movement were manipulated. Participants were presented with three different shapes (see Figure 2.3): a rounded triangle (or egg curve), a double ellipse (Limaçon of Pascal) and a three-petal rose (trefoil), centered with respect to the x and y axes of the monitor. The dot moved along these paths either in clockwise or anticlockwise directions. Each participant completed a total of 54 trials; with each shape being presented 18 times (9 times with the dot moving clockwise and 9 times anticlockwise). The order of the shape presentation was random.

Data processing and analysis.

Eye movements. The proprietary algorithm of the Eyelink II tracker automatically identified fixations during the on-line data recording and processing steps. Although the data was recorded binocularly, during the data analysis phase we only used the data obtained tracking the movements of the right eye. Saccade threshold was set to 30°/sec for velocity and 8000°/sec^2 for acceleration, with a saccade amplitude threshold of 0.2°, and short (less than 100 milliseconds in duration) fixations were removed. As the fixations could be scattered away from the path contour (see for instance Coen-Cagli et al. (2009), who describe a similar phenomenon), we divided the screen into square bins 100 pixel wide and counted the number and the total duration of the fixations inside each bin. We then divided the fixations according to their location on the screen: on the path, outside or inside the area delineated by the path. For every trial we calculated the total duration spent for the three classes of fixations, classified according to their locations. This procedure allowed us to determine whether participants were looking at the path itself, at the area defined by the contour (i.e., for the fixations classified as laying *inside* of the figure) or at the rest of the screen.

Hand and Arm movements. The 2D coordinates of the stylus were filtered with a 5th order low-pass Butterworth filter with cutoff frequency of 8 Hz . The start and the end of each movement were defined using a relative speed threshold (25% of mean speed).

For each subject, we assessed the accuracy of movement reproduction by comparing the hand movements with the original path shape. In order to measure the similarity of the the 2D shape of the movement, we reparametrized the data to constant Euclidean arc-length (see Viviani et al., 2009). This process allows for a resample of the data which space every point of a specific segment of each trajectory uniformly, keeping the speed constant during all the movement This is particularly important for high-curvature segments or for other parts of the movements which are executed at lower speeds because these parts might be oversampled with respect to the straight ones in the raw data. However, if from one hand this transformation decreases the chances of artifacts in the Procrustes' analysis (see later) due to the oversampling of high-curvature areas, the information about the dynamic features of the imitative performance gets lost as trade off.

A second step in the data processing and analysis was to assess the distance, or dissimilarity, between hand movements reproducing the same shape or between every movement and the original model path. This was obtained using reflectionless Procrustes Analysis (Bookstein, 1997; Kendall, 1989), a mathematical tool that finds the best way of overlapping two figures. This is computed with a set of Euclidean transformations (scaling, translation and rotation) that minimizes the measure of distance, *d*, between two curves. This distance is the sum of squared errors standardized by a measure

of the scale of the curves. While *d* can be used as index of overall similitude of the two curves, the components of the transformation provide additional information about the motor performance such as the rotation angle between the original model and its reproduction or the scaling of the latter with respect to the former. Procrustes Analysis was computed on reparametrized data, resampled to a fixed amount of points (210, as the original videos), using the Statistics Toolbox for Matlab (The Mathworks, Natick, United States). Therefore, it will be a measure of the accuracy in the *spatial* domain or of the similarity between the *shapes* being traced. Information regarding the kinematic aspect of the movement, such as the speed profile, will not be provided for the reasons discussed before.

Data analysis

Eye movement and hand movements were analyzed with a linear mixed effects model ANOVA, with shape (3 levels: egg curve, limaçon or trefoil), direction of movement (2 levels: clockwise and anticlockwise) and repetitions (9 trials) as fixed effect factors and participants as random effect factor.

For eye movements, the dependent variable considered was the time of fixation expressed as percentage of the total duration of fixations during each trial, which was calculated for the following areas of the screen (as defined above):

    i. the path of the shape
    ii. the area enclosed by the path
    iii. the area of the screen outside the path

We then determined whether fixations that were recorded near the path of the shape were near local extrema in curvature (in the same visual bin as defined above, see Figure 2.4). Curvature, or the amount by which a line deviates from being straight, was computed numerically by means of a Matlab implementation of the approach outlined in Boutin (2000), and maxima were detected via application of the first derivative test.

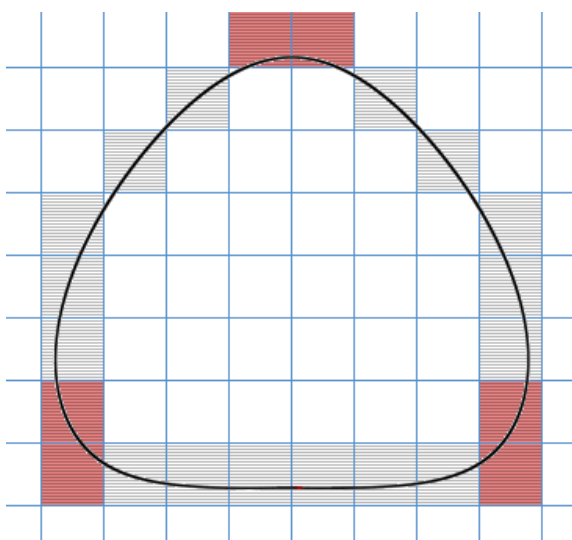**Figure 2.4 – partitioning the screen into visual bins and defining the categories (gray=path, red=high curvature regions)**

In order to determine whether the amount of fixations near maxima in curvature is significantly higher than what could be expected by chance we first computed for each shape the probability to "hit" randomly extrema in

curvature simply by taking the ratio between the number of bins (as defined in the methods) that contain an extrema in curvature and the number of bins crossed by the path of the dot: for the egg curve the probability is of 1/9, for the limaçon it is 2/15 and for the trefoil it is 1/9. We then computed the ratio between fixations near extrema in curvature and total fixations on the path for each trial and compared the observed ratios with the expected ones under the null hypothesis of homogeneous distribution of fixations along the path using one-sample t-test. The same procedure was adopted to verify whether the amount of fixation near maxima in curvature is higher than what would be predicted by considering the amount of time spent near high curvature segments by the moving dot. The dot is in high-curvature areas of the shapes for 20.8% of total time when tracing the egg curve, for 12.8% of the time when tracing the limaçon and for 12.8% of the time when tracing the trefoil.

For hand movement, the dependent variable considered were the Procrustes Distance (*d*), the total time of the movement (t), a measure of the size of the movement, the *scale*, and the rotation angle that provided the best fit between the reproduced movement and the model. The rotation angle and the scale are the result of the optimization algorithm of the Procrustes Analysis, and tell us how much a curve must be shrunk (or enlarged) and rotated to better match another curve. Therefore, a scale of 1.15 means that the curve must be enlarged by a factor of 1.15 and is thus smaller than the model with which it's being compared. Obviously, two identical curves do not need to be rotated or scaled to achieve the best possible match: the scaling will then be 1 and the angle 0.

Post hoc analysis was conducted by means of pairwise multiple comparisons on the marginal means and by splitting the dataset along relevant factors to investigate interactions.

2.3 Results

Eye movements

For the fixation time on the path itself, linear mixed-effects model ANOVA showed a significant main effects of shape of the gesture ($F_{2,647}= 28.191$, $p<0.001$) and of the number of repetitions ($F_{8,637=}3.311$, $p=0.001$). Across all trials, subjects spent more time fixating the path of the trefoil than the other two shapes ($p<0.001$ for the comparison between trefoil (72% of total fixation time) and egg-shape (51%); $p<0.001$ for the comparison between trefoil and limaçon (56%).
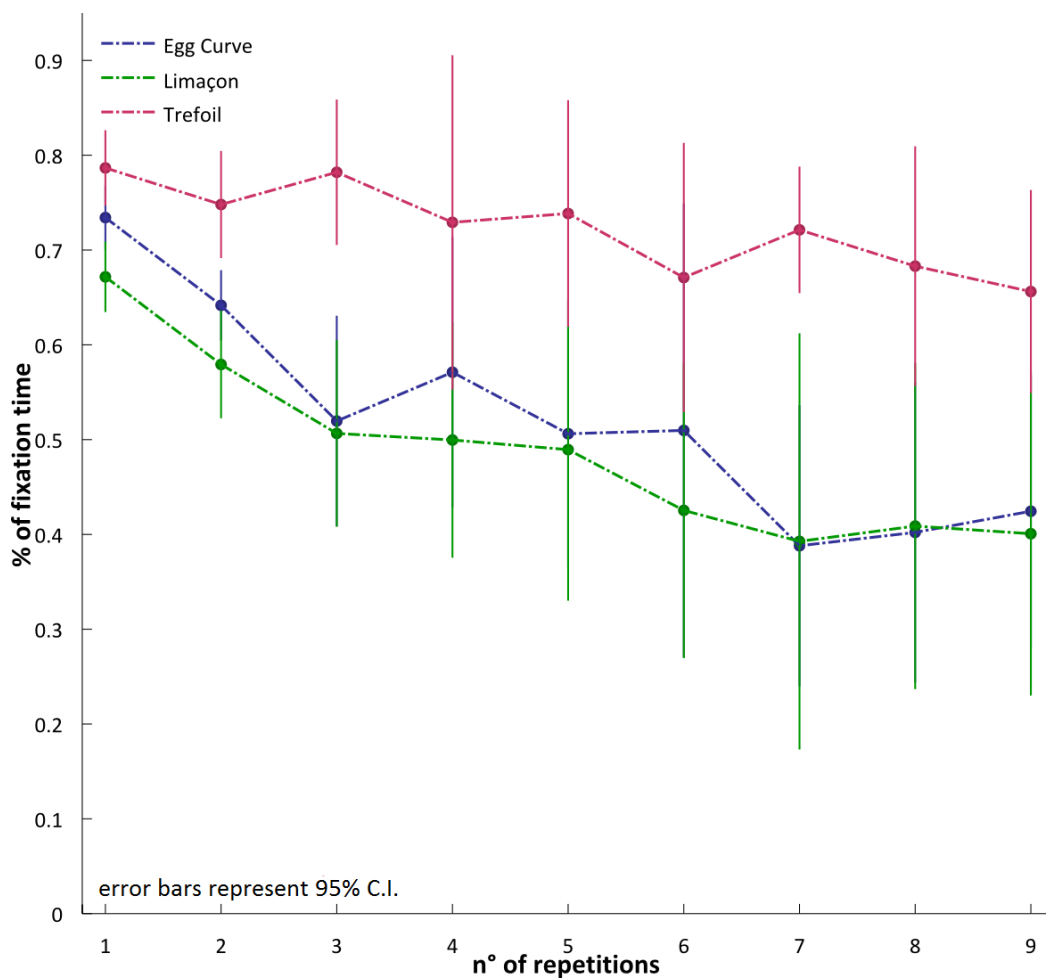
Figure 2.5 - % of total fixation time on the path by repetitions and stimulus

As shown in Figure 2.5, the time spent fixating the path of the shape decreased as the experiment proceeded. Post hoc analysis revealed that participants gazed significantly more along the path during first repetition than during the last four ($p=0.048$ for repetition 6, $p=0.048$ for repetition 7, $p=0.013$ for

repetition 8 and $p<0.001$ for repetition 9). No other post-hoc contrast was significant. No other effect was significant and there was no significant interaction between the factors.

For the time spent fixating outside the path, the main effect of repetition ($F_{8,620}=2.447$ p=0.013) was significant. However, post hoc analysis revealed no significant difference between the repetitions. We also found that the two-way interaction between shape and repetition was significant ($F_{16,622}=1.897$, $p=0.018$). Post hoc analysis conducted by splitting the dataset based on the shape of the path revealed the effect of repetitions for the egg curve ($F_{8,196}=4.49$, $p<0.001$) and for the limaçon ($F_{8,204}=3.178$, $p=0.002$). The three-way interaction between repetition, stimulus and direction ($F_{16,622}=2.137$, $p=0.006$) was found to be significant as well.

For the time spent fixating in the area delineated by the path the main effect of shape ($F_{2,625}=36.785$, $p<0.001$) was found to be significant: participants spent less time gazing inside of the area delineated by the path of the trefoil (16% of total fixation time) than of the limaçon (36%, $p<0.001$) or of the egg curve (34%, $p<0.001$). Also the main effect of repetition ($F_{8,635}=3.669$, $p<0.001$) was significant (see Figure 2.6): post hoc analysis revealed that the effect of repetitions for this variable was similar to the one obtained for he time spent gazing at the path traced by the dot: the first repetition was significantly different from the sixth ($p=0.21$), seventh (trend, $p=0.58$), eight ($p=0.44$) and ninth ($p<0.001$).

No other contrast was revealed to be significant by the post-hoc analysis and no other effect was statistically significant.
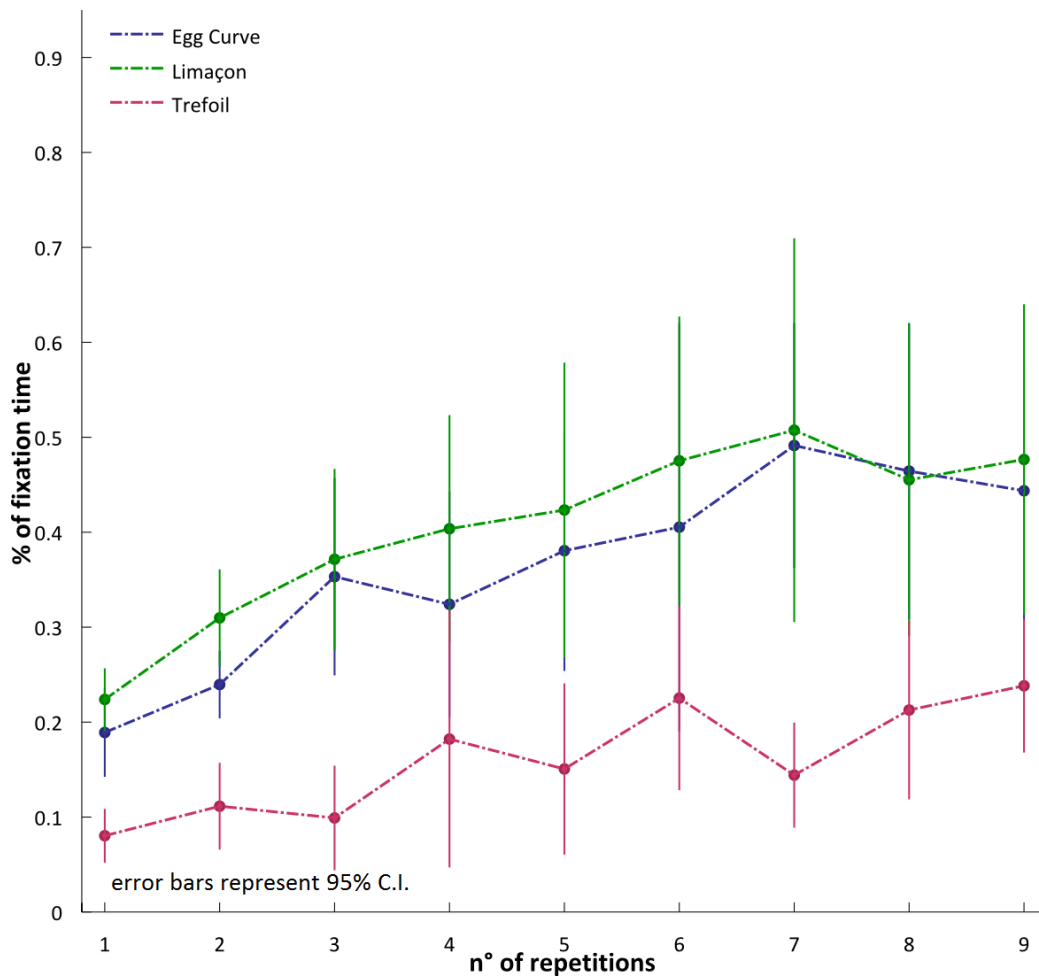
Figure 2.6 - % of total fixation time inside the area defined by path by repetitions and stimulus

To further explore the change in the location gazed by the participants in this study, we calculated the frequencies of fixations on the path, along and outside the path for each trial. Then, we divided the trials in different groups: we assigned a trial to category A if the participant spent the majority of fixations (more than 50% of the total fixation time for the trial) gazing along the path; if on the contrary the opposite pattern (less than 50% of total fixation time was spent fixating on the path) was found, the trial was assigned to category B. Table 2.1 shows the amount of trials belonging in category A (path) and category B (not path), divided by repetition number

		Repetition number									Total
		1	2	3	4	5	6	7	8	9	
Location of majority of fixations	**Path (A)**	70	69	56	36	48	38	43	50	38	*448*
	Not Path (B)	0	4	16	37	25	33	31	25	38	*209*
Total		70	73	72	73	73	71	74	75	76	*657*

Table 2.1: Classification of trials by location of fixations and repetition number

As expected, we found an interaction between the number of repetitions and the location of the majority of fixations in that given trial. The number of trials that belongs to category A decreases in the later repetitions (from the third one), and that trials belonging to category B increases (corrected $\chi^2(8,N=657) = 87.39$, $p<0.001$).

The two behaviors are characterized by the different percentages of fixation time spent looking along the paths of the dots (behavior A: 73.72% (SD 10.08) of fixation time, behavior B: 25.22% (SD 13.73), t-test:$t(209)=29.94$, $p<0.001$), which is greater for behavior A, for the different percentages of fixation times spent looking at the area delimited by the path (behavior A: 16.39% (SD 9.01), behavior B: 61.13 (SD 15.71), t-test:$t(209)=27.63$, $p<0.001$), which is greater for behavior B and also for the amount of fixation directed on the areas of the screen outside of the path (behavior A: 9.89% (SD 4.62), behavior B: 13.65 (SD 2.90), t-test:$t(209)=7.36$, $p<0.001$) , which is greater for behavior B.

The percentage of fixation recorded near extrema in curvature is greater than the one predicted by the hypothesis of uniform amount of fixation along the path. The result was significant for the egg curve ($t(N=209) = 14.456$, $p <0.001$, 46.828% of fixations centered near extrema in curvature), for the limaçon ($t(N=231)=15.198$, $p < 0.001$, 52.351% of fixations centered near extrema) and for the trefoil ($t(N=217)= 7.98$, $p < 0.001$, 24.207% of fixations centered near extrema). The percentage of fixation near extrema in curvature is also greater than the one predicted on the basis of the time that the dot spent near high curvature segments. . The result was significant for the egg curve ($t(N=209) = 14.653$, $p <0.001$), for the limaçon ($t(N=231)=11.075$, $p < 0.001$, 52.351% of fixations centered near extrema) and for the trefoil ($t(N=217)= 6.950$, $p < 0.001$, 24.207% of fixations centered near extrema).

There was no difference in the number of fixations near high curvature segments between the limaçon and the egg curve($t(N=209) = 1.095$, $p =$ n.s.), but there was difference between the trefoil and the egg-curve($t(N=209) = 6.08$, $p < 0.001$.) and the trefoil and the limaçon ($t(N=217) = 5.09$, $p < 0.001$.).

Discussion. It was found that both the shape and the number of repetitions influenced the location of the fixations of the participants. The differences between the shapes can be explained by considering that the trefoil is quite different from the egg curve and the limaçon, as the area enclosed by the trefoil is much smaller than in the other two cases, and the path crosses itself three times - participants were more likely to fixate towards the center of the path traced by the dot and this behavior was found to be less prone to changes than the fixations while watching the videos of the egg-curve or of the trefoil. Indeed, participants spent more time gazing on the path traced by the dot when the shape represented was the trefoil than when the shape was the limaçon or the egg-curve, but there was no significant difference between the latter two.

The effect of repetition, though, seems to be independent of the shape. The shift of the fixations from the path traced by the dot either towards the center of the area enclosed by the path or towards the one outside of the path could simply be due to getting used to the stimuli, which are relatively simple, and therefore from a drop of the attention level or from the effect of learning: subjects pay less attention to the stimuli because they have learned the task and therefore only need to recognize the next one. The effect of the number of repetitions on the percentage of time spent gazing outside the area enclosed by the path while significant it is probably not meaningful: fixating outside the area enclosed by the dot movement cannot be beneficial to completing the experimental task.

The fact that subjects consistently spent more time fixating near high curvature segments of the curve could be due to the presence of the imitation task and thus for motor control reasons. Extrema in curvature are relevant to motor control theories (Viviani & Flash, 1995), and a study (Reina & Schwartz, 2003) showed that they are fixated more in a curve-tracing task. In agreement with the findings of the Reina and Schwartz, in our experiment participants fixated near high-curvature segments from the beginning of the experiment.

Arm movements

Mixed linear model ANOVA with participants as random factor and shape, and repetitions of movement as fixed-effects was performed on the Procrustes distances. The results paralleled somehow the eye movement data: the main effect of the shape of the gesture ($F_{2,644}$=143.533, p<0.001) was found to be significant. Participants found the trefoil (Procrustes'$d = .104$) to be harder to reproduce than both the limaçon (p<0.001, d=.047) and the egg curve (p<0.001, d=.034). The direction of the movement showed a trend towards statistical significance ($F_{1,644}$=3.168, p=0.076), and reproducing the gestures in counterclockwise direction was slightly easier easier for the participants than moving in

clockwise direction. The interaction between shape of the movement and direction (see Figure 2.7) was found to be significant ($F_{2,644}$=7.730, $p<0.001$): considering clockwise motion, all comparisons are significant: participants were more accurate in reproducing the egg curve than both the limaçon and the trefoil ($p<0.001$ in both cases) and were more accurate in reproducing the limaçon than the trefoil ($p<0.001$), while when the participants traced the gestures in counterclockwise motion they were less accurate when tracing the trefoil than the limaçon or the egg curves ($p<0.001$) but the difference between the egg curve and the limaçon was not significant. Also the three way interaction between repetition, shape and direction of movement was significant ($F_{16,644}$=1.797, $p=0.028$). Notably, no main effect of the number of repetitions was found, and no other interaction was statistically significant.
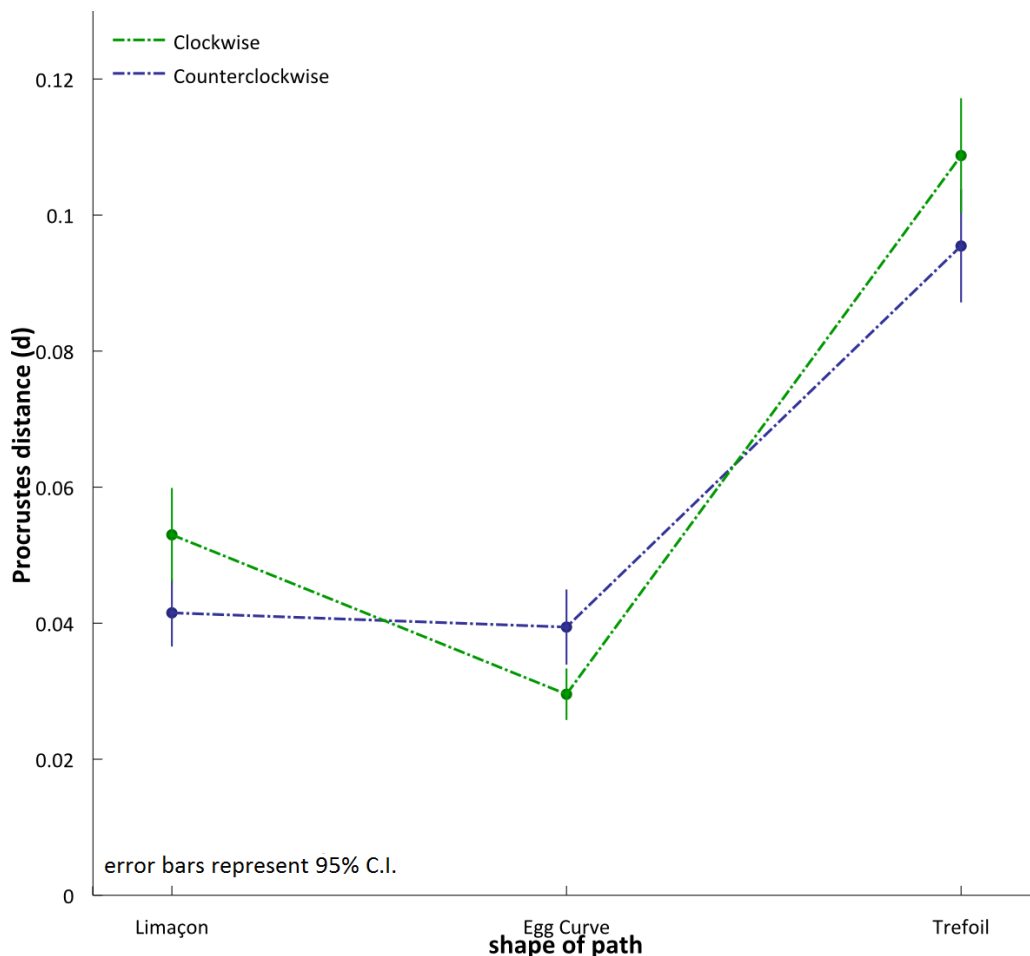
Figure 2.7- Accuracy (procrustes distance) by direction and shape of path

To further explore the effect of learning during the performance of the motor imitation task, we ran a mixed model linear ANOVA on movement duration and on the parameters of two of the transformations computed by the Procrustes' analysis: scaling and angle of rotation. The main effect of the shape of the movement was found to be significant for movement time ($F_{2,644}$=7.871, $p<0.001$), since participants could draw more quickly the egg curve (4400 milliseconds, average time considering all repetitions) and the limaçon (4587 milliseconds) than the trefoil (4951 milliseconds – both

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comparisons significant, $p < 0.001$). Also the main effect of repetition ($F_{8,644}$=2.563, $p<0.01$) and direction ($F_{2,644}$=5.344, $p<0.005$) were significant , with counterclockwise (4555 milliseconds) gestures being executed slightly faster than clockwise movements (4737 milliseconds). The main effect of repetition was examined in more detail: post hoc analysis revealed that participants learned to reproduce more quickly the movements as they became more practiced with the task: on average, the first repetition of a gesture required more time than the seventh (trend, p=.041), the eight (p=.002) and the ninth (p=.004); the second repetition required more time than the seventh (trend, p=.006), the eight (p>.001) and the ninth (p>.001), but not than the third or fourth trial, suggesting a gradual process (see Figure 2.8).
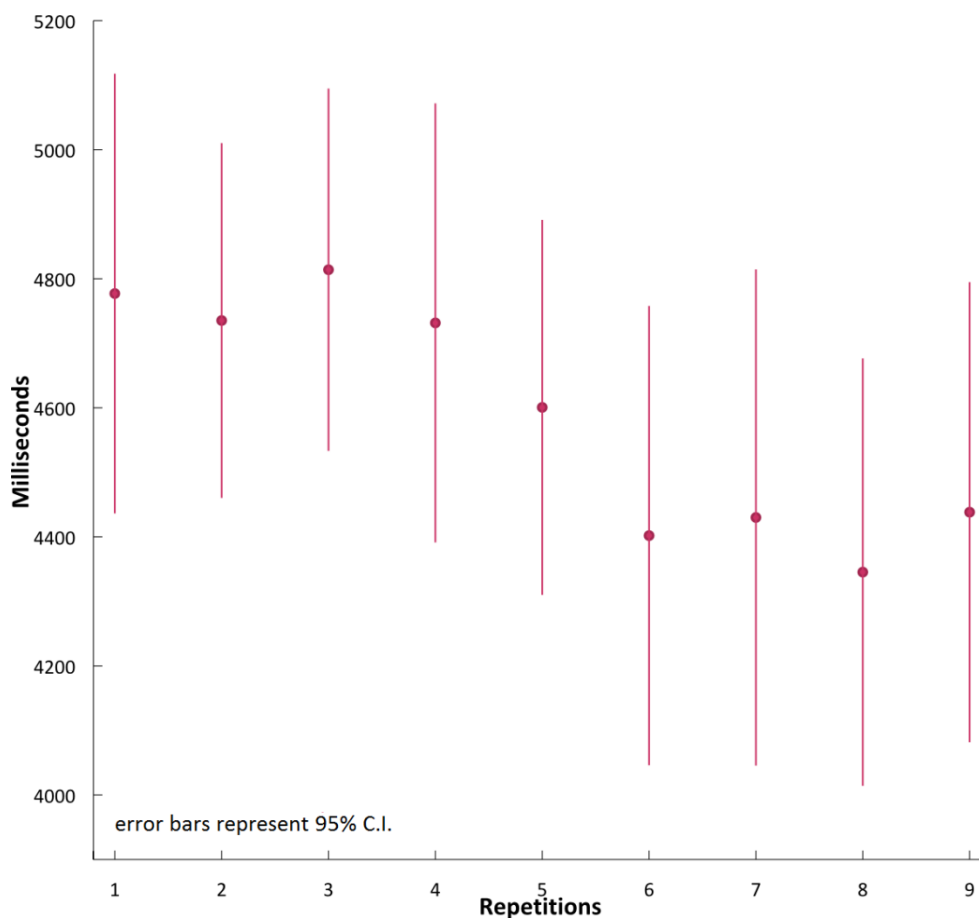
Figure 2.8 - Movement times by repetitions

The main effect of repetitions was found to be significant for rotation angle ($F_{8,644}$=2.76, p=0.005; see Figure 2.9): post hoc analysis reveals that after just the first repetition, participants greatly reduced the difference of the orientation of the gestures they produced with the models (pairwise contrasts show a statistically significance from the mean rotation angle of the first repetition and of subsequent ones – p <0.05 for all comparisons). Also, the interaction between number or repetitions and shape was

found to be significant ($F_{16,644}$=2.050, p<0.01): post hoc analysis revealed that the interaction is driven by the main effect of the number of repetitions when considering only the trials that used the trefoil as stimulus ($F_{8,207}$=2.837 p=0.005), since the main effect of the number of repetitions is not significant either for the limaçon or the egg curve.
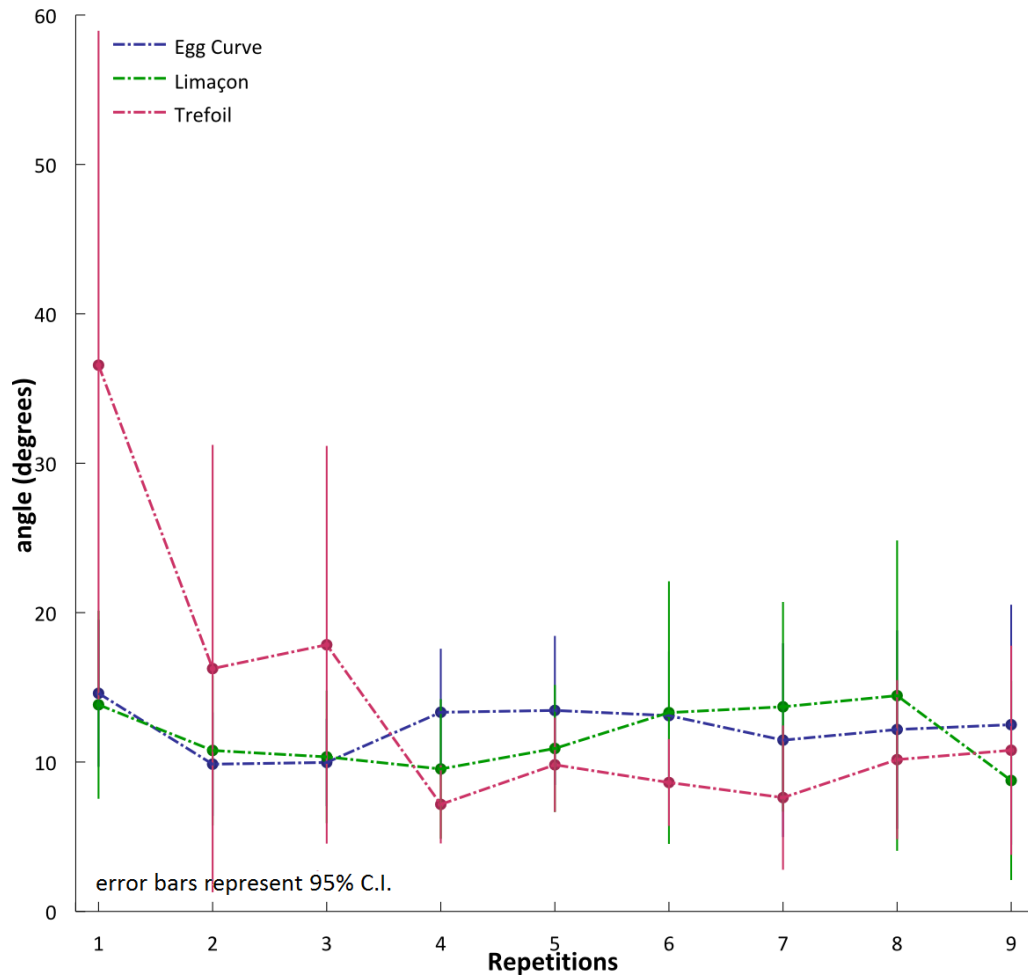
Figure 2.9 - Angle of rotation by repetitions and shape of the path

The main effects of repetition ($F_{8,644}$=2.837 p=0.005), shape ($F_{2,644}$=2.837 p=0.005) and direction ($F_{1,644}$=2.837 p=0.005) were significant for the scale of the reproduced gesture (see figure 2.10). Participants shrunk the egg-curve by a factor of 1.122 when they were reproducing it, the limaçon was shrunk by a factor of 1.052 and the trefoil by 1.017 (thereby being more accurate with the latter than with the former: p<0.001 for both comparisons). Also, participants reduced the scale of the reproduced gesture more when tracing it clockwise (1.095) than counterclockwise (1.032). Post-hoc analysis of the main effect of repetitions revealed that the effect is mainly due to the difference between the first trial and the other ones: while no pairwise comparison reaches significance, there are trends (.05< p < 0.1)

in the comparisons between the first repetition and the second, sixth, seventh and ninth ones. No interaction was found to be significant.
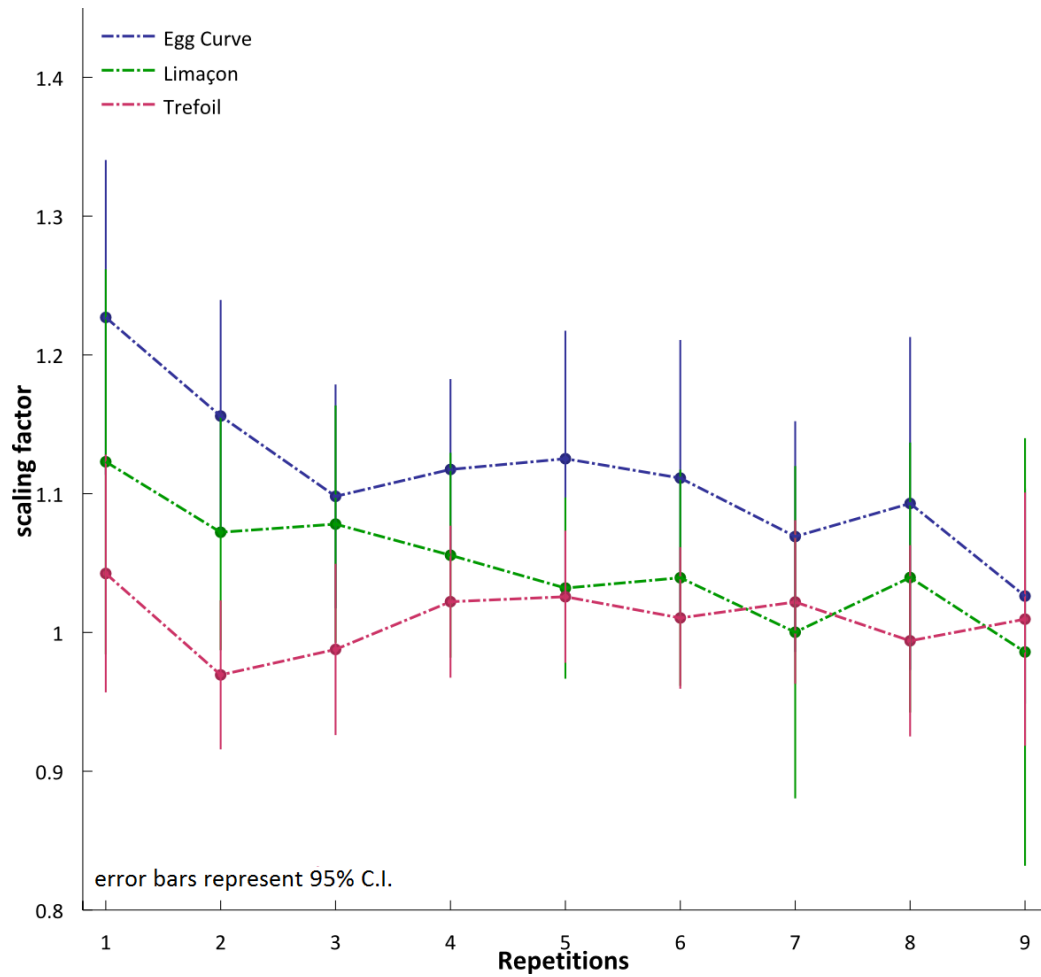
Figure 2.10 – Scale of the movements by repetitions and shape of path

Discussion. Participants' accuracy of motor performance was modulated by several factors: the gesture that was being imitated, the number of repetitions (and therefore learning) and the direction of movement. Faithfulness to the model as measured by the Procrustes distance, *d*, did not improve as a function of the number of repetitions. However, other features of the model were reproduced with increasing accuracy as the experiment progressed: participants were able to reduce the angle of rotation between their gesture and the original stimuli (although this effect was driven by only one shape, the trefoil) and the difference in the scale. Although participants did speed up their execution of the movements as the experiment progressed, they were not able to match the speed of the stimuli. While the learning of features such as the scale and the rotation angle happened between the first and second trial, the improvement in execution time was a more gradual phenomenon.

All considered, counterclockwise movements were reproduced slightly more faithfully than clockwise ones. This effect could be explained with the notion that counterclockwise movements are preferred when using the right hand, as clockwise are preferred for the left hand (Bauer & Miller, 1982).

2.4 General discussion

In the present study we investigated the relationship between perceptual processes and motor performance and the effect of learning during imitation of *non-biological* movements. In particular, we aimed at verifying if motor laws, such as 2/3 power law or minimum jerk model, could be applied to both components of imitation: perception and action. We predicted that, during perception of movement detection, fixations would to be directed along the path traced by the dot and, in particular, they would be attracted to the areas of high curvature of the path from the first trial (Land et al., 1994; Land & Tatler, 2001; Reina & Schwartz, 2003). The results confirmed these predictions: subjects spent a significant amount of time fixating the path and, specifically, high curvature parts of the path. However, we found that participants' behavior was modulated by the number of repetitions of each different stimulus: participants were more likely to fixate the path traced by the moving dot in the first few trials, while in later repetitions of the same movement a different behavior was sometimes observed. Subjects spent more time looking at the center of the screen, sporadically saccading towards the path, but quickly moved back towards the center of the screen. This latter behavior was evident during later trials: the frequency of the 'active' tracking behavior diminished from the third repetition of the observed movement, but remained the most frequent strategy used by the participants in this study.

Fixations along the path of the moving dot were often concentrated near high-curvature segments of the shape. This could be due to the kinematics of the stimulus: as the dot moves according to the 2/3 power law, which states that high curvature points are the sections of a curve where velocity of the movement decreases, participants could fixate near high curvature areas as the dot slows down there. However, an alternative explanation is that participants fixated high curvature points as these are the most relevant feature for motor planning, as high curvature parts of the path of a movement have been proposed as via-points in the minimum jerk model (Flash & Haendzel, 1985), in the minimum torque change model (Kawato et al., 1990) and as possible segmentation points in the framework of the 2/3 power law. As our participants watched near extrema in curvature more than it could be predicted by accounting for the dots kinematics, our data support the second hypothesis. Future studies, however, will have to better disentangle the two components, for instance by altering the kinematics of the point, either using alternative models of biological human motion or by perturbing the movement such as to make it clearly unnatural and non-biological.

We proposed that the shift between gaze behavior A and B was due to the progressive perceptual habituation to the visual stimuli, as well as to the dynamic training of the motor task. To investigate this hypothesis, we asked participants whether they were aware of any change in their gaze behavior at the end of the experimental session. Eleven out of 13 participants were aware of a change in their gaze

behavior and eight of them explicitly declared that the reason for this was that they have learned the stimulus and the motor task.

An alternative account of these results is that the gaze behavior was modified by a decrease in attention related to fatigue or boredom. However, this is probably not the case, for two main reasons: on average, the third repetition of a given stimulus occurred after 18 trials. As a trial lasted less than 30 seconds, the sudden appearance of behavior B happened on average after 8-9 minutes after the start of the experimental session. Second, this result is in line with previous studies (Maryott et al., 2011); Agam & Sekuler, 2008)) that have shown a consistent improvement of imitative/copying performance after one or two presentation of the model.

Therefore, practice can modulate the gaze behavior: even if stimuli were presented in a random order, subjects quickly learn to recognize the shapes. This allowed them to identify the movement following the first frames of the video, with the only source of uncertainty being the direction of the movement of the dot. A comparable result was found in a recent study by Crespi et al. (2012), who found that expert and novice billiard players had different scanpaths while observing videos of pre-recorded billiard shots and by previous studies (Humphrey & Underwood, 2009; Reingold et al., 2001) that found similar differences in the scanpaths of novice and expert subjects during tasks such as playing chess or observing a work of art. For instance, in the work by Crespi et al. (2012), novices displayed pattern of eye movements compatible with a mental simulation of the whole trajectory of the ball, but professional players explored less the table and instead focused on few crucial points from which the outcome of the shot could be predicted using formal rules. In the same way, in this experiment "naïve" subjects (i.e.: subjects at the beginning of the experiment) displayed scan-paths that followed the path of the dot, while "expert" subjects (i.e.: subjects already acquainted with the stimuli) needed less fixations,

Even if participants did not end up faithfully reproducing the gestures, they did learn some aspects of the task: they corrected the orientation and the size of their reproduction after just one trial for each different gesture, and kept improving in subsequent trials. This result is consistent with Maryott et al. (2011) and Agam and Sekuler (2008), who noticed similar improvement after just one or two trials in their experiments. It must also be noted that while participants were not specifically instructed to reproduce the timing of the movement and could keep their own pace, they constantly increased their speed of execution of the gesture. This result could simply be due to the familiarization with the task, but could also demonstrate the learning of a feature of the model that they were not requested to emulate. As no participant was faster than the model in any trial the results cannot clearly support any hypothesis at this stage. Other features, such as local isochrony during imitation, and

imitation of the speed profile as well as the path of the movement were not investigated. In our task, the physical constraints (such as the position of the tablet and of the fact that participants were keeping their head on a chin rest) added to the difficulty of the task and made the movements less natural – as a result, the speed profiles of the reproduced gestures were not always comparable with the original model. Future studies investigating this issue adopting a more ecological setup, could address these behavioral aspects and expand upon the analysis presented here..

Even if participants' performance improved with practice, they never seemed to mirror the original shape. As a speculative interpretation of this evidence, we propose that each participant created his own mental representation of the movement during the learning phase and used it as motor template to execute the following trials. This strategy might have been more advantageous in terms of time and cognitive demand than monitoring and comparing their movement with the original shape.

The main result of the present study consisted in validating the link between perception and action in non-ecological imitation tasks and in showing that movement laws can be applied and account for action as well as perception. For instance, we showed that high curvature segments represent highly salient targets for ocular fixation during some tasks such as tracing shapes (Reina & Schwartz, 2003) or driving (Land & Tatler, 2001). We also confirmed that humans do not learn the importance of high curvature segments after studying a given task: as in Reina and Schwartz paper, our participants fixated near high curvature parts of the path of the stimuli from the first trials. Once the new task is learnt, or at least understood, a new, 'resting' strategy emerges in perception. Observing how this 'restful gazing' appears with the third repetition of the different stimuli and that on average the second repetition shows great improvements with respect to the first one, we believe that the co-occurrence of the two phenomena is not a spurious link but rather the result of visuomotor integration or possibly of a wider strategy of executing task such as the one we used in this study.

Chapter 3

Grasp to use or to move common objects? An exploratory study of motor control in aging

3.1 Introduction

Grasping is a motor act which is often part of more complex everyday actions and it is normally performed with a goal. We can grasp an object to use it or to move it in a different location, or to throw it away. Indeed, different studies showed that the kinematic parameters of grasping are influenced not only by the properties of the object to be grasped but also by the end goal of the task. Marteniuk et al. (1987) authored one of the first studies showing the effect of the task goal on the kinematic characteristics of grasping. In this study, participants were asked to grasp an object and either to throw it in a large bin or to fit it into a tight fitting well. These authors showed that even the initial part of the task, when participants grasped the object, was strongly influenced by the final goal of the action. In particular, when the second part of the movement required a fine action, such as to fit the object correctly into the bin, participants' initial grasping movements were characterized by lower peak velocities and a longer deceleration phase, that is kinematic parameters considered as indicators of high level of motor control.

Afterwards, Gentilucci, Negrotti, and Gangitano (1997) investigated whether the spatial extent of a subsequent transport movement affected the initial grasp of an object. Participants were asked to grasp an object, which was presented at a fixed spatial location, and to bring it to different final positions, near and far with respect to the initial location of the object. Although the task goal was consistent across conditions, the manipulation of the distance between initial and final target locations affected some kinematic parameters of the first grasping movement: the peak velocity of the reaching movement increased along with the length of the second (placing) movement. This evidence suggests that the different movements required to accomplish a single task are related and do not simply represent a sequence of independent motor acts. In other words, the extrinsic characteristics of the action to be performed after the initial grasp of the object, such as the distance or the precision requirements, have an impact on the initial grasp formation.

Other studies (Ansuini et al., 2006; 2008) investigated the effect of the task on the kinematics of grasping by extending the measures to other parameters. Thus, in addition to the transport and grasping components of thumb and index fingers, the Ansuini and collaborators considered the flexion and extension of the joints of each single finger of the hand. In their first study, participants were asked to grasp an object, to lift it, and to place it in a big niche or in a smaller one. The results showed that the goal of the task influenced not only the reaching speed, with movements being faster in placing the objects in the larger than smaller niche, but also the pre-shaping of the hand fingers. In the large niche condition, the ring finger and the little finger were not gradually flexed and extended as in the other conditions, suggesting that the lower demand for precision of the final goal action affected the initial grasp formation. Taken together these studies suggest that, when considering a goal-directed motor act that is composed of multiple movements (i.e., grasping an object and then placing it at a different spatial location), the characteristics of the final movement (i.e., distance from the final position of the placing motion), and the goal (i.e., accurate placing in a small niche vs. throwing the object in a bin), can influence both transport and grasp components of the first movement.

Different studies (Riecker et al., 2006; Goggin & Stelmach, 1990; Shiffman, 1992; Roy et al., 1993; 2010) showed that although pointing, grasping and moving objects are relatively simple tasks, aging has an impact on the performance of these motor acts with a reduction in hand functionality from the age of 65 years (see for a review Carmeli, Patish, & Coleman, 2003) . The hallmarks of this phenomenon are longer reaction times (Riecker et al., 2006), loss of strength (Shiffman, 1992; Voorbij & Steenbekkers, 2001), slower movement execution and longer deceleration phases during pointing tasks (Warabi et Al., 1986; Goggin & Stelmach 1990; Shiffman, 1992; Roy et al., 1993; Roy et al., 2010) and a general slowing down of the performance (Welford, 1988). Among the physical changes that might contribute to this decay, Carmeli et al. (1993) listed the decrease of muscle mass, changes in the composition of tendons leading to lower tensile strength, arthritis and nerve alterations. However, the decrease of reaction times and movement speed in aging has not been always observed (Riecker et al., 2006) and it does not necessarily imply a deterioration of motor control or loss of accuracy. For instance, the decrease in velocity, often observed, might be a secondary effect of the strategy that older adults use to complete the motor task, which aims at limiting the number of errors in their motor performance (Welford, 1984). This hypothesis suggests that elderly participants might be rather concerned with the accuracy of their motor performance and for this reason they might increase their safety margins in different motor tasks. In line with this interpretation, Cole (1991) found that elderly participants used more force to grasp objects than young adults, and attributed part of this difference to a strategic tendency to reduce the risk of slippage of the objects. Another possible cause of the differences in performance between young and elderly people may be related to the overall fitness level

of the individuals. For instance, Weir et al. (2010) found no difference in the duration of deceleration phase between young and old participants and argued that their sample was composed of healthy and active elderly people, while in previous literature the fitness level of the elderly group was not specified.

An alternative explanation of the differences in motor performance between young and old subject has been proposed by Bennett and Castiello (1994) who pointed out at the difficulty of the task. The authors suggested that elderly people may show a poor performance in the classical experimental tasks used to explore motor control in aging because of their novelty and low ecological value. In their 1994 paper, the authors hypothesized that the difference in motor performance between older and young adults can be explained with the former requiring longer learning periods to adapt to a motor task which is not part of their daily life. A direct prediction based on this hypothesis is that the observed difference in performance would be reduced in more ecological motor task. In their study, Bennett and Castiello (1994) did not confirm this prediction and, instead, found longer movement times and deceleration phases for elderly participants than for young adults. Rather than embracing a purely physiological explanation of the phenomenon, the authors attributed the difference in performance between young and elderly participants as the outcome of different strategies in performing the actions: on average, elderly people exhibited longer deceleration phases than the younger. As longer deceleration phases have been previously shown to correlate with higher precision requirements of the task and with a greater number of corrective submovements in approaching the target, the authors suggested that elderly people were moving more slowly than young participants in order to avoid errors and compensate for the slight loss of coordination between the two components of grasping (transport and grip). This hypothesis has not been bearded out in a recent study (Bock & Steinberg, 2012) in which the performance of elderly and young adults was compared in two tasks of different ecological values. While the motor aspect was the same, the final goal of the task was manipulated. In one condition, the movement was meaningless and the participants were asked to executed the movement under explicit instructions, while in the other condition, which the authors described as more ecological, participants executed the action as part of a more complex movement required to play a computer game. In this case the movements were self-initiated and had a specific goal (beating the game and winning a small monetary reward). Elderly participants showed deterioration in different parameters of the motor performance, but they fare worse in the more ecological task. However, as the authors noted, this might be due to the greater experience of youngsters with computers and electronic devices, and their results might not be generalizable to more ecological tasks.

While it is known that intrinsic characteristics of the object to be grasped influence the kinematic characteristics of the movement (see Brenner & Smeets, 1998, for a review), to the best of our knowledge no study has investigated to date the interplay between ageing, the task goal, and the

characteristics of the objects being manipulated. The main aim of the present study was to explore whether the goal of the motor task modulates the changes observed in aging. In particular, I aimed at exploring the hypothesis that the ecological value of the motor task might reduce the often reported differences between young and older participants in a grasping task (Bennet & Castiello, 1994). Therefore, and elderly participants were asked to perform everyday actions such as reaching, simple grasping, grasping to move and grasping to use common objects.

In Experiments 1 and 2 (grasping to move and grasping to use) the goal of the first movement was the same (to grasp an object), while the final goal of the motor task varied. In Experiment 1, participants were required to move the object back to the starting position, while in Experiment 2 participants were asked to bring the object back at the starting position and to use it. In Experiment 3, participants were required to reach and point an object; while in Experiment 4 participants were asked to reach and grasp the same object. As the objects used in Experiments 1 and 2 were different from the one used in Experiments 3 and 4, our study is structured as two pairs of experimental tasks. The data of each experiment will be presented independently, but data of Experiment 1 will be also compared with the data of Experiment 2, and the data of Experiment 3 with the data of Experiment 4. In this way, I will assess the specific role of the final goal of the task in the two different sets of experiments. I considered the goal of Experiments 1 and 2 to be more ecological than the one of Experiments 3 and 4, which are more similar to classical laboratory tasks used to explore grasping movements.

Following the hypothesis of Bennett and Castiello (1994), I expected the performance between elderly and young participants in Experiments 1 and 2 to be more similar, while more pronounced differences would appear in in experiments 3 and 4. Overall in line with the literature (Goggin & Stelmach 1990; Shiffman, 1992; Roy et. al, 1993; 2010), I expected the kinematics of elderly to be characterized by an increase in movement times, longer deceleration phases (Bennett & Castiello, 1994; Weir et al., 1998), and an increase in maximum grip aperture. Due to the explorative nature of this study, no definitive predictions were formulated in respect to the interaction of aging with the extrinsic or intrinsic characteristics of the objects. Instead, I predicted that any effect due to the size of the objects, the distance or the side would be presented in both groups (young and elderly).

3.2 Methods and materials

Participants

Sixteen participants took part in the study of whom 8 elderly (67-75 years old; 2 women) and 8 young adults (19-25 years old; 4 women). They were all right handed, with normal or corrected to normal vision, were paid for their participation and all gave informed consent prior to their participation in the present study, in line with the guidelines of the Declaration of Helsinki. The study was approved by the Ethics Committee of SISSA.

Procedure

Participants presented with four different experiments, in which they were asked (i) to grasp objects and then move them to a predefined point (Experiment 1), (ii) to grasp objects and mimic their use using a predefined target (Experiment 2), (iii) to execute reaching movements (Experiment 3) and (iiii) to grasp objects without performing additional actions (Experiment 4). A similar setup was used for all the four experiments (see Figure 3.1). However, the main distinction in the set up among experiments was that the near location (3 and 4 in Figure 3.1) was used only in Experiments 3 and 4.

Participants were first tested for handedness (via the Edinburgh Handedness Inventory), and experimenters verified that participants could reliably distinguish and correctly reach and grasp the different objects in all positions and experimental conditions. After a practice session, subjects took part in Experiment 1 (grasp to move) and Experiment 2 (grasp to move), which lasted on average 1 hour and participants were offered the chance to take a break after its completion. Depending on the participants' time availability, Experiment 3 and 4 took place right after the break or in a subsequent day.

General set up

Participants sat comfortably in front of a black wooden board, with their body midline aligned with the midline of the board itself. Five positions were marked on the board by means of round black stickers (10 cm wide). The starting point (SP in Figure 3.1) was aligned with the vertical midline of the board and distinguished from the other disk by mean of a smaller concentric green disk. The other disks were placed so that their centres laid along imaginary lines departing to the left and to the right of the starting point with a 45° angle with respect to the midline, and were placed at 10 cm (near condition) and 40 cm (far condition) from the SP. While objects were placed at the far locations in all the experiments, objects were placed in the near locations only in Experiment 3 and 4. A fixation target was implemented by means of a LED placed along the board midline, 30 cm away from the SP. The

objects used in Experiments 1 and 2 rested on small padded supports, to minimize the auditory noise produced when the experimenter placed the objects on the board and allow for a more comfortable grasp of the objects.

Before each trial started, subjects were asked to maintain their eyes closed and to rest their hand at the starting point location, with index and thumb fingers pointing at the centre of the starting point area. Then, participants heard a recorded voice asking them to open the eyes ('*apra gli* occhi') and they were instructed to look at the fixation point (see Figure 3.2). After two seconds from the end of the recorded voice, an auditory tone was played as signal for the initiation of the movement. The tone was a had a duration of 250 milliseconds and a frequency of about 1000 Hz, and participants were instructed to start the movement as soon as they heard the tone, but not earlier than that since data were recorded after the tone. Trials on which participants started the movement before the presentation of the auditory tone were marked during the experimental session and repeated at the end of each block. Once the action was completed, participants were asked to move their hand back at the starting point location and to close their eyes. The subsequent trial started after few seconds (~ 6.5 sec), time necessary to change the arrangement of the objects on the table.

In all the experiments, participants were presented with two conditions: they were instructed to keep fixation at the LED during the actual execution of the movement ('fixed' eye movements) in half of the trials, while in the other half the LED turned off with the auditory tone and participants were asked to look at the object while performing the action ('free' eye movements). Participants' fixation at the LED was monitored, on-line by the experimenter with a small webcam facing participants' eyes.

Each movement was recorded for a predefined amount of time. This varied among experiments tasks (6 sec when grasping to use 4 sec when grasping to move, 3 sec when grasping, 2 sec when reaching) since it was estimated as the maximum amount of time necessary to perform each action. This was done in order to keep the time interval between trials as constant as possible. However, since longer movement times were not considered as a reason to exclude subjects or trials from the subsequent analysis, recording times were prolonged for the whole experiment when participants were too slow in performing the tasks.
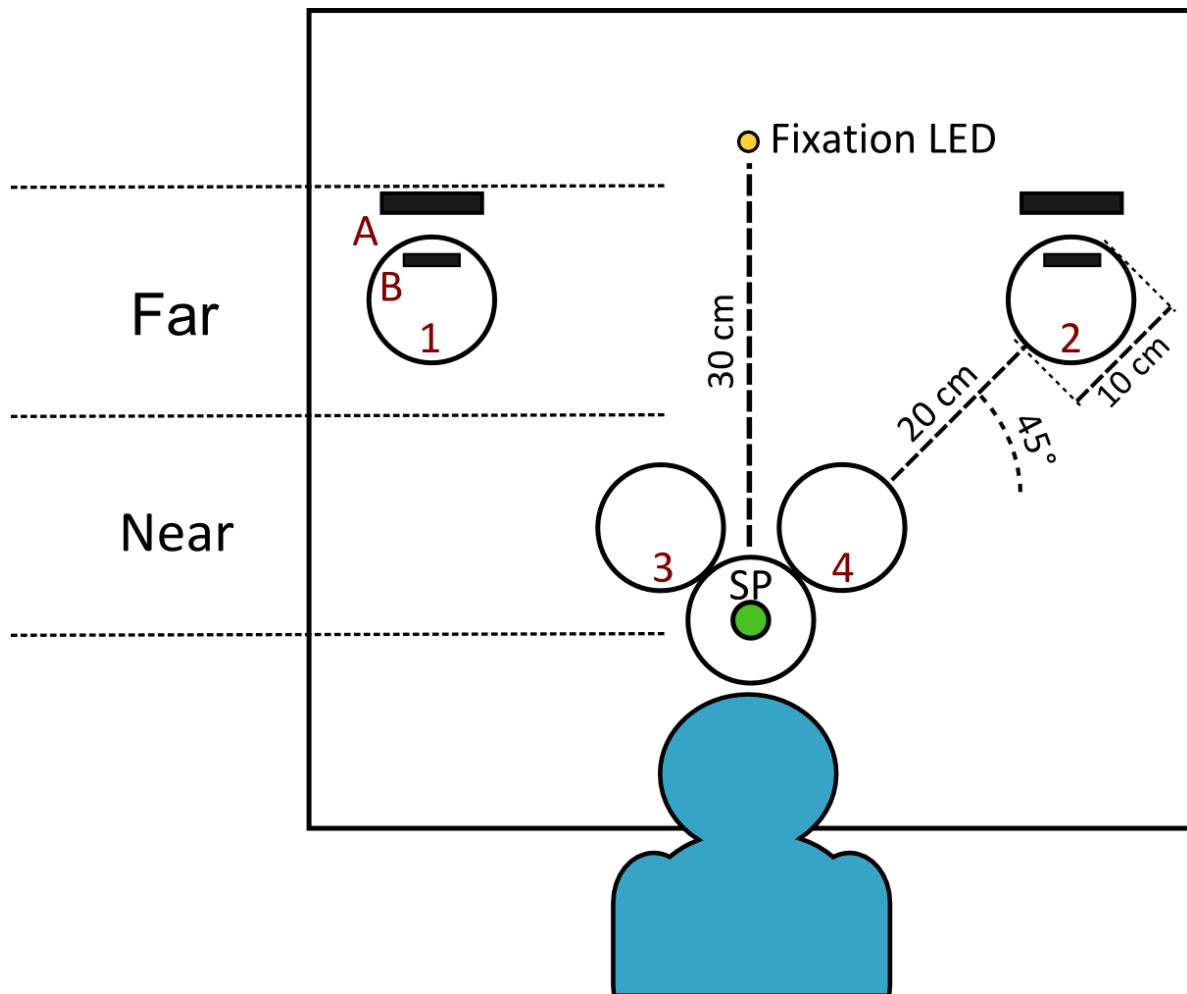
Figure 3.1- Experimental setup. SP is the starting position, 1, 2, 3 and 4 represent the disks marking the possible locations of the objects (only positions 1 and 2 for Experiment 1. A and B represents the supports which raised slightly the objects in Experiments 1 and 2 to allow for an easier grasp.

The spatial and kinematic parameters of the movements were recorded using an Ascension MiniBIRD electromagnetic tracker operating at 100 Hz. Markers were attached on the top of the index and thumb fingers of the right hand using straps made of Velcro™, in a comfortable position to allow for an as easy as possible grip on the objects. A digital camera (Canon Legria FS306) recorded the participants' hands during the task to exclude trials in which instructions were not followed. Trials marked as incorrect during the experimental sessions were repeated at the end of respective blocks whenever participants (i) failed to follow instructions, (ii) failed to perform the reaching movement in the allotted time, (iii) did not use the object when requested or (iiii) when they did not respect the instructions about eye movements (keeping the fixation on the LED/looking at the objects)

Figure 3.2 – Flowchart of the events in the a single trial

Experiments 1 and 2: Grasp to move and grasp to use.

In both tasks participants were presented with a single object placed at one of the two possible locations (left-far or right-far) and were asked to grasp and move it (Experiment 1) or grasp and use it (Experiment 2) at the starting position. So, in Experiment 1 participants were instructed to move the object to the starting position and leave it there, while in Experiment 2 they were asked additionally to use the object at the starting point location.

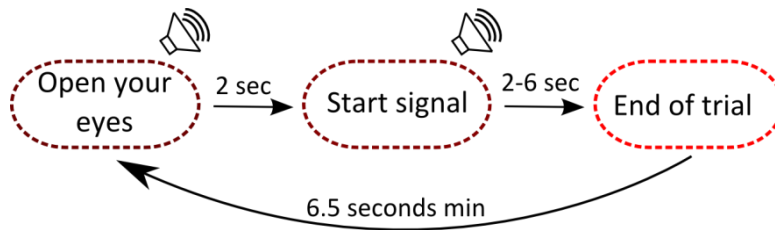Participants were presented with three types of objects (brush, tweezers and fork) in two sizes (small and big), for a total of six objects. The objects could be placed with the handle facing towards the participants or away from them, on their left or on right side. As described in the general set up, participants were asked to perform each action in two conditions: keeping fixation on the central LED or looking at the object location. To sum up, in each experiment I manipulated the eye movements (fixed or free gaze location), the size of the object (big, small), the orientation (upward and downward), the side (right and left) and the object type (fork, brush, tweezers/tongs). Each possible experimental condition was repeated two times, for a total of 96 trials for each experiment. Trials were divided in four blocks of 24 and in each block the factor Eye movements (LED fixation/free gazing) was manipulated according to an ABBA schedule. This trial order was reversed for the second participant and so on, while the order was counterbalanced between groups.

Experiments 3 and 4: Reach and Grasp.

In these experiments, participants were asked to reach (Experiment 3) or to reach and grasp (Experiment 4) two possible objects: a small pencil eraser or a bigger whiteboard eraser. The objects could be placed either on the near or far disk location, on the left or on the right side of the participants. As in Experiments 1 and 2, participants were instructed to keep fixation on the LED in

half of the trials, while they were asked to look at the objects in the other half. In this set of experiments, I manipulated the size of the objects (small and big), the side (right and left), the distance (near and far) and eye movements (fixed or free).

Each possible experimental condition was repeated three times, for a total of 48 trials. For each experiments, trials were divided in two blocks of 24 in which the vision (LED fixation/free gazing) was manipulated and alternated between participants.

Data reduction and dependent variables

The sampled coordinates of the sensors for each trial were filtered with a high-pass second-order Butterworth filter, with a frequency cut-off of 10 Hz, and analysed using customised software written in LabVIEW™ (National Instruments). Movement onset and offset were determined by comparison of markers' speed against a threshold of 50 millimeters/s, and subsequent analysis was restricted to the parsed reaching movements. To provide a description of the movements we considered the first reaching movement which was common to all the trials and computed the following variables:

- Reaction time (RT) – The duration in milliseconds between the auditory tone and movement onset
- Movement time (MT) – The duration in milliseconds between the movement onset and offset
- Maximum grip aperture (MGA) – The distance in millimetres between the sensor placed on the index finger and the sensor placed on the thumb
- Normalized time to peak velocity (nTPV) – The duration of acceleration phase, expressed as percentage of movement time
- Normalized time to maximum grip aperture (nTMGA) – The time interval between movement start and maximum grip aperture, expressed as percentage of movement time

As in Experiment 3 (reaching) participants were not required to grasp, MGA and tMGA were not computed for the last two experiments.

Analysis

Linear mixed-effects model ANOVAs in SPSS, with type III sums of squares, were performed on the computed variables to maximize statistical power, given the small number of repetitions for each

condition. We performed two different analyses: between experiments and within each experiment. When analyzing data from a single experiment, participants were entered as random factor, while all experimental manipulations were entered as fixed factors. When comparing different tasks (reach versus grasp; grasp to move versus grasp to use), group, task and condition were entered in the analysis as fixed factors as they were the key manipulations of interest in the present study, while all other factors were entered as random effect factors.

Therefore, when analyzing individually Experiment 1 or Experiment 2 the fixed effect factors considered were size (2 levels: big and small), object (3 levels: fork, brush, pliers), orientation (2 levels: congruent or incongruent), side (2 levels: right or left), eye movements (2 level: free or fixed) and group (2 levels: young or old) resulting in a 2x3x2x2x2x2 design. When comparing Experiment 1 with Experiment 2, the fixed effect factors were group (2 levels: young or old), eye movements (2 levels: free or fixed) and task (2 levels: grasp to move or grasp to use), resulting in a 2x2x2 design.

When analyzing individually Experiment 3 or Experiment 4 the fixed effect factors considered were size (2 levels: big and small), distance (2 levels: near or far), side (2 levels: right or left), eye movement (2 level: free or fixed) and group (2 levels: young or old) resulting in a 2x2x2x2x2 design. When comparing Experiment 3 with Experiment 4 the fixed effect factors were group (2 levels: young or old), eye movements (2 levels: free or fixed) and task (2 levels: grasp to move or grasp to use), resulting in a 2x2x2 design.

Post hoc analyses were conducted by splitting the dataset by the factors driving the significant interactions, while keeping all other factors as fixed (or random) effects like in the original Linear Mixed-Effects model ANOVA.

3.3 Results

As stated in the Methods section, the results of each experiment will be described and commented independently, but also contrasted two by two. In Section 1, Experiment 1 and Experiment 2 will be discussed, while the results of Experiment 3 and 4 will be presented in Section 3.

Experiment 1 – Grasp to move

Effect of group and eye movements.

The analysis revealed that the *main effect of the group* was significant only for **nTPV** ($F_{1,14}$= 24.34, p<0.001) and **MGA** ($F_{1,14}$= 5.07, p<0.05). Older participants had a shorter acceleration phase (29.46% of movement time) than young adults (39.23%) as well as a larger maximum grip aperture (85.64 mm vs. 77.37 mm).

The *main effect of eye movements* was significant for **nTPV** ($F_{1,1328}$= 26.93, p<0.001) and **MGA** ($F_{1,1328}$= 69.8, p<0.001).The acceleration phase was slightly longer (35.30 %) and the grip less wide (79.15 mm) when subjects could look at the objects than when they were asked to keep fixation on the LED (33.17% of movement time and 84.04 mm as maximum grip aperture). There was a trend towards significance in main effect of eye movements for **RT** ($F_{1,1328}$= 3.302, p=0.069): reaction times were faster when participants looked at the LED (508 ms) than when they were free to look at the objects (538 ms).

The *interaction group by eye movements* was significant for **MT** ($F_{1,1328}$= 11.25, p<0.005). As shown in Figure 3.3, young participants were faster in the free condition rather than in the fix condition, (p<0.05), while elderly were faster in the fix condition than in the free (p<0.05). No significant difference was found when comparing the two groups in fix or free conditions.
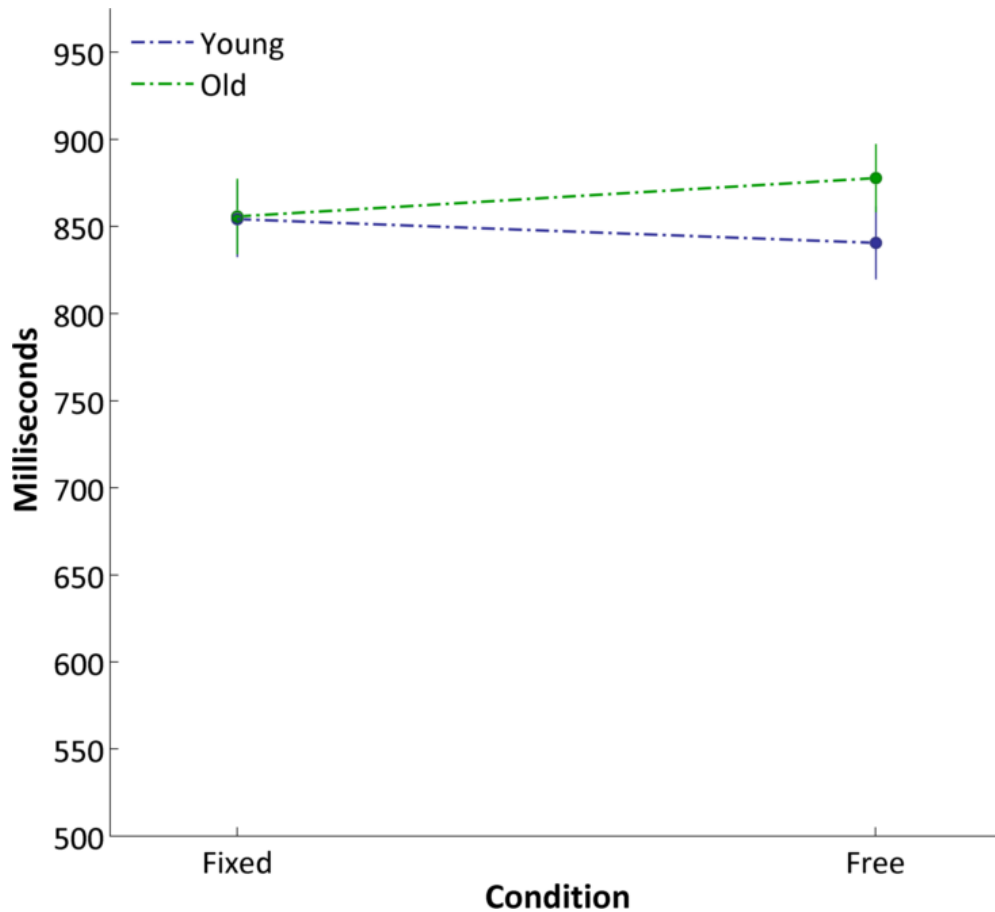
Figure 3.3 - Movement times of young and old participants in free and fixed eye movements conditions (Experiment 1: Grasp to Move)

The interaction *group by eye movements* was also significant for **nTPV** ($F_{1,1328}$= 4.76, $p<0.05$).Post hoc analysis revealed that for both groups ($p < 0.05$ in both comparisons), acceleration phase was shorter when participants when fixating the LED than when looking at the object. Furthermore, elderly participants showed a shorter acceleration phase than young adults in both conditions ($p < 0.05$). Finally for **RT**, there was a trend towards significance in the interaction *group by eye movements* ($F_{1,1328}$= 3.75 , $p=0.053$, see Figure 3.4).

General effects observed across groups.

Effect of side. The location of the object (right or left side of the participants' body midline) modulated the transport component parameters. The main effect of side was significant for **MT** ($F_{1,1328}$= 662.2, p<0.001) and for **nTPV**($F_{1,1328}$= 13.31, p<0.001). Movements were faster when performed towards the right (777 ms) than towards the left (937 ms), with a longer acceleration phase when objects were placed on the left (34,96%) rather than on the right side of the participants (32.75%). The main effect of side was also significant for **MGA** ($F_{1,1328}$= 13.8, p<0.001), that was slightly bigger on the left (82.44 mm) than on the right (80.76 mm); and for the **nTMGA** ($F_{1,1328}$= 9.7, p<0.005), which occurred later when the objects were placed on the right (71.75% of movement) than on the left (68.47%). There was a trend towards significance in the main effect of *side* for **RT** ($F_{1,1328}$= 3.318, p=0.053), as participants reacted faster when objects were placed on the right (460 ms) than on the left (475 ms).

Effect of size. Main effect of size was significant for **MT** ($F_{1,1328}$= 49.42, $p<0.001$), with faster movements when grasping big (834 ms) than small objects (880 ms). The main effect of size was also significant for **MGA** ($F_{1,1328}$= 69.8, $p<0.001$), with the grasp being wider (95.01 mm) for big objects than for small ones (68.316 mm), and for the **nTMGA** ($F_{1,1328}$= 87.5, $p<0.001$), with the maximum aperture occurring later in the movement when grasping big objects (74.01% of the movement duration versus 66.55% for small objects).

Effect of orientation. The main effect of orientation was significant for transport component parameters: **MT** ($F_{1,1328}$= 24.35, $p<0.001$), as movement were faster when the objects were placed in congruent (842 ms) than incongruent orientation (872 ms), and **nTPV** ($F_{1,1328}$= 4.76, $p<0.05$), as acceleration phases were slightly longer when reaching for objects placed in congruent orientation (34.65% vs. 33.82% for incongruent). The analysis also revealed that effect of orientation was significant for **MGA** ($F_{1,1328}$= 10.4, $p<0.001$), with a slightly larger (82.34 mm vs. 80.84 mm) grip when grasping objects placed in incongruent orientation. There was a trend towards significance in the main effect of the orientation for **RT** ($F_{1,1328}$= 3.59, $p=0.058$), as participants seemed to react faster with objects places in congruent (461 ms) than in incongruent orientation (475 ms).

Effect of object. The main effect of the type of object was significant only for **MT** ($F_{2,1328}$= 5.36, $p<0.01$): reaching for one of the brushes took longer ($p<0.05$) than reaching for the tongs/tweezers or one of the forks. (Brush: 872 millisecond; Fork: 856 ms; Tongs/Tweezers: 843 ms).

Comments Experiment 1

A key result of Experiment 1 was that older participants did not show a significant decrease in MT with respect to young adults. These results met our expectations as I considered this experimental task to be ecological and easy to be performed by old adults. Our results are in line with at least a previous study which showed no slowing down of movement execution in elderly people: Carnahan et al. (1998), found no difference in between young and elderly in the initiation times of a grasping movement, and actually their sample of elderly participants was faster than young adults.

Nevertheless, in the present experiment elderly participants' deceleration phases accounted for a longer portion of the movement than it did for young participants. This result is in agreement with previous evidence (Ketcham et al., 2002; Welsh, Higgins, and Elliott, 2007) and can be considered as the possible reflection of finer motor control in the approach rather than reaching phase of the target (Chua and Elliott, 1993). Longer deceleration phases in elderly have been interpreted as the possible outcome of a conservative strategy, which aims at minimizing errors (Welsh et al., 2007). In support of

this hypothesis, we found that elderly participants consistently used a wider grip than younger adults, a behavior that could be interpreted as a possible strategy aiming at reducing grasping errors.

The ideal speed profile of a reaching movement is symmetrical, with roughly equal acceleration and deceleration phases, but this model does not describe adequately the performance of either young or elderly participants of the present study. For both groups the portion of movement composed by the deceleration phase was longer when fixating the LED then when looking at the object. Notwithstanding the longer approach phase, older participants were faster (in terms of both MT *and RT*) when fixating the LED than when looking at the objects. This result was not expected, and will be discussed in more detail in the general discussion. In general, when the movements were performed while keeping the fixation on the LED, there was an overall increase in the maximum grip aperture. This effect is in agreement with previous studies (Sivak and MacKenzie,1990; Brown, Halpert, and Goodale, 2005) which showed an increase in maximum grip aperture when objects are presented in the peripheral visual field.

Implicit and explicit characteristics of the stimuli influenced participants' performance in a predictable manner. I found that subject were faster, more accurate in the production of their grip and had a longer acceleration phase when grasping objects placed to the right rather than to the left side. This right handers' preference for moving the right hand towards the right hemispace, which was found to be valid for both groups (young and old), is a well-known effect (Fisk & Goodale, 1985, Simon & Reeve, 1990). Likewise, I found that movements were faster when reaching big targets, as it would have predicted by postulating a speed-accuracy trade-off similar to the one proposed by Fitts (Fitts and Peterson, 1964). In relation to the orientation of the objects, we did not expect a modulation of transport or grasping parameters in this grasp-to-move task, since the completion of the task would not benefit specifically from the correct grasp of the object. On the contrary, an effect of the orientation of the object was observed, as participants were faster in terms of MT, slightly (as the effect did not reach significance) faster in terms of RT and more accurate (as they had a narrower maximum grip aperture) in the grip formation. This could be explained with stimulus-response compatibility effect described by Tucker & Ellis (2001). The authors asked participants to categorize artifact versus natural objects by grasping the response device with a power or a precision grip. Participants did more errors in the categorization when there was incompatibility between the grasp elicited by the size of the object and the one required to correctly categorize the item presented. Notably, this effect was present even if participants were not required to manipulate the objects. It is therefore plausible to suggest that that the same phenomenon might also account for the present result. An alternative hypothesis is that movement times were longer in the incompatible orientation because participants were executing longer movement in order to grasp the objects from the handle. To verify this hypothesis, we

computed the distance between the starting point and the final position of the thumb during the first (grasping) submovement. I found that the main effect of orientation was not significant for this measure ($F_{1,1328}= 0.11$, p=n.s.). To further analyze this result I performed a regression analysis with the distance as independent variable and movement time as dependent. I found that MT were actually *inversely* related to this distance, ruling out this explanation both for small ($b = -.272$, $t(717) = -7.58$, $p < .001$, corrected R^2=0.073) and big objects ($b = -.090$, $t(718) = -.405$, $p =.016$, corrected R^2=0.007).

Experiment 2 – Grasp to use

Effect of group and eye movements

Effect of group. The analysis showed a significant main effect of the group only for **nTPV** ($F_{1,14}= 918.6$, $p<0.001$) . Older participants had a shorter acceleration phase (30.7% of movement) than young adults (37.98%). For **RT**, old people seemed to be faster than young (452 versus 576 ms), but the main effect of the group did not reach significance ($F_{1,13.92}= 4.09$, p=0.063).

Effect of eye movements. I found that the main effect of eye movements was significant for **nTPV** ($F_{1,1263}= 17.64$, $p<0.001$) and **MGA** ($F_{1,1263}= 154.37$, $p<0.001$). The acceleration phase was slightly longer (35.25% of movement) when subject could look at the object rather than fixating the LED (33.34%) and the grip was less wide (77.86 mm) in the free than in the fix condition (84.06 mm). The main effect of *eye movements* was also significant for **RT** ($F_{1,1263}= 11.16$, p=0.001). **RT** were shorter when participant fixed the LED (508 ms) than when were free to look at the objects (538 ms).

The interaction between *group and eye movements* was significant when considering **MT** ($F_{1,1263}= 5.22$, $p<0.05$). Post hoc analysis showed that this significant interaction was driven by the performance of elderly participants, who were faster when fixating the LED than when looking at the objects ($p<0.5$) (Figure 3.5). This interaction was significant also for **MGA** ($F_{1,1263}= 18.51$, $p<0.001$), as both groups of participants showed a bigger finger aperture when fixating the LED than when they were free to look at objects ($p<0.001$ for both groups), and a trend towards significance (p=0.058) in the difference between groups for the fixed condition, with old people showing an overall larger grasp than young adults.
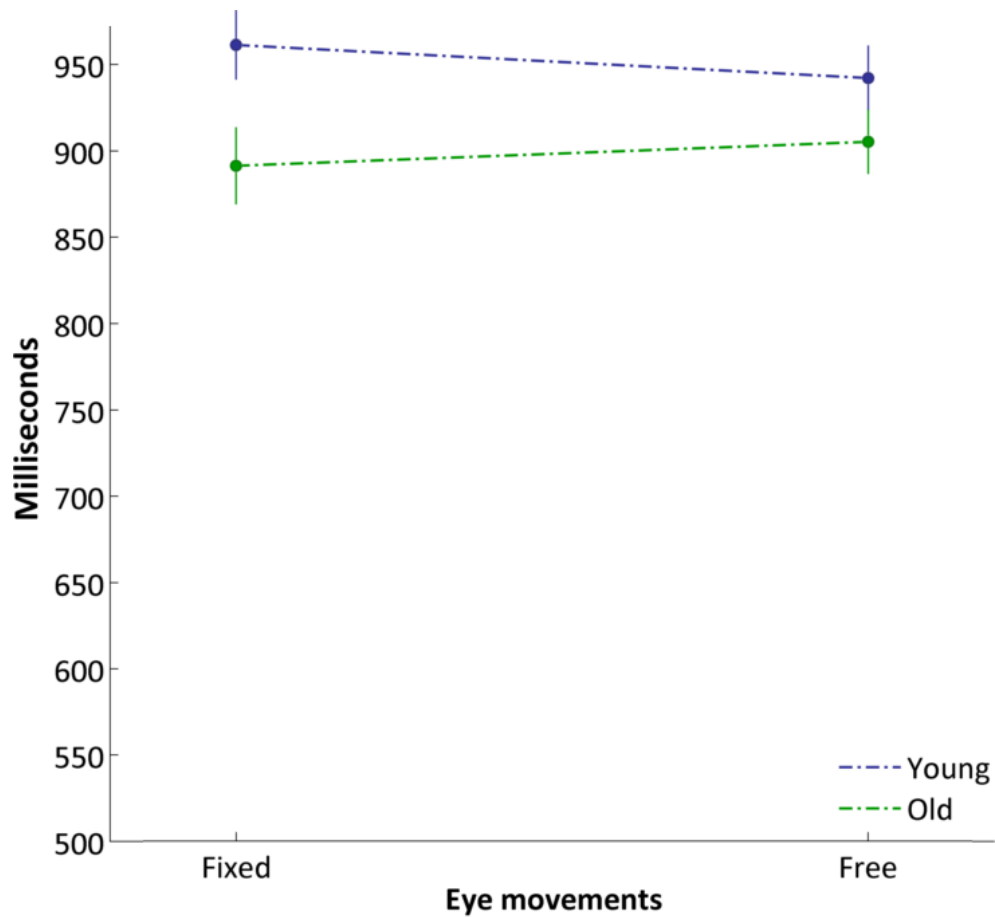
Finally, the interaction *group by eye movements* was also significant for **RT** ($F_{1,1263}$= 5.22, $p<0.05$) (Figure 3.6). The effect was only significant for elderly participants ($p<0.001$), who were faster in reacting when fixating the LED (425 ms) than when looking at the objects (480 ms).
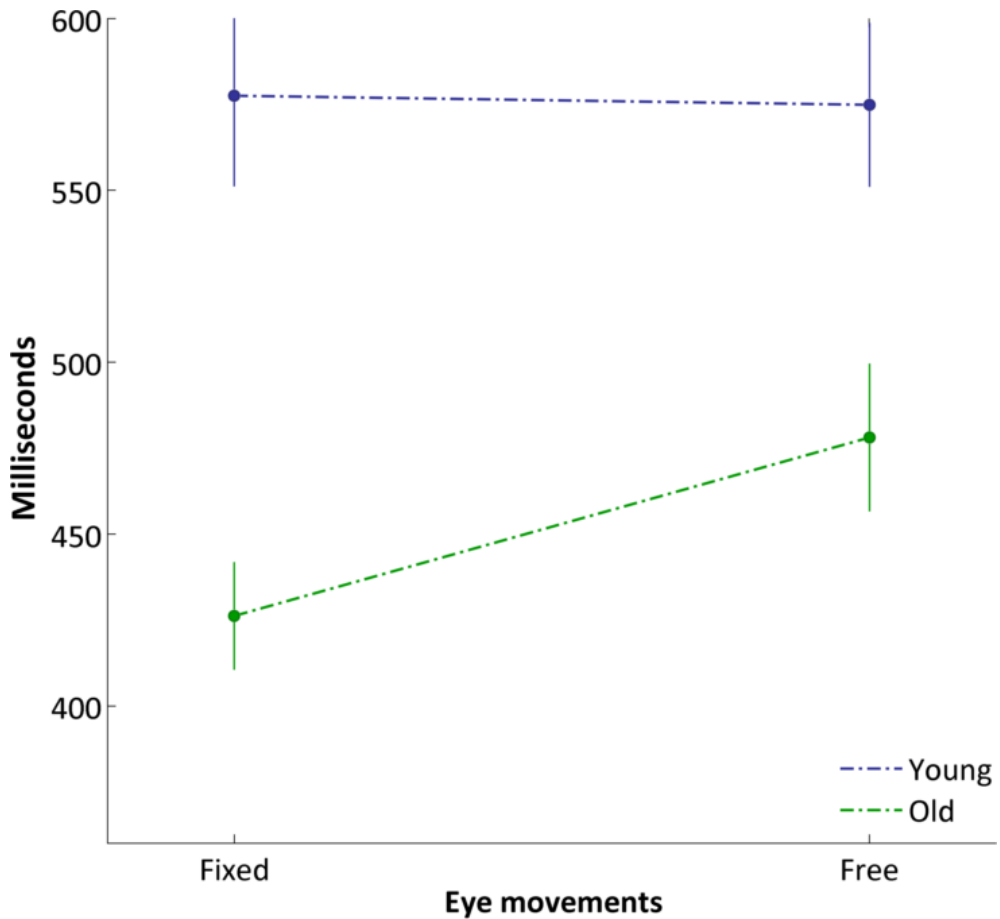
Figure 3.6 - Reaction times of young and older adults in fix and free Eye movements conditions (Experiment 2: Grasp to Use)

General effects observed across groups

Effect of side. The analysis showed a significant main effect of side for both transport (**MT** $F_{1,1263}$= 571.4, $p<0.001$; **nTPV** $F_{1,1263}$= 33.7, $p<0.001$) and grasping components (**MGA** $F_{1,1263}$= 9.58, $p<0.005$; **nTMGA** $F_{1,1263}$= 5.19, $p<0.05$). Movements were faster when performed towards the right (847 ms) than towards the left (1000 ms), with a longer acceleration phase when objects were placed on the left (35.66% of movement) rather than on the right side of the participants (32.9%). The grip was bigger on the left (81.67 mm) than on the right (80.2 mm) and participants needed more time to reach the maximum aperture when the objects were placed on the right (69.51% of movement) than on the left (67.43%).

Effect of size. The main effect of size was significant for **MT** ($F_{1,1263}$= 9.41, $p<0.005$), with faster movements when grasping big objects (913 ms) than smaller one (934 ms). Similar results were obtained for the grasp formation: **MGA** was wider when participants grasped big (93.82 mm) rather than small objects (68.0 mm) ($F_{1,1263}$= 27.35, $p<0.001$), and **nTMGA** occurred later in movement

when participants were asked to grasp big (72.22%) rather than small objects (64.71%) ($F_{1,1263}$= 71.9, p<0.001). The effect of size was also significant for **RT** ($F_{1,1263}$= 16.08, *p*<0.001), as participants were faster with big objects (505 ms) than with small objects (541 ms).

Effect of orientation. A significant main effect of orientation was found for **MT** ($F_{1,1263}$= 51.1, *p*<0.001) and **nTMGA** ($F_{1,1263}$= 4.8, *p*<0.05). Movements were faster when the objects were placed in congruent (902 ms) than incongruent orientation (947 ms). More time was required to achieve the **MGA** when grasping objects placed in incongruent (69.21%) than congruent orientation (67.75%).

Effect of object. The main effect of the type of object was significant for **MT** ($F_{2,1263}$= 9.29, *p*<0.001), for **nTPV** ($F_{2,1263}$= 4.64, *p*<0.05), and for the **MGA** ($F_{2,1263}$= 9.29, *p*<0.001). Movements were faster when grasping one of the two brushes (907 ms) rather than the forks (923 ms) or the tong/tweezers (940 ms, *p*<0.05 for all comparisons). Participants took also more time to reach the PV for the brushes (35.14% of movements) than for the tongs/tweezers (33.69%), while they showed similar nTPV in the other comparisons between objects. Finally, the MGA was wider when grasping the tongs/tweezers (87.23 mm) than the brushes (77.48 mm) or forks (78.14, *p*<0.001 for both comparisons)

Comments Experiment 2

Implicit and explicit characteristics of the stimuli as well as the eye movements (fixed/free) had an impact on both transport and grasp formation in a similar way as in Experiment 1. For instance, movements were faster when grasping big rather than small objects, when the movement was directed towards the right than the left side of the participants and when the objects were placed in compatible rather than incompatible orientation. A notable difference was that the main effect of the factor *object* was significant not only for movement times, but also for the duration of acceleration phases and for the maximum grip aperture. Furthermore, in the present experiment the kind of object to be grasped became of a certain importance, supporting the prediction that the type of object would modulate participants' performance when the task involved the actual use of the object rather than the simple moving action.

As in Experiment 1, the observed effect of the *orientation* of the object could not be explained with a shorter length of movements, as a longer spatial length of the movements did not entail a longer temporal duration but actually a shorter one both for small (*b* = -.247, *t*(682) = -6.69, *p* < .001, corrected R^2=0.06) and big objects *(b* = -.104, *t*(683) = -.2.72, *p* =.007, corrected R^2=0.009).

Older people were faster when grasping objects while keeping fixation on the LED than when they were free to look at the object. However, the significant interaction between target of eye fixation (objects or LED) and group was significant also for the maximum grip aperture in the present experiment. While both groups opened their grasp more in the fix rather than free condition, the difference between the two groups was noteworthy only when participants were required to fixate the LED. In the comment section of Experiment 1, I proposed that older participants opened the grip more in order to avoid grasping errors, an hypothesis that could account for the results of Experiment 2 too. Finally, reaction times were faster when participants fixate the LED, but this result was mainly due to the performance of elderly subjects, who were faster than young adults in this condition. The same reason, such as better performance of elderly when fixating the LED, might account for the difference in speed between elderly and young participants.

Comparison between Experiment 1 and 2

Effect of task. The analysis showed a significant main effect of the experiment (Grasp-to-move versus Grasp-to-use) for **MT** ($F_{1,2275}$=253.02, $p<0.001$), which were longer when participants grasped to use (923 ms) grasped to move the objects (857 ms), and for **RT** ($F_{1,2275}$=71.65, $p<0.001$), that were faster in the grasp to move (464 ms) than in the grasp to use (512 ms) experiment. The main effect of the task was also significant for **MGA** ($F_{1,2276}$=4.40, $p<0.05$) and **nTMGA** ($F_{1,2277}$=7.30, $p<0.01$). Participants opened the grasp slightly more when grasping to move (81.6 mm) than grasping to use (80.94%). and reached maximum grip aperture earlier when grasping to use (78.5% of the movements) than when grasping to move (80.2%) experiment.

Effect of group. A main effect of the group was significant only for the **nTPV** ($F_{1,14}$=18.05, $p<0.005$). Shorter acceleration periods were found for elderly participants (30.1% of movement) than for young ones (38.6%).

Effect of eye movements. Main effect of eye movements was significant for **nTPV** ($F_{1,2776}$=14.34, $p<0.001$), as shorter acceleration periods were evident when subjects were grasping keeping fixation on the LED (33.25% of movements) than when they were free to look at the objects (35.28%). The analysis also showed a significant main effect for **MGA** ($F_{1,2276}$=168.88, $p<0.001$), as participants opened the grasp more when keeping fixation on the LED (84.05 mm) than when they were free to look at the objects (78.52 mm) and for **RT** ($F_{1,2776}$=11.87, $p<0.005$), as participants were faster when fixating the LED (480 ms) than when looking at the objects (497 ms).

The analysis showed that the interactions *group by eye movements* ($F_{1,2776}$=11.52, $p<0.001$) and *group by task* ($F_{1,2776}$=30.24, $p<0.001$) were significant for the **RT**. Reaction times of young participants were longer in use than move ($p<0.001$) and the same effect was found for older adults ($p< 0.05$); and there was a trend towards significance in difference between groups when participants grasped to use ($p= 0.06$), with older participants being faster than young ones (Figure 3.7)

Figure 3.4 – RT of young and old adults in the two different tasks (left panel) and in fixed and free eye movement conditions (right panel)

The interactions *group by eye movements* ($F_{1,2776}$=11.54, $p<0.001$) and *group by task* ($F_{1,2776}$=27.45, $p<0.001$) were significant for **MT.** Both groups were faster when grasping to move than grasping to use ($p<0.001$) and showed similar MT when grasping to move, but elderly were slightly faster ($p=0.06$) than young adults when asked to grasp to use an object. On the other hand, elderly were slightly faster than young participants in the fix condition ($p=0.069$) (Figure 3.8).
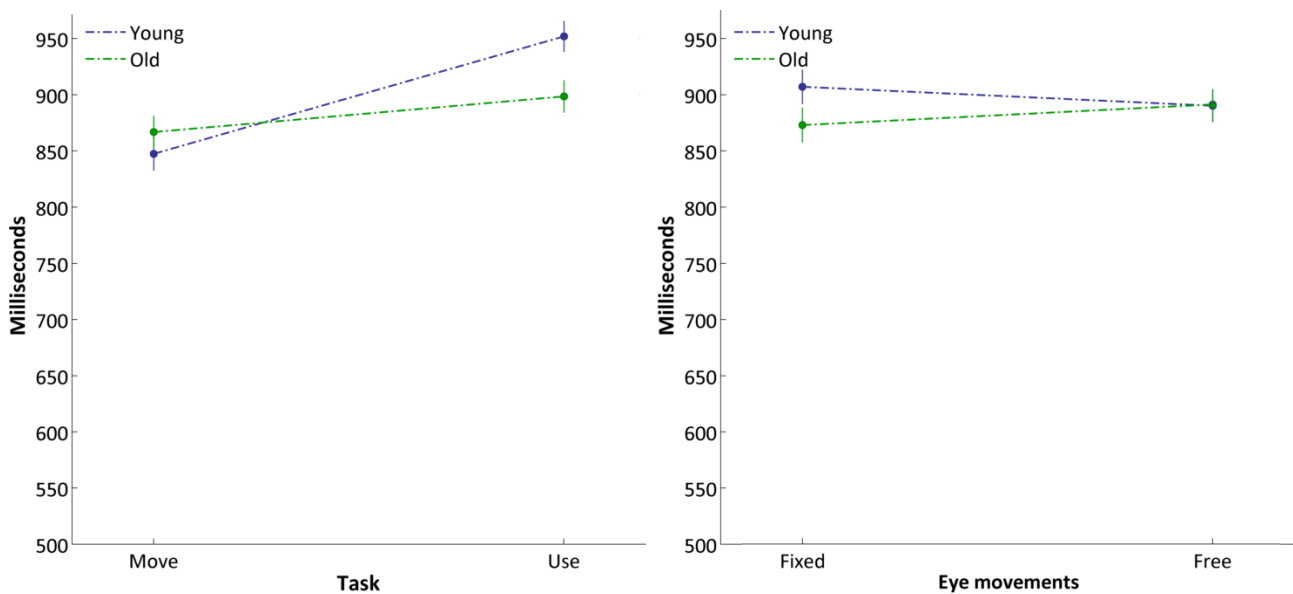
Figure 3.8- MT of young and old adults in the two different tasks (left panel) and in fixed and free eye movement conditions (right panel)

The interaction *Group by task* ($F_{1,2776}$=14.14 $p<0.001$) was also significant for the **nTPV**: elderly people had shorter acceleration phases than young adults, in both grasp-to-use and grasp-to-move experiments ($p<0.001$ in both comparisons). However, while acceleration phases of young participants were longer in grasping to move than in grasping to use ($p<0.01$), this trend was reversed for elderly adults ($p<0.05$) (Figure 3.9).
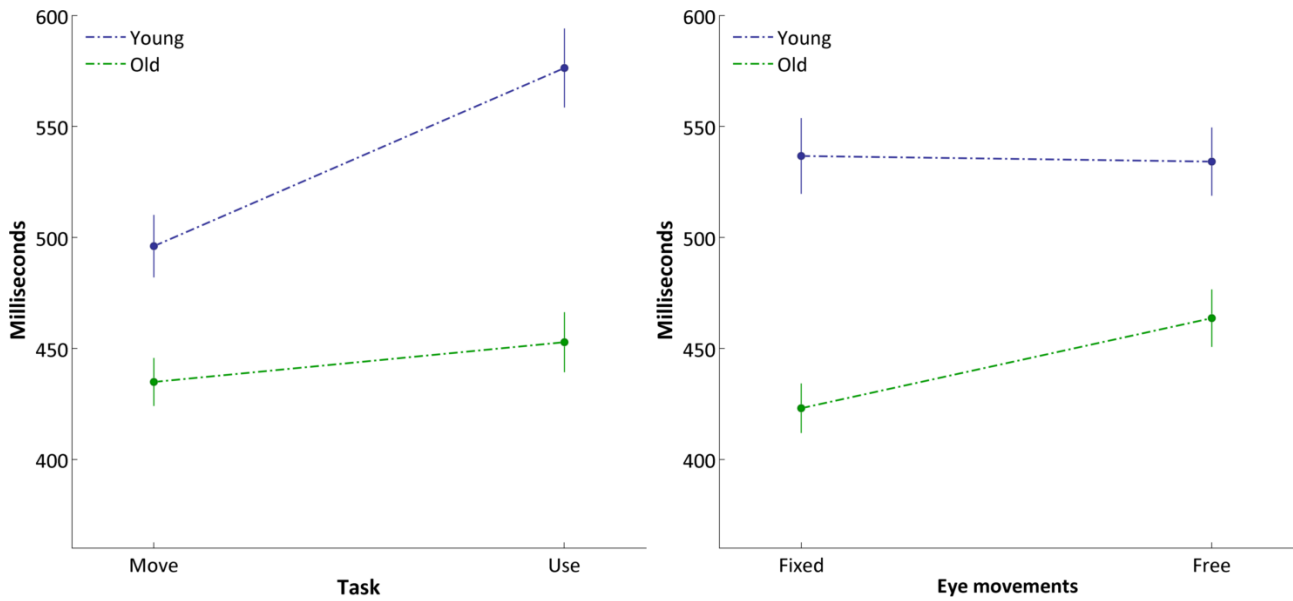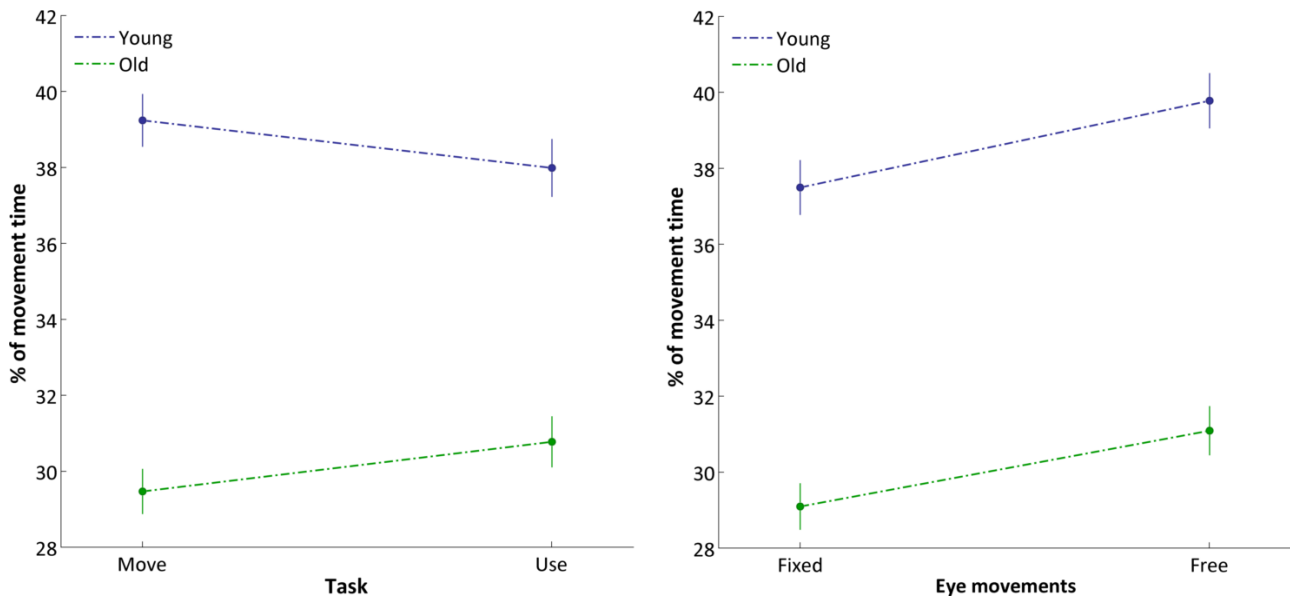

Figure 3.9- nTPV of young and old adults in the two different tasks (left panel) and in fix and free eye movement conditions (right panel)

The interaction *group by task* ($F_{1,2776}$=7.6 $p<0.01$) was significant for **MGA**: older participants opened the grip more when grasping to move than when grasping to use ($p<0.001$), while consistent peroformance across experiments was observed in young adults, and a significant difference between the two groups of participants was observed only in grasp-to-use task ($p<0.05$), as older people opened the grip more. Also the interaction *Group x Eye movements* was significant for **MGA** ($F_{1,2776}$=12.35 $p<0.001$) and **nTMGA** ($F_{1,2776}$=3.87 $p<0.05$). Post hoc analyses showed that MGA was smaller in free than in fix condition for both groups ($p<0.001$), but the groups differed only when fixating the LED, with elderly participants showing a larger MGA than young participants. Post hoc analyses for the nTMGA revealed that although it did not reach significance ($p=0.059$), young participants reached the MGA first in free than fixed eye movements condition. All other interactions were non-significant.

This comparison between Experiment 1 and Experiment 2 allowed us to assess the influence of the task on grasping parameters. In agreement with the literature (Ansuini et al.,, 2006; 2008), the final goal of the action influenced all the kinematic parameters taken into account, with the exception of the length of acceleration phases.

This follow-up comparison between the performances in two experiments showed that the task goal modulated the grasping parameters in a different way for elderly and young adults. For instance, an impact of the task on grasping parameters in young adults emerged in nTPV, which occurred earlier in grasping to use than in grasping to move Experiment. On the contrary, older participants showed the opposite trend: the acceleration phases were shorter in grasping to move than in grasping to use, thus reducing the gap in the performance with young adults. Furthermore, elderly people were slightly faster in terms of both RT and MT than young adults when the task required to grasp-to-use the object, but no such effect was noted in grasp-to-move Experiment. These results are partially in line with the study of Carnahan et al. (1998), who showed that elderly people had shorter movement times in a grasping task, and might be explained with the fact that elderly people may perform as well as young adults in ecological task. However, neither Bennett and Castiello (1994) nor Bock and Steinberg (2012) did confirm this hypothesis in their studies.

While both groups were slower in grasping to use than in grasping to move common objects, this effect was reduced for elderly participants, showing a specific advantage of the grasp-to-use task. However, since both grasp-to-use and grasp-to-move experiments have in different degree some ecological value, performance in the reach and grasp experiments (Experiment 3 and 4) allowed us to explore kinematics parameters in a less ecological and daily life type of tasks.

Experiment 3 – Reach

Effect of group and eye movements.

Effect of group. The main effect of the group was not significant for any of the variables considered in this study.

Effect of eye movements. The main effect of eye movements was only significant for **RT** ($F_{1,633}$=11.11 p=0.001). Participants were reacting faster when fixating the LED (388 ms) than when they were looking at the objects (409 ms).

The interaction between *Group* and *Eye movements* was significant for **RT** ($F_{1,633}$=6.25 p=0.01). The difference was significant only for elderly people ($p<0.01$), who were faster to react when fixating the LED than when looking at the objects. The interaction was also significant for **MT** ($F_{1,633}$=15.993 $p<0.001$). The effect of eye movements was significant both for young people ($p<0.005$) and elderly ($p<0.01$), but while young people were faster when looking at the objects, elderly were faster when fixating the LED during the movement.

General effects observed across groups.

Effect of side. The main effect of side was significant for **MT** ($F_{1,633}$=213.1 $p<0.001$) and **nTPV** ($F_{1,633}$=145 $p<0.001$). Participants were faster when moving in the right half of the space (529 vs 616 seconds) and reached peak velocity earlier when moving towards the right (35.5% of movement duration) than towards the left side (38.2%).

Effect of size. The main effect of size was only significant for **MT** ($F_{1,633}$=38.9$p<0.001$). Participants were faster when reaching big (552 ms) than small objects (593 ms).

Effect of distance. The main effect of distance was only significant for **MT** ($F_{1,633}$=1103.12 $p<0.001$). Participants were faster when reaching objects placed at near (467 ms) than far locations(692 ms)

Comments Experiment 3

I considered this experiment to be less ecological than the previous two, since participants were simply required to point with the two fingers at the objects, an action which is not often performed in everyday situations. Therefore, I predicted that elderly participants would perform this task worse than younger adults.

Overall, older adults showed a similar performance than young adults since the main effect of the group was not significant for any of the variables I took into consideration. However, older adults benefited more than young adults when action was performed keeping fixation at the LED, as shown by the decrease in both reaction and movement times in elderly people. This advantage was not observed in young people who were instead faster in executing the movement while looking at the

objects, but showed no difference in the reaction times. Therefore, it seems that elderly participants benefit from tasks more similar to the ones common in everyday life, even if they are not greatly impaired in less ecological ones.

The effects of size, distance and side were reconfirmed in this experiment as in the previous set of experiments and the predictions made on the basis of the existing literature (see comments of the previous section).

Experiment 4 – Grasp

Effect of group and eye movements.

Effect of group. A trend towards significance was found in the main effect of group for **MT** ($F_{1,12.9}$=4.134 p=0.063): young people were faster than older people when grasping the objects (639 versus 717 ms). The effect of group was significant also for **nTPV** ($F_{1,13.1}$=8.2 p<0.005). Young participants had a longer acceleration phase (36,9% of the movements) than elderly (29,6%).

Effect of eye movements. The main effect of eye movements only significant for the **nTPV** ($F_{1,605}$=4.08 p<0.05). Participants had shorter acceleration phases (32.1% of the movement) when fixating the LED than when they were free to look at the objects (34.2%).

The interaction between *Group* and *Eye movements* was significant for **RT** ($F_{1,609}$=33.93 p<0.001). This difference was significant for both elderly (*p<0.001*) and young (*p*=0.001) participants, but while elderly were faster to react when fixating the LED, the opposite trend was observed for young people The two groups differed only in the free eye movements condition (*p<0.05*). The interaction was also significant for **nTPV** ($F_{1,6113}$=4.928 p=0.027). The effect of eye movements was significant only for elderly participants (*p*=0.001), that had shorter acceleration phases when they were fixating the LED during the movement.

General effects observed across groups.

Effect of side. The main effect of side was significant for **MT** ($F_{1, 605}$=168.1 p<0.001) and **nTPV** ($F_{1, 605}$=11.7 p<0.005). Participants were faster when moving in the right half of the space (636 vs 724 seconds) than in the left part, and reached peak velocity earlier when moving towards the right (31.6% of movement duration) than the left (34.7%).

Effect of size. The main effect of size was not significant for any variable considered in this study.

Effect of distance. The main effect of distance was only significant for **MT** ($F_{1,605}$=1373.27 p<0.001). Participants were faster when reaching near objects (545 ms) than far objects (808 ms).

Comments Experiment 4

Unlike in the previous experiment, young adults had longer acceleration phases than elderly when grasping the objects, while the difference in movement times approached significance (with young being faster than old participants). In this study both Experiment 3 and Experiment 4 were conceived to be less-ecological tasks and as baseline measures. For instance, grasping an object meaningless in relation to the action is less ecological than using a brush or a fork. In line with this interpretation, older participants showed a slowing down of the performance in respect to young adults in this experiment.

The interaction between group and eye movements once more echoed the finding observed in the other experiments. Furthermore, as in Experiment 3 (reaching), side and distance affected the grasping parameters as predicted. The lack of the effect of the size on either reaction times or movement times was unexpected, as the factor *size* was significant in Experiment 3 (reaching). However, it could be explained considering the fact that when the object are in the near condition the distance from the SP is very short, and the effects on the transport component could be less easy to detect in a grasping task than in a reaching one. Indeed, when considering only the trials in the 'far' condition, the effect of size is significant (p=0.008), and movement is faster when grasping big (796 ms) than small (822 ms) objects.

Comparison between Experiment 3 and 4

Effect of task. A significant main effect of task was found for **MT** ($F_{1,1186}$=145 p<0.001), as movements were faster in reaching (572 ms) than in reaching to grasp (680 ms). The significant main effect of task was also found for the **nTPV**, which was longer in reaching (36.88% of movement) than in grasping (33.16%) ($F_{1,1297}$=12.99 p<0.001)

Effect of group. The analysis revealed a trend towards significance in the main effect of group for **MT** ($F_{1, 1186}$=3.137 p=0.076), with MT being shorter for young people (572 ms) than for elderly participants (655 ms). The main effect of the group was also significant for **nTPV**, as elderly people

exhibited a shorter (32.1% of movement) acceleration phase than young adults (37.73%; $F_{1,1084}$=83.0 p<0.001).

Effect of eye movements. The main effect eye movements was significant for **nTPV**, which was reached later when participants were free to look at the objects (33.1% of movement) than when fixating the LED (35.82%; $F_{1,1344}$=4.26 p<0.05).

The interaction *Experiment x Group* was significant for **MT** ($F_{1,398}$=4.53, p<0.05). Post hoc analysis revealed that both groups were faster in reach-to-point than in reach-to-grasp experiment (p<0.05), and that the difference between groups approached significance in grasping, as young participants were faster than elderly when reaching to grasp (p=0.063). The same interaction was significant also for n**TPV** ($F_{1,662}$=7.43 p<0.01): while the performance of the two groups was similar when reaching, young participants had longer acceleration phases than elderly in reaching to grasp (p<0.001). Post hoc analyses showed that the task had an effect for young people (longer acceleration phases when reaching, p<0.001), but not for elderly adults.

The interaction *Group by Eye movements* was significant for **MT** ($F_{1,345}$=4.17, p<0.05): young participants were faster than elderly in both conditions, but they showed a similar performance in free and fix conditions, and older adults were faster when fixating the LED than when looking at the objects (p<0.05) (figure 3.10). However, the difference between group reached significance only when participants were looking at the objects (p=0.05), with young participants being faster than older adults.
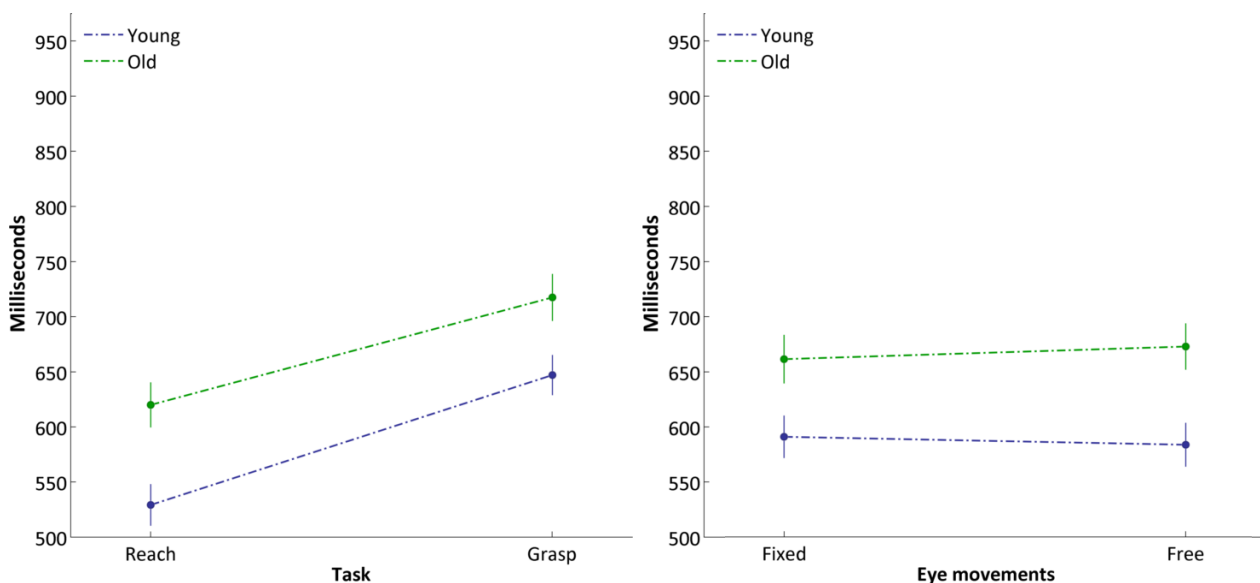
Figure 3.10 - MT of young and old adults in the two different tasks (left panel) and in fix and free eye movement conditions (right panel) in Experiments 3 and 4
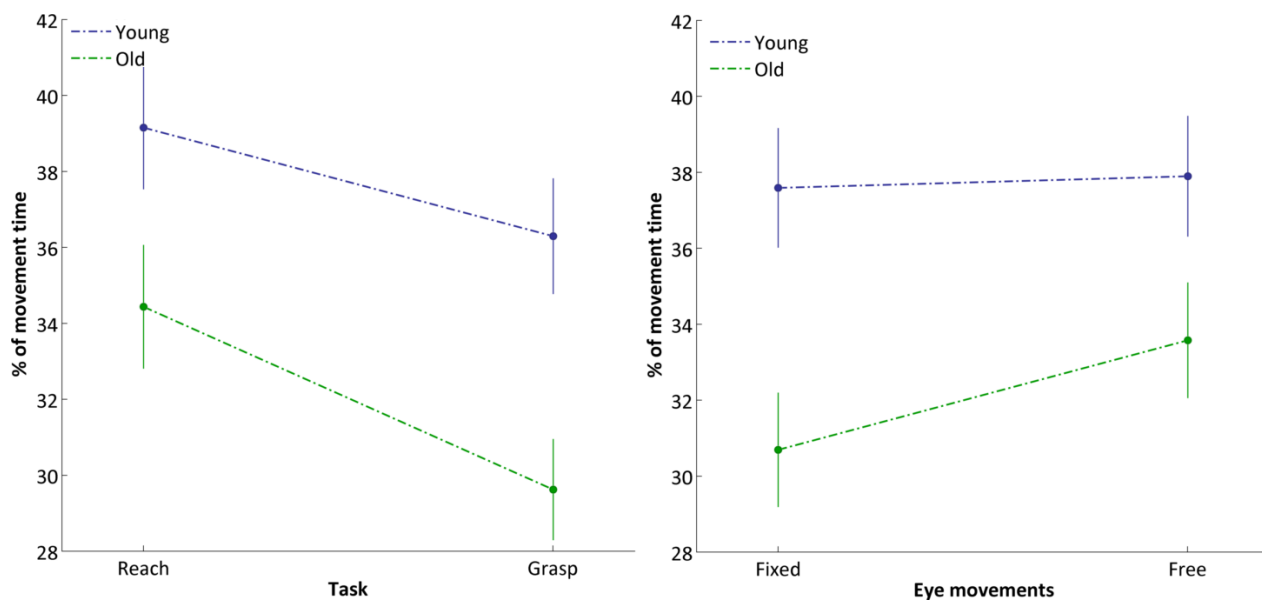
Figure 3.11 - nTPV of young and old adults in the two different tasks (left panel) and in fix and free eye movement conditions (right panel) - Experiments 3 and 4

The interaction *Group by Eye movements* was also significant for **nTPV** ($F_{1,1344}$=3.91 $p<0.05$), with older participants showing a shorter acceleration phase than young in both fix and free condition ($p<0.001$). For young participants there was no effect of eye movements, while old participants had shorter acceleration phase in fix than free condition ($p<0.001$) (see Figure 3.11).

Comments

In the first set of experiments, in which participants were asked to grasp and move (or use) common objects, older adults showed an average of the task to be performed in terms of RT and MT (more so when grasping to use than grasping to move). On the contrary, when older adults were presented with less ecological tasks, in which they were asked to grasp less familiar objects, such as erasers resembling a rectangular parallelepiped, a different trend emerged: they were slower than young adults and in grasping Experiment in particular. As in Experiments 1 and 2, in these sets of experiments too, older adults showed a longer deceleration phases than young adults and were faster in performing the movements when fixating the central LED than looking at the objects, while younger participants had a similar performance in both conditions.

To summarize, when grasping to move and especially when grasping to use elderly participants are faster than young ones, in reaching and grasping this trend seemed to be reversed. This result supports the hypothesis that elderly participants performed better in more ecological tasks than in laboratory types of tasks. Consistent evidence across experiment was that young participants generally perform better if they were looking at the objects than fixating the LED, while the opposite trend is true for elderly participants. Therefore, I suggest that this unexpected result is the outcome of genuine differences in motor planning between young and older participants, and are not simply due to the task or other factors that remained constant across Experiments 1 and 2.

3.4 General discussion

The present study aimed at exploring the effect of aging in a series of motor tasks, in which goal of the task and the associated ecological value was varied across experiments, from a more daily life-type tasks (Experiments 1 and 2), toward less common ones (Experiments 3 and 4). The results showed that transport and grasping parameters were modulated by the goal of the task and by aging. This result is even more striking, since I took into consideration the first part of the movement that is the act of reaching and/or grasping of presented objects, which was consistent within each set of experiments. In particular, the initial reaching and grasping action was the same in Experiments 1 and 2, since same manipulations and stimuli were used in both experiments. The only difference was in the specific instruction given to the participants, which consisted in "grasp to move" and "grasp to use" the object. In line with previous literature (Marteniuk et. al., 1987; Gentilucci, Negrotti, & Gangitano, 1997; Ansuini et al., 2006; Ansuini et al., 2008), I confirmed that some grasping parameters are modulated by the purpose of the task.

Although a direct comparison across all the four experiments was not carried out for methodological reasons, I was able to compare the experiment in pairs: Experiments 1 and 2 (grasp to use and grasp to move) and Experiment 3 and 4 (reaching-and-pointing or reaching-and-grasping).In the second set of experiments I found that reaching movements were faster than grasping ones, and a similar, trend was noted comparing movement times in the first set of experiments: grasp to move movements were faster than grasp to use ones. These observations suggest that the complexity of the motor task may elicit longer movement times. However, in first set of experiments, the relative length of acceleration phase was modulated by the task, but in different ways for elderly and young people; while in the second set of experiments, it was found that acceleration phase accounted for a larger part of the movement when reaching than when grasping in both groups.

The main result of this study was consistent across all four experiments and was that elderly participants were faster in terms of reaction times or movement times (or both, in Experiments 1 and 3) when they were asked to fixate the central LED rather than when they were looking at the objects. Although a direct comparison of all four experiments was not possible, it is worth nothing that older participants had slightly faster reaction times than young adults in Experiment 2, had longer acceleration phases in Experiment 2 than in Experiment 1 and were somewhat slower than young adults only in Experiments 3 and 4. I can therefore argue that elderly participants seem to have a comparative advantage in more ecological tasks. The effect was particularly evident when the location of eye fixation was manipulated.

The present results contrast with a recent study (Bock & Steinberg, 2012) showing a greater impairment of elderly people in self-initiated, goal-directed tasks than in more laboratory-like tasks, but it is in line with the idea that elderly participants could be as fast as young participants in ecological tasks like grasping (Bennett & Castiello, 1994). This study lends some support to this hypothesis, as elderly participants showed a similar performance of young adults in grasping tasks and was actually even faster when grasping to use.

Similar results from the present were found in a previous study (Carnahan et al., 1998), which showed that older participants were faster than young adults, when they were required simply to grasp and move objects, without any speed-accuracy tradeoff. In the present study, that different control strategies were sufficient to offset the difference between young adults and elderly people. While in grasp to use older adults were actually faster than young ones, it is possible that in tasks such as reaching or grasping meaningless object, button low level factors (loss of muscle mass, of tendon functionality, etc…) might have had a stronger influence to the movement speed.

Previous studies have shown that elderly patients compensate for their real (or perceived) motor deficits with different behavioral and neural mechanisms, such as longer deceleration phases (Bennett & Castiello, 1994; Weir et al., 1998; Ketcham et al., 2006), larger grip apertures or higher grasping forces (Cole, 1991): all these factors may be considered as different elements of a 'play it safe' strategy (Welsh et al., 2007). A possible neural substrate for this phenomenon could be found in the results of neuroimaging studies that showed an hyperactivation of wide motor, premotor and frontal brain areas (Mattay et al., 2002; Hutchinson et al., 2002; Riecker et al., 2006). Furthermore, it has been shown that this phenomenon is stronger for more difficult tasks (Heuninckx et al., 2005), suggesting a possible shift towards more controlled processing of movements. I propose that the differences between young and elderly subjects observed in the present experiments may be the result of such mechanisms: elderly participants could benefit from situations that require higher cognitive control, while young ones could have a relative advantage in the opposite condition. In our experiment, executing the movements when fixating the LED required a more tight control of both the eye and arm movements, and the need for such control was arguably increased in tasks such as grasp to use, which required grasping the objects in a more specific way to be accomplished successfully. The finding that movements executed when fixating the LED required longer deceleration phases support this hypothesis: both groups had longer acceleration phases and larger grip aperture when they could not directly look at the objects. This suggests that older adults may increase the level of motor control during motor tasks and apply strategies to avoid hitting the object instead of grasping it when objects are presented in the peripheral visual field (Sivak & MacKenzie, 1990, Brown et al., 2005) or when there is uncertainty about the position of the object to be grasped (Schlicht & Schracher, 2007).

Elderly participants had a larger maximum grasp aperture than young in Experiments 1 and 2, and opened the grasp more regardless which the object was presented, the position of the object on the board or the target of eye fixations. This can be interpreted as a mechanism geared towards the reduction of the number of errors during grasping, and thus as a part of the different strategy used by elderly and young participants in our study. The increase in the MGA can alternatively be interpreted as a decrease in accuracy (Carnahan et al., 1998), with older participants exhibiting some tradeoff between speed and reaction times on one side and grip accuracy on the other. The present study cannot support specifically the former or the latter interpretation, and further research is required to shed light on this point.

To conclude the present study shows that age-related changes affect the motor performance in grasping, but compensatory mechanisms seems to play a role in reducing the difference between old and young participants in terms of movement speed and reaction times. In particular, older adults could benefit from motor tasks that require higher control, while wider grip apertures and longer deceleration phases could contribute to compensate the changes in hand functionality by minimizing the errors without sacrificing execution speed.

Chapter 4

Perturbations in kinematic parameters of grasping and reaching following brain damage

4.1 Introduction

Amongst the most frequent outcomes of brain damage in humans there is a diminished ability to move in the space and to act purposefully. For instance, damage to primary motor cortices can initially cause flaccid paralysis of the limbs controlateral to the lesion and, in subacute and chronic stages, hemiparesis of the limbs contralateral to the lesion, lesions of the cerebellum can cause ataxia and lesions to the basal ganglia dyskinesia, tremors and dystonia. On the other hand, lesions of other brain areas such as the left parietal cortex can cause different a different kind of motor deficit, noticeable whether the limb used to perform the movements is ipsi- or contralateral with respect to the location of brain damage and not dependent on low level motor or sensory deficits. This kind of motor deficit is known as apraxia, and has been first described and linked with damage to the left parietal cortex by the seminal works of Liepmann (1908, 1913). Apraxia is a neuropsychological condition defined as "a disorder of skilled movement not caused by weakness, akinesia, deafferentation, abnormal tone or posture, movement disorders such as tremor or chorea, intellectual deterioration, poor comprehension, or uncooperativeness" (Heilman and Rothi, 1993) and has proven to be a complex entity to investigate: Liepmann himself identified two different forms of apraxia (*ideational apraxia,* or the inability to correctly generate the appropriate motor plan to execute an action or to use an object and *ideomotor apraxia,* that is characterized by an impairment of the production component of praxis systems), but since then different studies proposed further subcategorizations, giving rise to a complex taxonomy of apraxic syndromes (Petreska et al., 2007). While a full review of the literature of apraxia is outside the scope of this introduction, it is worth noting that while apraxic syndromes have been mostly been described in patients with left brain damage, some studies (Marchetti & Sala, 1997 Raymer et al., 1999) found severe apraxia in patients with unilateral right brain damage.

Apraxic errors have often been described from a qualitative point of view, using categories such as uncertainties in the execution of the movement, spatial errors, errors in the temporal sequence of movements, perseverations, parapraxias (right execution of a wrong movement), or tendency to use a

body part as a tool (for instance using bringing the index finger towards the teeth and moving it when demonstrating the act of teeth cleaning instead of mimicking the grasp of a toothbrush) (Rumiati et al., 2001). However, with the development of technology and with the increased availability of sophisticate measures of motion, some studies focused upon the analysis of the performance of apraxic patients from a kinematic point of view. For instance, Poizner et al. (1994) recorded the performance of apraxic patients while they were executing transitive gestures, such as unlocking a door or a cutting, using a 3D tracking system. Analyzing the kinematic data of patients and healthy controls, the authors pointed out at several differences between the groups: while control subjects exhibited a clear inverse relationship between speed and curvature (similar to the one predicted by the 2/3 power law) (Lacquaniti, Terzuolo & Viviani, 1983), this relationship was perturbed in patients. Another study (Haaland et al., 1999) found also evidence for a similar dissociation between the spatial and temporal aspect of movements. For instance, left brain damaged patients (LBD) with or without apraxia showed a similar performance to healthy controls when executing a simple reaching task. However, when feedback of the targets and/or of the hand was withdrawn, apraxic patients were more likely to commit spatial errors and were not able to execute the movements accurately.

As mentioned before, apraxic syndromes have been also observed in patients with unilateral brain damage confined to the right hemisphere. Indeed, different studies pointed out that both right and left hemispheres contributed to motor planning (Fisk & Goodale, 1988; Haaland & Harrington, 1989; Hermsdörfer et al., 1999; Schutler et al, 2001; Hermsdörfer and Goldenberg, 2002), but in different ways. In particular, the right hemisphere has been linked to on-line control of movements and closed-loop processing (Haaland & Harrington, 1996), while the left hemisphere with planning of open-loop and ballistic movements (Winstein & Pohl, 1995, Hermsdöfer et al., 1999b). This hypothesis did not find support in a recent study (Hermsdörfer et al. 2003), where performance of LBD and RBD patients was compared with healthy controls in different pointing tasks. The authors found that RBD patients performed similarly to the control group when pointing to external targets and showed no specific deficit when pointing towards smaller targets. Most importantly, patients with LBD showed prolonged approach phases. This effect was especially pronounced when higher accuracy was required (that is, when pointing towards smaller targets) and in this condition LBD patients also exhibited longer movement times. However, the authors did not found any differences in the duration of the initial acceleration phase between healthy controls and LBD patients, and therefore argued that the left hemisphere might not specifically involved in planning and execution of open-loop movements, but it may rather play a more general role in motor control, with a level of involvement dependent on task demands.

To summarize, there is still not clear consensus in the literature about the roles played by the right and the left hemisphere in motor control. This might be partly due to the difference across tasks and to the different aspects of the movements taken into account in different studies. However, even if the different studies diverge in the interpretation of the roles played by the left and right hemispheres, some studies (Hermsdörfer et al., 2003, Haaland et al, 1999) agree on the fact that apraxia might impair the representation of the arm configuration and of its relationship to the external space, as underlined by a greater impairment of performance of apraxic patients when they execute movements without external guidance or feedback.

While different studies analyzed the performance of patients with brain damage in a number of tasks, from pointing and prehension to one-handed shoe tying (Poole et al. 2009), to the best of our knowledge the performance of brain damaged patients in different tasks, which range from simple grasping to more complex actions have not been investigated in a single study. As discussed in Chapter 3, it has been shown that the goal of the task has an impact on the kinematics of grasping. For instance, two more recent studies on healthy subjects(Ansuini et al., 2006; Ansuini et al., 2008) investigated the effect of the task on the kinematics of grasping, considering the motion of each single finger of the hand. When participants were asked to grasp an object, to lift it, and to place it in a big or small niche, the goal of the task influenced not only the reaching speed, with movements being faster in placing the objects in the larger than smaller niche, but also the hand pre-shaping of the fingers (Ansuini et al., 2006). Furthermore, the different nature of the task goal (grasping a jug of water without any other goal versus grasping the jug to pour some water or to pass it to other persons) also influenced both grasp formation and transport parameters (Ansuini et al., 2008).

As in Chapter 3, in the present study participants were asked to perform different actions directed towards an object placed on the left or right side of their body midline: in Experiment 1, they were asked to grasp the objects to move them; in Experiment 2, to grasp the objects and then to use them on a predetermined target location. In Experiment 3, participants were asked to simply perform reaching movements toward the objects and touch them in the middle, while in Experiment 4 participants were required to grasp the objects without performing any further action afterwards.

In the present study, I explored the performance of a group of six LBD patients without apraxia and of a group of three patients with unilateral RBD on a series of motor tasks and compared their performance with healthy controls. As the control subjects were all right-handed but executed all the experiments with both hands, I analyzed first the effect of grasping kinematics of the hand used. Then, I compared the performance of control subjects using their left hand with LBD patients and the

performance of control subjects using their right hand with RBD patients. In the last section, I described as a single case one patient with LBD and limb apraxia.

An important manipulation involved the relation between eye and hand movements: in one condition participants were free to perform the action having full access to visual feedback (they could look at the object to be grasped), while in another condition they were asked to keep the fixation on a LED placed centrally in the workspace while performing the action (a manipulation similar to the one used in Fisk & Goodale, 1988). This experimental factor allowed us to explore the different effect on LBD and RBD patients of reducing the available visual feedback. In particular, if the left hemisphere is more implicated in the planning of open-loop, ballistic movements, I predicted that LBD patients would be impaired in the condition on which they were asked to grasp the objects while keeping fixation on the central LED. On the other side, I expected that RBD patients would show abnormally longer deceleration phases than controls in all condition, but especially so when the movement was more dependent on visual feedback (for instance, when looking at the objects and/or reaching toward smaller targets).

4.2 Methods and materials

Participants

A group of seven left brain damage (LBD) and three right brain damage (RBD) patients took part in the present study (see Table 4.1 for a summary of the demographic characteristics of the samples) and were asked to perform the motor tasks using their ipsilesional hand. Furthermore, a group of six adults matching for age the two patients' groups were also selected and were asked to perform the experimental task using both hands. Only one patient with LBD showed limb apraxia. This patient is not included in Table 1, and will be discussed as a single case study. Patients and control subjects were matched for age [t (10)=1.1, n.s. for the LBD and t (2.1)=-0.1, n.s. for the RBD].

Table 4.3 - Age, sex and scholarity of the three groups of participants

	Age		Scolarity		Males	Females
	Mean	SD	Mean	SD		
Controls	61.8	5.7	13.83	3.76	3	3
LBD	53.57	8.12	12.28	5.28	4	2
RBD	64	20.29	7.66	0.57	2	1

All participants had normal or corrected to normal vision. Control subjects were paid for their participation and all participants gave informed consent prior to their participation in the present study, in line with the guidelines of the Declaration of Helsinki. The study was approved by the Ethics Committee of SISSA.

Preliminary tasks

Patients and control subjects were asked to name and use the six objects used in the study described in Chapter 3 (forks, tweezers, pliers, brushes of small and large sizes). The accuracy in the use of the objects was assed using a score ranging from 0 to 2 (0: use is not correct; 1: the patient show the use of the object only after the second attempt; 2: the patient is able to show the correct use on the first attempt). None of the patients or of the control subjects showed difficulties in naming or using the object, with the exception of VS (see Single case description). Participants' ability to recognize and reach the objects when fixating the central LED was also assessed. No participants were excluded on the basis of his or her inability to reach or grasp the objects, as all control subjects scored 12/12 points in both using and naming tasks, and all patients scored at least 1 point in each naming/using task.

Left Brain Damage (LBD) group

Table 4.2 shows the average scores of patients with LBD on several neuropsychological tests, measuring different cognitive domains. As expected patients showed language problems and impairment in other cognitive domain, being in most of the cases attention and executive functions. No patient included in the LBD group showed limb apraxia, but two subjects (CS and AM) showed symptoms of bucco-facial apraxia, scoring respectively 17/24 and 9/24 points in the relative subscale (De Renzi et al, 1980). The results of each subject are reported in Appendix B, along with a more detailed description of the tests used in each case.

Table 4.4 - Performance of the LBD group on neuropsychological tasks

		Mean (SD)
Language		
Aachener Aphasie Test (AAT) (Luzzatti et al., 1996)	Errors in Token test	25.1 (10.4)
	Repetition:	116.6 (20.9)
	Written Language:	65.8 (17.5)
	Denomination:	78 (21)
	Comprehension:	102.1 (5.1)
Apraxia		
(De Renzi et al., 1980; Tessari et al.,)	Ideomotor	61 (5)
	Ideational	12
	Bucco-facial	19 (7)
Intelligence		
Raven (0-36) (Carlesimo et al., 1995) (n=4)		31 (6)
Attention and Executive functions		
Attentional matrices (n=5)		31 (7)
Weigl (Spinnler e Tognoni, 1987) (n=4)		10 (4)
Memory		
Digit span (Orsini e coll., 1987) (n=4)		4 (1)
Corsi span (Spinnler e Tognoni, 1987) (n=5)		5 (1)

Right Brain Damage (RBD) group

At the onset of the stroke, all RBD patients presented left hemiplegia, but they showed only mild difficulties at the moment of testing. Two of the three RBD patients had mild form of neglect, as demonstrated with a pathological score (107, 112) in the Behavioural Inattention test (Wilson et al 1995), but they were able to compensate the deficit in everyday life. They were able to perform the experiments and to keep fixation at the central LED while reaching the objects. All RBD patients were screened with a set of neuropsychological tests and the results are reported in Table 4.3.

Table 4.5 – Performance of the RBD group on preliminary neuropsychological tests. * mild, **moderate, * severe impairment**

Name	CDP	EC	VV
Age	42	68	82
Education	8	8	7
Lesion side	temporo-parietal	Fronto-parietal	Fronto-temporal
Neuropsychological tests			
Raven (Carlesimo et al., 1995)	22	21	25
Attentional Matrices (Spinnler e Tognoni, 1987)	19*	33	
Phonemic Fluency (Carlesimo et al., 1995)	18	21	
Semantic Fluency (Novelli et al., 1986)	34	48	
Vebal Fluency (Carlesimo et al., 1995)			35
Weigl (Spinnler and Tognoni, 1987)	10		6
Digit Span Forward (Orsini e coll., 1987)	3	5	4
Digit Span Backward (Orsini e coll., 1987)	3	4	2*
15 Rey words (imm)	44		
16 Rey diff (max 15)	10		
Span corsi (Spinnler e Tognoni, 1987)		4	4
Corsi Leaning phase		0*	
Rey Figure IMM (Wilson et al 1995)	25*	21.5*	19.5*
Rey Figure DIFF (Wilson et al 1995)	13.5	9*	11.5
Behavioral Inattention Test (BIT)	107*	112*	135
Test delle Campanelle (Biancardi e Stoppa, 1997).	30 (4 sx)	26 (5sx-3dx)	
Visual Object and Space Perception Battery (VOSP)			Letters 16* Silhouettes 13* Objects decision 10*
OTHER		Paced Auditory Serial Addition Test 4*	Language difficulties

Experimental setup and procedure

The experimental setup was very similar to the one described in more detail in Chapter 3, and will be shortly summarized here. All participants executed four different experimental tasks: they were asked to grasp objects and then move them to a predefined point (Experiment 1), to grasp objects and mimic their use using a predefined target (Experiment 2), to execute reaching movements (Experiment 3) and to grasp objects without performing additional actions (Experiment 4). A similar setup was used for all the four experiments (Figure 4.1). However, the main distinction among experiments was that the near location (3 and 4 in Figure 4.1) was used only in Experiments 3 and 4.

The experimental setup was described in detail in Chapter 3 and will be not described again here. However, in order to be able to test all patients with all the four experimental tasks I reduced the number of objects used from 6 to 2 (only big and small fork).

Data reduction and dependent variables

The sampled coordinates of the sensors for each trial were filtered with a high-pass second-order Butterworth filter, with a frequency cut-off of 10 Hz, and analysed using customised software written in LabVIEW™ (National Instruments). Movement onset and offset were determined by comparison of the speed against a threshold of 50 millimeters/s, and sub-sequent analysis was restricted to the parsed movements. To provide a description of the movements I considered the first reaching movement which was common to all the trials and computed the following kinematic variables

- Reaction time (RT) – The duration in milliseconds between the auditory tone and movement onset
- Movement time (MT) – The duration in milliseconds between the movement onset and offset
- Maximum grip aperture (MGA) – The distance in millimetres between the sensor placed on the index finger and the sensor placed on the thumb
- Normalized time to peak velocity (nTPV) – The duration of acceleration phase, expressed as percentage of movement time
- Normalized time to maximum grip aperture (nTMGA) – The time interval between movement start and maximum grip aperture, expressed as percentage of movement time

As in Experiment 3 (reaching) participants were not required to grasp, MGA and tMGA were not computed for the last two experiments.

Analysis

Linear mixed-effects model ANOVAs in SPSS, with type III sums of squares, were performed on the computed variables to maximize statistical power, given the small number of repetitions for each possible condition. I performed two different analyses: between experiments and within each experiment. When analyzing data from a single experiment, participants were entered as random factor, while all experimental manipulations were entered as fixed factors. When comparing different tasks (reach versus grasp; grasp to move versus grasp to use), group, task and condition were entered in the analysis as fixed factors as they were the key manipulations of interest in the present study, while all other factors were entered as random effect factors.

Therefore, when analyzing individually Experiment 1 or Experiment 2 the fixed effect factors considered were size (2 levels: big and small), orientation (2 levels: congruent or incongruent), side (2 levels: right or left), eye movements (2 level: free or fixed) and group (2 levels: patients or controls) resulting in a 2x2x2x2x2 design. When comparing Experiment 1 with Experiment 2, the fixed effect factors were group (2 levels: control subjects or patients), eye movements (2 levels: free or fixed) and task (2 levels: grasp to move or grasp to use), resulting in a 2x2x2 design.

When analyzing individually Experiment 3 or Experiment 4 the fixed effect factors considered were size (2 levels: big and small), distance (2 levels: near or far), side (2 levels: right or left), eye movements (2 level: free or fixed) and group (2 levels: patients or controls) resulting in a 2x2x2x2x2 design. When comparing Experiment 3 with Experiment 4 the fixed effect factors were group (2 levels: patients or controls), eye movements (2 levels: free or fixed) and task (2 levels: grasp to move or grasp to use), resulting in a 2x2x2 design.

Post hoc analyses were conducted by splitting the dataset by the factors driving the significant interactions, while keeping all other factors as fixed (or random) effects like in the original ANOVA.

Before analyzing the performance of patients I analyzed the performance of control subjects, comparing first Experiment 1 and 2 and then Experiment 3 and 4, as described above. However, as the control subjects performed the experiments once with the right and once with the left hand, the factor 'hand' (left or right) replaced the factor 'group', therefore obtaining a 2x2x2 design (task x hand x eye movements).

4.3 Results

Control subjects

First, I analyzed the performance of control subject in the experimental tasks, comparing grasp to move against grasp to use, and reach against grasp, to assess the effect of the hand on the grasping and reaching movements. Control subjects performed the experiments with both the right and the left hand. The results of this analysis are reported in Appendix B. In brief, the analysis confirmed the preference of each hand for moving in its own hemispace (Fisk & Goodale, 1985, Simon and Reeve, 1990), as showed by the differences in MT and nTPV, and the influence of the goal on the kinematic parameters of grasping.

Patients with left brain damage (LBD) versus controls

After this preliminary analysis, I compared the performance of patients with LBD with control subjects using their left hand. As in described in the materials and methods section, I analyzed the differences between groups in each experiment (grasp to move, grasp to use, reach and grasp) and then comparing grasp to move with grasp to use and reach to grasp.

Experiment 1: Grasp to move

Main effect of the group. As shown in Table 4.4, the main effect of the group was significant for the reaction times (**RT** $F_{1,10}$=208.38 $p<0.001$), as healthy controls were faster than LBD in starting the movement.

Main effect of the size. The effect of the size was significant for the maximum grip aperture (**MGA** $F_{1,332}$=459.23 $p<0.001$), that was larger for larger objects.

Main effect of the side. The main effect of the side was significant for several parameters: movement times (**MT** $F_{1,332}$=93.34 $p<0.001$), maximum grip aperture (**MGA** $F_{1,332}$=6.39 $p<0.05$), and normalized length of acceleration phases (**nTPV** $F_{1,332}$=15.46 $p<0.001$). Movement times and acceleration phases were longer and grip apertures were larger when objects were placed on the right rather than on the left side.

Main effect of the orientation: The main effect of the objects orientation (congruent or incongruent) was not significant for any parameter.

Table 4.4 - Means and SEM of the kinematic parameters referred to the main effects (grasp to move, patients and controls)

	Mean	SEM	Mean	SEM
Group	Control		LBD	
RT	565.28 ms	11.65	751.45 ms	30.95
Size	Small		Big	

MGA	*69.04 mm*	*0.875*	<u>*93.21 mm*</u>	*1.077*
Side		*Left*		*Right*
MT	*896.72 ms*	*14.578*	<u>*1052.46 ms*</u>	*17.117*
MGA	*79.90 mm*	*1.175*	<u>*82.67 mm*</u>	*1.451*
nTPV	*31.36%*	*0.510*	<u>*34.41%*</u>	*0.674*

The interaction *group by side* was significant for movement times (**MT** $F_{1,332}$=5.24 p<0.05). Both groups were faster when objects were placed on the left half (p<0.001 for both groups) rather than on the right of the workspace. The performance of the two groups did not differ when the objects were placed on the left nor when the objects were placed on the right, as healthy controls were faster than LBD.

The interaction *group by size* was significant for the maximum grip aperture (**MGA** $F_{1,332}$=9.070 p<0.005).Both groups opened the grip more for big objects than for small ones (p<0.001 for both groups) and no other contrast was significant.

The interaction *group by eye movements* movement times (**MT** $F_{1,332}$=30.40 p<0.001) and maximum grip apertures (**MGA** $F_{1,332}$=17.72 p<0.001). LBD had shorter movement times when looking at the objects than when fixating the LED (p<0.001), while the opposite pattern was found for control subjects (p<0.001). When participants looked at the object there was no difference between groups, but when they were asked to perform the action while fixating the LED, control subjects were faster than LBD (p<0.05). LBD showed a bigger maximum grip aperture when they were moving while fixating the LED (p<0.001) than when looking at the objects, but control subjects showed the opposite effect and adopted a larger grasp when they were looking at the objects rather than fixating the LED (p<0.05).
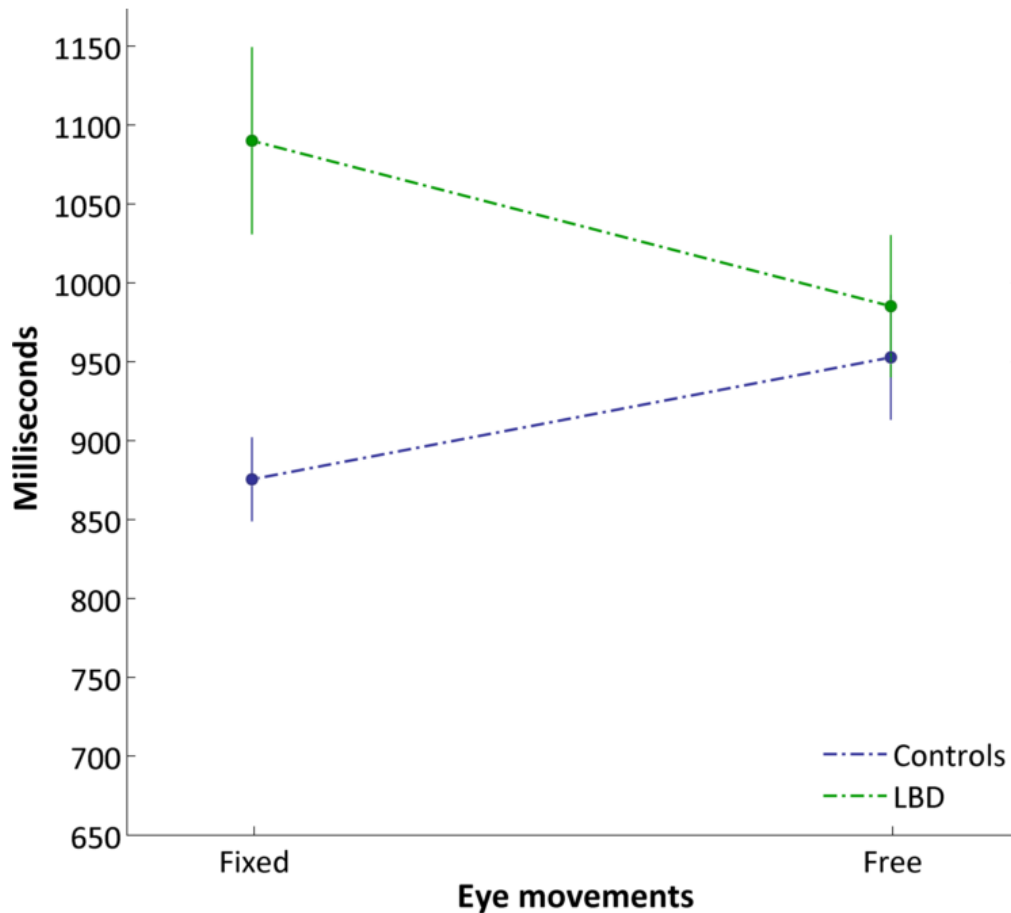
Figure 4.1 – Movement times (MT) of LBD patients and controls in free and fixed eye movements conditions (Experiment 1: Grasp to Move)

The interaction *group by eye movements* was significant also for the normalized length of acceleration phases (**nTPV** $F_{1,332}$=10.55 $p<0.001$). Controls subjects had longer acceleration phases when fixating the LED rather than looking at the objects ($p<0.001$), but the effect was not significant for LBD. When LBD were looking at the objects to be grasped, they showed longer acceleration phases than control subjects, but they showed a similar performance when fixating the LED.

Figure 4.2 – Normalized time to peak velocity (nTPV) of LBD patients and controls in free and fixed eye movements conditions (Experiment 1: Grasp to Move)

Experiment 2: Grasp to Use

Main effect of the group. The main effect of the group (controls - LBD) was not significant for any parameter.

Main effect of the eye movements. The main effect of the eye movements (fixating the LED or looking at the objects) was not significant for any parameter.

Main effect of the size. The main effect of size was significant for the grasp parameters (see Table 4): Maximum grip aperture (**MGA** $F_{1,305}$=535.90 p<0.001) and normalized time to maximum grip aperture (**nTMGA** $F_{1,305}$=11.62 p<0.001). When grasping bigger objects participants used a bigger grip and showed longer times to reach the maximum grip aperture (Table 4.5)

Main effect of the side. The main effect of the side was significant for several parameters: movement times **MT**($F_{1,305}$=84.73 p<0.001), maximum grip aperture ($F_{1,305}$=5.95 p<0.05), and normalized length of

acceleration phases ($F_{1,305}$=50.80 p<0.001). Movement times and acceleration phases were longer and grip apertures were larger when objects were placed on the right rather than on the left.

Main effect of the orientation. The main effect of orientation was significant for movement times (**MT** $F_{1,305}$=16.68 p<0.001), which were faster with objects placed in congruent orientations.

Table 4.5 - Means and SEM of the kinematic parameters referred to the main effects (grasp to use, LBD patients and controls)

	Mean	SEM	Mean	SEM
Size	*Small*		*Big*	
MGA	*66.49 mm*	*0.822*	*91.17 mm*	*1.031*
nTMGA	*69.82%*	*1.399*	*74.80%*	*0.845*
Side	*Left*		*Right*	
MT	*916.22 ms*	*12.986*	*1062.24 ms*	*13.622*
MGA	*77.73 mm*	*1.180*	*80.05 mm*	*1.453*
nTPV	*29.63%*	*0.545*	*35.77%*	*0.785*
Orientation	*Down*		*Up*	
MT	*1024.34 ms*	*14.917*	*954.97 ms*	*13.412*

The interaction *group by eye movements* was significant for different parameters: movement times (**MT** $F_{t,305}$=32.25 p<0.001), maximum grip apertures (**MGA** $F_{1,305}$=17.38 p<0.001) and normalized times to peak velocity(**nTPV** $F_{1,305}$=8.61 p=0.001) . As for the previous experiment, LBD had shorter movement times when looking at the objects rather than when fixating the LED (p<0.005) and the opposite pattern was observed for controls (p<0.001). The difference between the groups was not significant when participants looked at the objects, but when fixating the LED, LBD were slower than control subjects (p<0.05). In a similar way, patients adopted a larger grip when fixating the LED than when looking at the objects (p<0.05), but the reverse effect was observed for control subjects (p<0.001). The difference between the groups was not significant when participants looked at the objects, but when fixating the LED, LBD used a wider grip than control subjects (p<0.05). Finally, control subjects had longer acceleration phases when fixating the LED than when looking at the objects (p=0.05), while an opposite trend emerged for LBD, without reaching significance (p=.12)

Figure 4.3 – Movement times (MT) of LBD patients and controls in free and fixed eye movements conditions (Experiment 2: Grasp to Use)
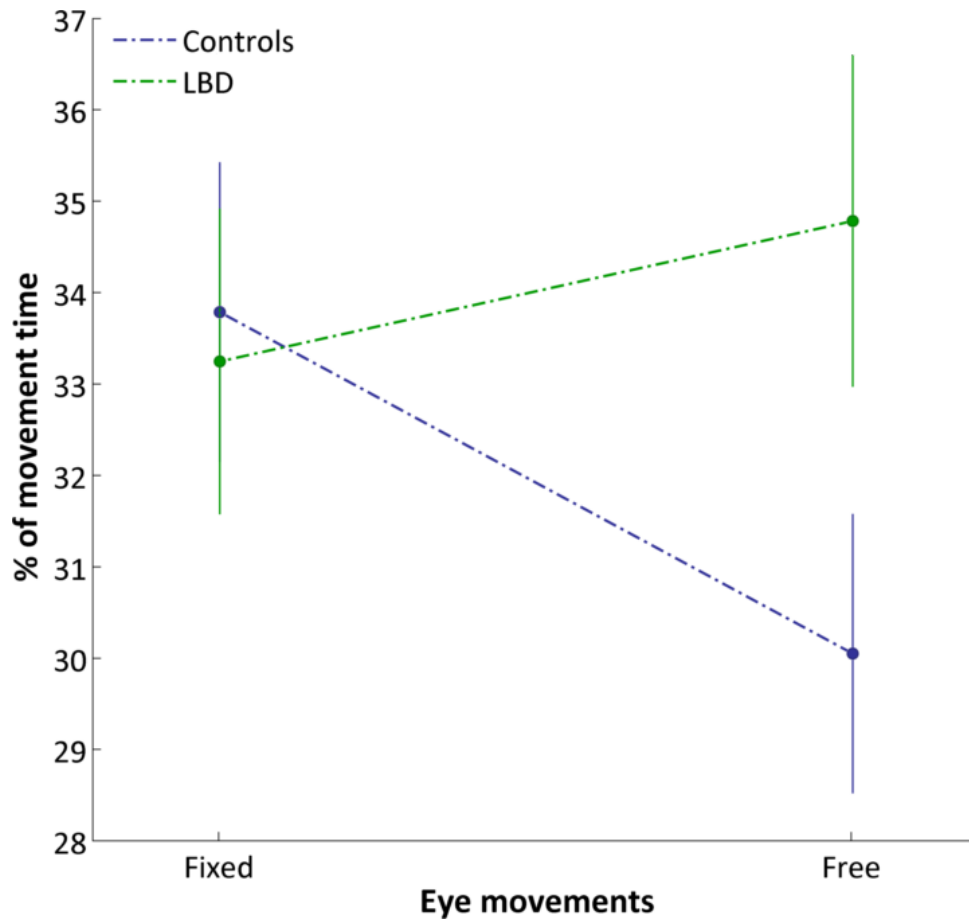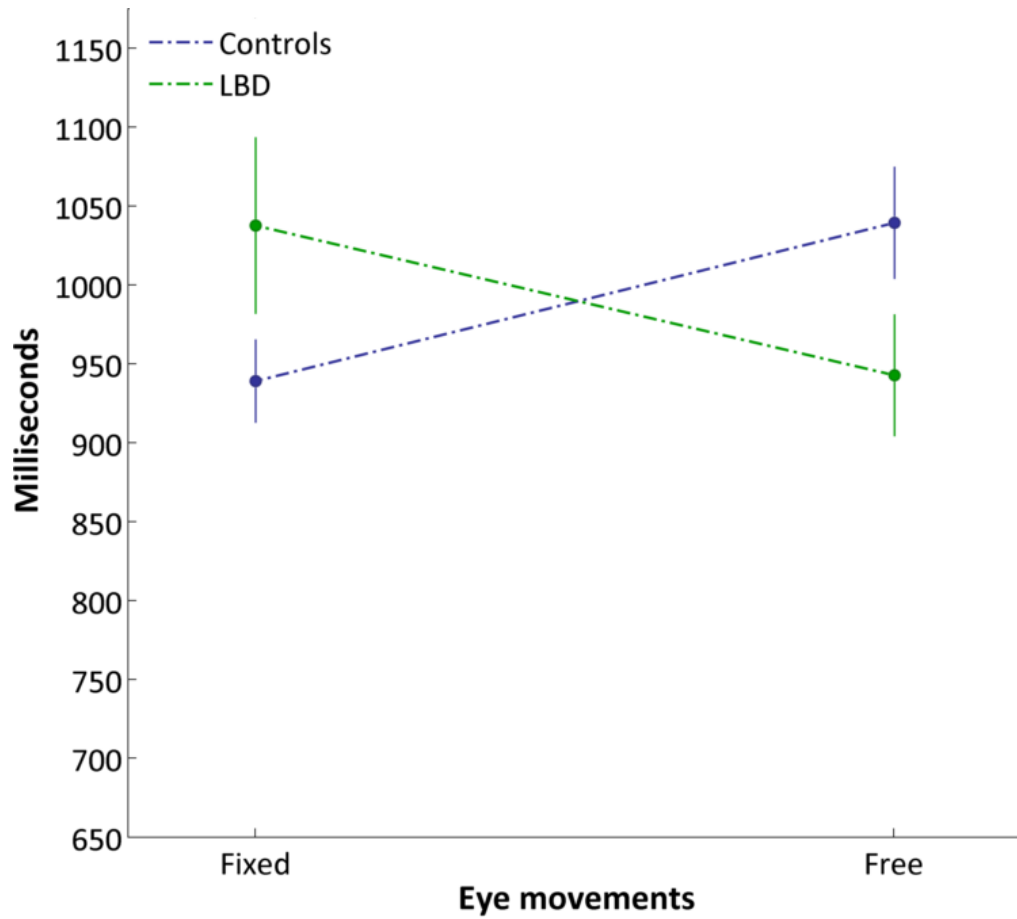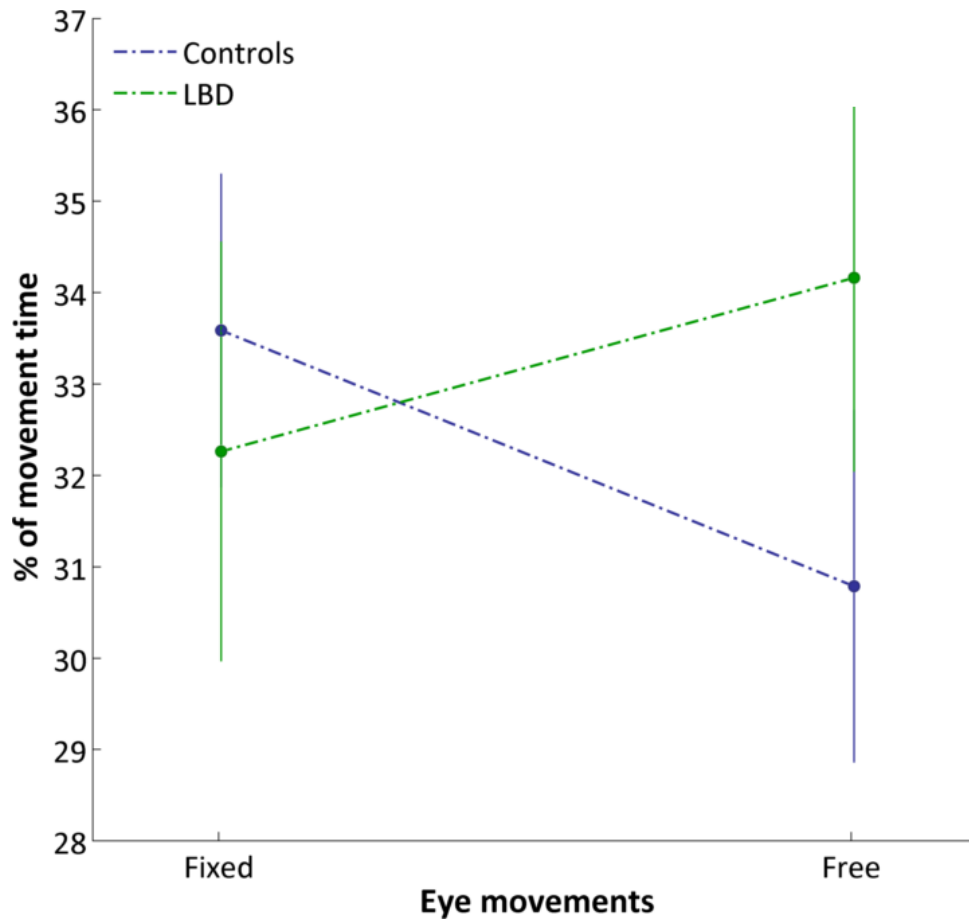
Figure 4.4 – Normalized time to peak velocity (nTPV) of LBD patients and controls in free and fixed eye movements conditions (Experiment 1: Grasp to Move)

The interaction *group by side* was significant for movement times (**MT** $F_{1,305}$=18.06 $p<0.001$). While for both groups movement were faster when objects were placed on the left half of the workspace ($p<0.001$ in both cases, controls were faster than LBD patients on the right ($p<0.05$), but patients were faster than controls on the left ($p<0.05$).

The interaction *group by size* was significant for the normalized times to maximum grip aperture (**nTMGA** $F_{1,304}$=3.73 $p=0.05$). The interaction is driven by within group effects: patients required more time to reach the maximum grip aperture when grasping big objects rather than small ones ($p<0.001$), but this difference was not significant for control subjects.

The interaction *group by eye movements by side* was significant for reaction times (**RT** $F_{1,303}$=4.91 $p<0.05$). LBD were slower to react than control subjects only when they were asked to fixate the LED and grasp the objects presented on the right side ($p<0.05$) .

Comparison between Experiment 1 and Experiment 2

Main effect of the group. The main effect of the group was significant for reaction times (**RT** $F_{1,10}$=5.66 p<0.05), as patients were slower than control subjects in initiating the movement (see Table 4.6)

Main effect of the Experiment: Although the comparison did not reach significance (**MT**: $F_{1,702}$=2.89 p=0.089), longer movement durations were observed in use rather than move Experiment. In this last Experiment, normalized times to grip aperture were longer than in grasp to use (**nTMGA** $F_{1,702}$=4.47 p<0.05).

Main effect of the eye movements: The main effect of the eye movements (fixating the LED or looking at the objects) was not significant for any parameter.

Table 4.6 - Means and SEM of the kinematic parameters referred to the main effects (grasp to use and grasp to move, LBD patients and controls)

	Mean	SEM	Mean	SEM
Group	*Control*		*Patients*	
RT	*565.28 ms*	*9.137*	*747.05 ms*	*23.362*
Task	*Move*		*Use*	
MT	*637.53 ms*	*0.935*	*989.65 ms*	*10.180*
nTMGA	*81.29%*	*0.702*	*78.90%*	*0.825*

The interaction *group by task* was significant for different parameters: reaction times (**RT** $F_{1,703}$=5.46 p<0.005), movement times (**MT** $F_{1,703}$=13.90 p<0.001) and maximum grip apertures (**MGA** $F_{1,703}$=7.48 p<0.005, Figure 4.5). Interestingly, when considering the LBD patients, there were no significant differences between grasp to move and grasp to use Experiments for any of the kinematic variables considered in the present study. On the contrary a modulation of the performance was observed in the control group: participants were faster when grasping to move than when grasping to use in terms of both **RT** (p<0.001) and **MT** (p<0.001), and had a wider maximum grip aperture in grasp to move than in grasp to use (p<0.005). Overall, the difference between the LBD and controls was not significant in grasping to use, but LBD showed slower reaction times than control subjects and movement duration in grasping to move tasks (p≤0.05 in both comparisons).

The interaction *group by eye movements* was significant for different parameters: movement times (**MT** $F_{1,703}$=45.33 p<0.001), maximum grip aperture (**MGA** $F_{1,703}$=15.33 p<0.001) and normalized times to peak velocity (**nTPV** $F_{1,702}$=14.62 p<0.001). While LBD were faster when looking at the objects than when fixating the LED (p<0.001), the opposite effect was noted for control subjects (p<0.001)(Figure 4.6a). When the participants looked at the objects to be grasped there was no difference in movement times between the groups, but when fixating the LED patients were slower than controls (p<0.001). A similar (but opposite) trend was noted for the maximum grip aperture: patients opened the grip more when fixating the LED than when looking at the objects (p<0.01), but control subjects opened the grip more when looking at the objects than when fixating the LED (p<0.005). The difference in MGA between the groups was only significant when participants fixated the LED, and patients opened the grip more than control subjects (p<0.001). Finally, the acceleration phases of controls were longer when they fixated the LED than when they looked at the objects (p<0.001). While there was no difference between groups in the nTPV when participants fixated the LED, patients had longer acceleration phases than controls (trend, p=0.08) when they could look at the objects (Figure 4.6b).
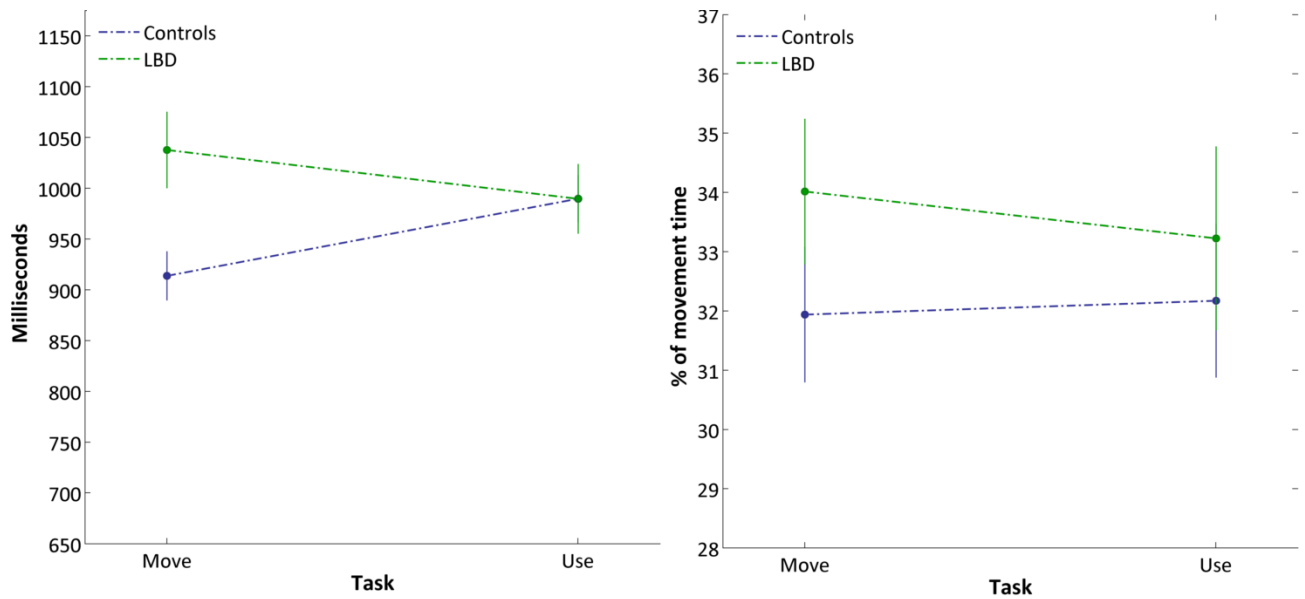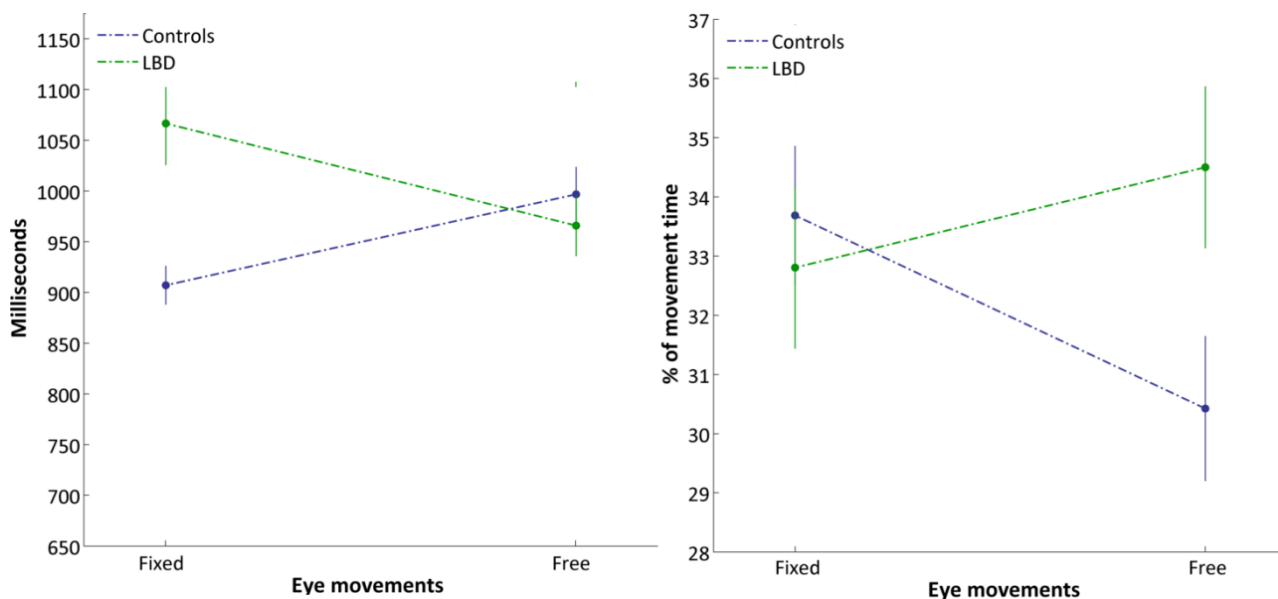
Figure 4.6 – Movement times (MT, left) and normalized times to peak velocity (nTPV, right) of LBD patients and controls in free and fix eye movements conditions (Experiments 1 and 2: Grasp to Move and Grasp to Use)

Comments to Experiments 1 and 2

The comparison between patients and healthy controls in Experiment 1 and 2 shows that some of the results found in the analysis of the kinematic parameters of control subjects are confirmed in LBD patients. For instance, both groups had shorter movement times and longer acceleration phases when the objects were placed in the left hemispace. This was expected, as both groups were using their left hand to grasp the objects.

I also found that LBD patients were slower than controls in initiating the movements. Previous studies investigating pointing and reaching movements in patients with unilateral left brain damage did not report significant differences in reaction times between patients and healthy controls (Fisk & Goodale, 1988; Haaland et al, 1999; Hermsdöfer, 1999). However, it is possible that our experiments imposed a higher load on motor control systems during the planning or pre-planning phases, and therefore made noticeable differences between groups that could not be noticed with simpler tasks. On the other hand, LBD patients showed similar movement time to control subjects. Although this result is in contrast with some previous studies, that found longer movement times for patients with left brain damage (Fisk & Goodale, 1988; Winstein et al., 1995; Hermsdörfer et al., 1999b), this effect is not replicated consistently in the literature. For instance, non-apraxic LBD patients did not differ from control in movement times in aiming tasks (Haaland et al., 1999).

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An interesting aspect of the present results is the interactions *experiment by group* and *eye movements by group*. In particular, while our control subjects benefitted from the condition on which they were required to grasp the objects while keeping fixation on the central LED, patients with LBD did not and therefore their performance was quite similar in this condition. It can be argued that participants relied more on visual feedback and online control mechanisms when grasping while looking at the objects, and on tactile and proprioceptive feedbacks from previous trials when grasping the objects while fixating the LED. In the same way, grasping an object with the only goal to move it arguably has lower accuracy requirements and a reduced need for online control than grasping an object to use it on a predefined target Performance in these condition might depend on pre-planned ballistic movements, with a lower precision requirements and lesser reliance on online feedback mechanisms, which have been posited to be altered in LBD (Hermsdorfer at al., 1999).

Interestingly, when considering the LBD group I found that the kinematic parameters of the transport component were not significantly modulated by the task: for instance, LBD patients had similar reaction and movement times in grasp to reach and grasp to use. Instead, healthy control subjects modulated their performance in accordance with the goal of the task, with movement duration being longer in grasping to use than grasping to move(as did both young and elderly participants of the study reported in Chapter 3). It is therefore possible that LBD patients suffer from a loss of cognitive flexibility and while they are able to execute the task correctly, they do not modulate their strategy according to the task requirements. It is possible that LBD patients always grasp as if they were required to use it, in order to minimize the changes in their movements during the trial and to reduce the errors, in a way similar to what described for elderly people in Chapter 3.

Experiment 3: Reach

Main effect of the group. The main effect of the group (controls or LBD patients) was not significant for any of the grasping parameter.

Main effect of the eye movements. The main effect of the eye movements (see Table 4.7) was significant for the movement times (**MT** $F_{1,148}=6.3$ $p<0.05$), which were longer in fix rather than free condition

Main effect of the side. The main effect of the side was significant for movement times **MT**($F_{1,148}=19.06$ $p<0.001$), which were longer on the right rather than on the left side of the working space.

Main effect of the distance. The main effect distance was significant for movement times **(MT** $F_{1,158}$=185.27 p<0.001), which were faster with objects placed in near position and for the normalized times to peak velocity (**nTPV** $F_{1,148}$=4.64 p<0.05) which occourred later for the objects placed in the far positions.

Table 4.7 - Means and SEM of the kinematic parameters referred to the main effects (reach, LBD patients and controls)

	Mean	SEM	Mean	SEM
Eye movements	*Fix*		*Free*	
MT	*748.01 ms*	*24.477*	*689.34 ms*	*19.874*
Distance	*Near*		*Far*	
MT	*581.02 ms*	*14.512*	*857.69 ms*	*19.704*
nTPV	*32.66%*	*1.713*	*36.48%*	*0.896*
Side	*Left*		*Right*	
MT	*732.33 ms*	*19.990*	*815.06 ms*	*24.121*

The interaction group by eye movements was shown as a trend for reaction times but did not reach significance (**RT** $F_{1,148}$=3.34 p=0.07).

Experiment 4: Grasp

Main effect of the group. The main effect of the group (controls and LBD patients) was not significant for any of the explored parameters.

Main effect of the eye movements. The main effect of eye movements (fixation on the LED or looking the objects) was not significant for any of the explored parameters.

Main effect of the size. The main effect of the size was significant for the reaction times (**RT** $F_{1,133}$=7.54 p<0.01) and for the movement times (**MT** $F_{1,133}$=3.83 p=0.05), which were longer with small rather than big objects.

Main effect of the side. The main effect of the side was significant for the movement times (**MT** $F_{1,133}$=25.61 p<0.001) and for the duration of acceleration phases (**nTPV** $F_{1,133}$=3.72 p=0.05), both being longer on the right rather than on the left side.

Main effect of the distance. The main effect distance was significant for movement times (**MT** $F_{1,133}$=239.63 p<0.001) and for the normalized times to peak velocity (**nTPV** $F_{1,133}$ 3.97 p<0.05), both being longer in the far rather than near location.

Table 4.8 - Means and SEM of the kinematic parameters referred to the main effects (reach, LBD patients and controls)

	Mean	SEM	Mean	SEM
Distance	*Near*		*Far*	
MT	*638.37 ms*	*14.437*	*907.93 ms*	*17.441*
nTPV	*31.55%*	*1.623*	*35.49%*	*1.060*
Size	*Small*		*Big*	
RT	*633.02 ms*	*30.655*	*543.33 ms*	*22.009*
MT	*789.42 ms*	*23.031*	*758.62 ms*	*19.444*
Side	*Left*		*Right*	
MT	*732.33 ms*	*20.058*	*815.06 mm*	*22.253*
nTPV	*31.70%*	*1.090*	*35.34%*	*1.596*

The interaction *group by side* was significant only for movement times (**MT** $F_{1,133}$=4.18 $p<0.05$). Both groups were faster when the objects were placed on the left rather than on the right ($p<0.005$ for patients, $p<0.05$ for control subjects), but none of the other contrast was significant.

The interaction *group by distance* was significant for reaction times (**RT** $F_{1,133}$=4.93$p<0.05$) and movement times (**MT** $F_{1,133}$=8.95 $p<0.01$). Patients were faster to react when the objects were placed in near than in far positions ($p<0.05$). Both groups had shorter movement times when the objects were placed in near rather than far positions ($p<0.001$ in both cases), but control subjects had longer movement times than LBD patients only in the near condition ($p=0.05$).

Comparison between Experiment 3 and 4

Main effect of the group. The main effect of the group (controls or LBD patients) was not significant for any parameter.

Main effect of the task. The main effect of the task (see Table 8) was significant for the movement times (**MT** $F_{1,351}$=6.05 $p=0.01$)

Main effect of the eye movements. Although it did not reach significance, movement times were slightly longer when participants were looking at the LED rather than at the objects (**MT** $F_{1,346}$=3.54 $p=0.06$).

	Mean	SEM	Mean	SEM
Task	*Reach*		*Grasp*	
MT	*725.07 ms*	*15.901*	*772.93 ms*	*15.274*
Eye movements	*Fixed*		*Free*	
MT	*768.49 ms*	*16.614*	*727.25 ms*	*14.626*

The interaction *group by task* was significant for movement times (**MT** $F_{1,351}=7.78$ $p<0.01$) The only significant contrast was for control participants, who required more time in grasping than reaching ($p<0.05$), while the difference was not significant for LBD patients (see Figure 4.7).

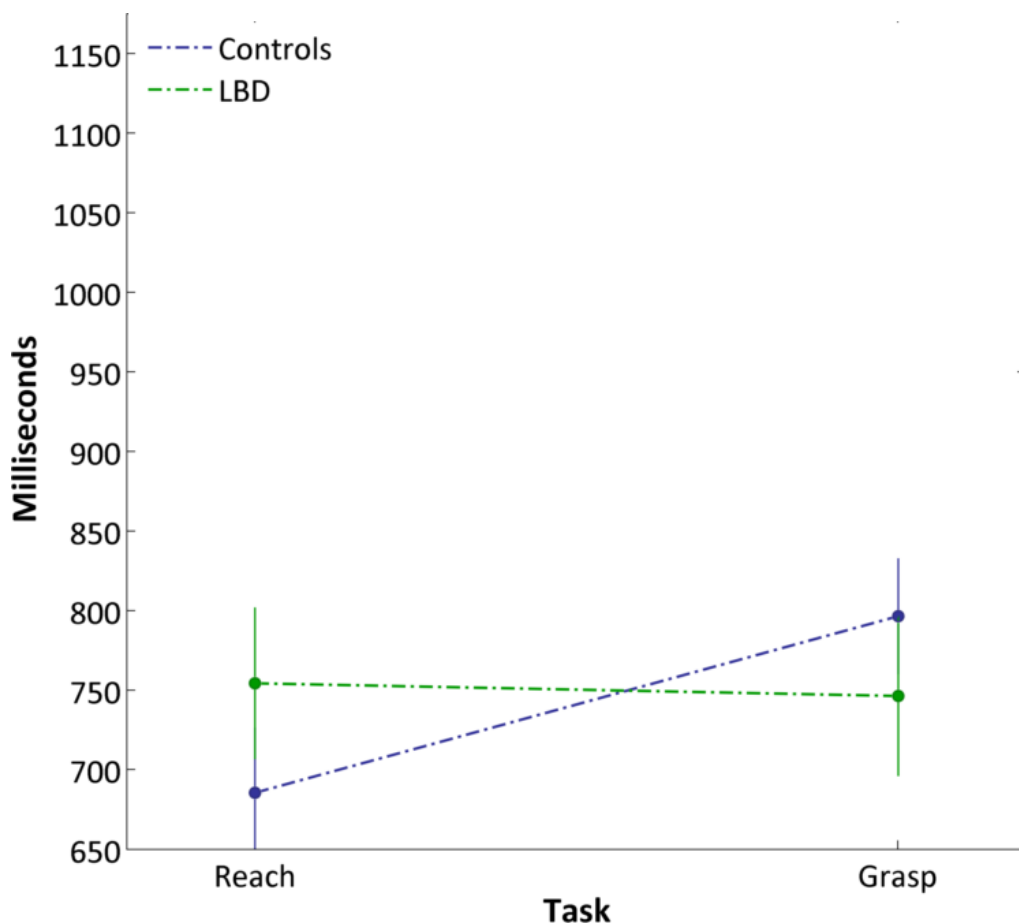**Figure 4.7– Movement times of LBD patients and controls in Experiment 3 and 4: Reach and Grasp**

The interaction *group by eye movements* was significant for reaction times (**RT** $F_{1,139}=4.58$ $p<0.05$). Patients reaction times were longer when they fixated the LED than when they looked at the objects ($p<0.05$), while the difference was not significant for control subjects. While the two group were not

significantly different either when looking at the objects or fixating the LED, control subjects were slightly faster than patients in the latter conditions and patients but slower in the former.

Comments to Experiments 3 and 4

Experiments 3 (reach) and 4 (grasp) were less sensible to detect differences between control subjects and patients with LBD, as the two groups did not differ in any of the parameters taken into consideration in this study. This is in agreement with the results described in Chapter 3 using the same set of tasks: while the groups differed in some kinematic parameters in Experiments 1 and 2, there were no major differences the second set of experiments. It is therefore possible that using this experimental setup the differences between groups can be elicited only using tasks that place higher loads on cognitive and motor systems.

Even so, comparing the performance of control subjects and LBD patients in Experiment 3 and 4 replicated some results observed with Experiment 1 and 2. In particular, I observed that while healthy controls did modulate some kinematic parameters of grasping (MT and nTPV) in function of the goal, patients did not. I did not find a significant main effect of the *eye movement* factor on movement times. However, I found that the interaction between group and eye movements was significant for reaction times, asLBD were slower the healthy controls only when they executed the movements while fixating the LED, a result similar to the one discussed in the comments to Experiments 1 and 2.

Patients with right brain damage (RBD) versus controls

To verify whether the difference noted between the LBD patients and healthy controls were specifically related to the damage at the left hemisphere, I compared the RBD patients with the control subjects using their right hand. However, as the number of subjects with RBD recruited was very small, the analysis will be limited to the comparison of the performances within the two sets of experiments: grasp to use and grasp to move on one side and reach and grasp on the other.

Experiment 1 and 2: Grasp to move and grasp to use.

Main effect of the group. The main effect of the group (controls or RBD patients) was significant for the normalized times to maximum grip aperture (**nTMGA** $F_{1,7}$= 5.4 , p=0.05), that were longer for control subjects than for RBD patients (Table 4.12)

Main effect of the task. The main effect of the task (grasp to move or grasp to use) was significant for the maximum grip aperture (**MGA** $F_{1,538}$= 3.8, p=0.05), for reaction times (**RT** $F_{1,541}$= 5.13, p<0.05) and for the normalized time to peak velocity (**nTPV** $F_{1,538}$= 6.99, p<0.01). Reaction times were longer in grasp to move than in grasp to use, maximum grip aperture were bigger in grasp to use and acceleration phases were longer when grasping to move than when grasping to use.

Main effect of the eye movements. The main effect of eye movements was significant for movement times (**MT** $F_{1,539}$= 15.6 , p<0.001) and a trend for reaction times (**RT** $F_{1,541}$= 3.58 , p=0.058). Both reaction times and movement times were longer when participants looked at the objects rather than looking at the LED.

Table 6.12 - Means and SEM of the kinematic parameters referred to the main effects (grasp to move and grasp to use, RBD patients and controls)

	Mean	SEM	Mean	SEM
Eye movements	*Fixed*		*Free*	
MT	*919.12 ms*	*15.334*	*971.48 ms*	*13.606*
RT	*752.17 ms*	*36.204*	*804.54 ms*	*41.203*
Task	*Move*		*Use*	
RT	*811.26 ms*	*43.186*	*746.58 ms*	*34.194*
MGA	*82.04 mm*	*1.139*	*83.50 mm*	*1.236*
nTPV	*33.02%*	*0.572*	*30.64%*	*0.670*
Group	*Controls*		*RBD patients*	
nTMGA	*74.27%*	*0.514*	*70.43%*	*1.109*

The interaction *group by task* was significant for the reaction times (**RT** $F_{1,539}$= 3.7 , p=0.05) and for maximum grip aperture (**MGA** $F_{1,539}$= 11.43 p<0.001) Maximum grip aperture was different between groups only when they grasped to use (*p*<0.05), as RBD patients opened the grip more. Furthermore, while patients opened the grip more in grasp to move than in grasp to use (*p*<0.001), healthy controls showed the opposite effect (*p*<0.05).

The interaction *group by eye movements* was significant for the maximum grip aperture (**MGA** $F_{1,539}$= 12.56 p<0.001). The difference between groups was only significant when participants grasped while fixating the LED (*p*<0.05), as RBD had a wider grip than control patients. Furthermore, RBD opened the grip more when fixating the LED than when looking at the objects (*p*<0.001), while the opposite trend was observed for control subjects (*p*<0.05) (Figure 4.8).
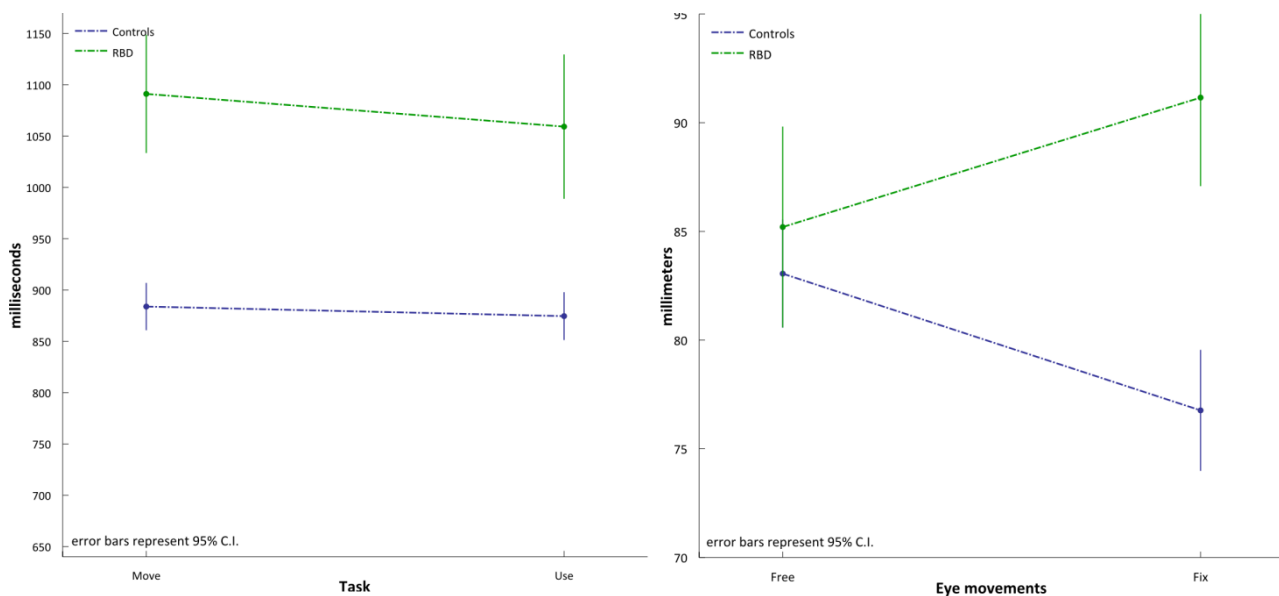
Figure 4.8 – Movement times (MT) of RBD and controls in Experiments 1 and 2 (left) and maximum grip aperture (MGAof RBD patients and controls in free and fix eye movements conditions (Exp. 1 and 2, right)

Experiment 3 and 4: Reach and Grasp.

Main effect of the group. The main effect of the group (controls or RBD patients) was not significant for any of the variables examined.

Main effect of the task. The main effect of the task (grasp to move or grasp to use) was significant for the movement times (**MT** $F_{1,307}$= 19.61, p<0.001), for reaction times (**RT** $F_{1,303}$= 6.89, p<0.01) and for the normalized time to peak velocity (**nTPV** $F_{1,306}$=21.38, p<0.001). Reaction times and movements

times were longer when grasping than when reaching, and acceleration phases were longer when reaching than when grasping (Table 4.11).

Main effect of the eye movements. The main effect of eye movements (looking at the objects or fixating the LED) was not significant for any of the variables examined.

Table 4.11 - Means and SEM of the kinematic parameters referred to the main effects (reach and grasp, RBD patients and controls)

	Mean	**SEM**	**Mean**	**SEM**
Task	*Reach*		*Grasp*	
RT	*725.25 ms*	*47.059*	*747.85 ms*	*41.972*
MT	*662.40 ms*	*18.717*	*775.64 ms*	*17.059*
nTPV	*38.29%*	*1.486*	*31.46*	*0.862*

Comments

Patients with RBD were not, on average, slower than control subjects either in terms of movement times or reaction times, nor did they display lengthened approach phase, in contrast with some previous studies (Fisk & Goodale, 1988; Hermsdörfer et al, 1999). However, it is worth noting that none of the effects described for LBD patients was replicated in the RBD group. In particular, patients with RBD modulated grasping parameters as function of the task, while LBD patients did not.

In contrast with patients with left brain damage, RBD patients were not worse than controls when moving when moving while fixating the LED. However, if the right hemisphere was specifically involved in visuospatial integration and in the online control of closed-loop movements, I would have expected RBD patients to shown a relatively greater impairment in performance in grasping while looking at the objects, and especially so when grasping small objects. However, the fact that I did not find any such result might be due to the small sample size of the group. Therefore, the present observations do not constitute enough experimental evidence to draw definitive conclusion and future studies should be devoted to explore this issue in a larger sample of patients.

Single case (VS)

Amongst the patients with left brain damage, only one patient (VS) showed limb apraxia. When she took part in the experiment, VS was a 48 years old woman with 8 years of education, right handed, who suffered from an ischaemic infarct, which involved parietal and posterior areas of the left hemisphere. Due to the wide spatial extent of the lesion, the areas interested included areas involved in linguistic competences (left angular gyrus, left supramarginal gyrus and superior temporal sulcus as well as Broadmann areas 44 and 45), the left middle temporal gyrus, the inferior left prefrontal gyrus and the left premotor cortex (see Figure 4.9)

VS showed severe hemiplegia on the right side of the body and severe impairment in language production. However, language comprehension was less impaired than production, as shown by the Aachener Aphasie Test. This patient showed normal performance in Raven matrices and in visual search (see Table 4.12) and also showed difficulties in using and reading numbers as evidenced by a pathological score in the EC301 Battery (Deloche e coll., 1993). Most importantly, VS showed difficulties in imitating gestures (obtaining a score of 42/72 in the test described in De Renzi et al., 1980) and bucco-facial apraxia (obtaining a score of 7/249).

Table 4.12 - Neuropsychological assessment of VS (* mild, ** moderate, * severe impairment)**

Test	Score
Aachener Aphasie Test (AAT) (Luzzatti et al., 1996)	
Token test	*42/50****
Repetitions	*61/150****
Written language	*22/90***
Denomination	*35/120****
Comprehension	*93/120**
Raven Progressive Matrices (Carlesimo et al., 1995)	*34/36*
Attentional Matrices (Spinnler and Tognoni, 1987)	*39/60*

This patient was presented with the experiments seven months after the onset of the stroke: she still presented hemiplegia at the right side of the body and was sitting on a wheelchair. In the preliminary tasks, she was able to denominate all the 6 presented objects, but she showed mild difficulties in using them (accuracy score of 7/12, see Materials and Methods). For instance, she was able to grasp the forks or the brushes and pointed them correctly towards the target, but she managed to demonstrate their use only on the second (or subsequent) attempts.
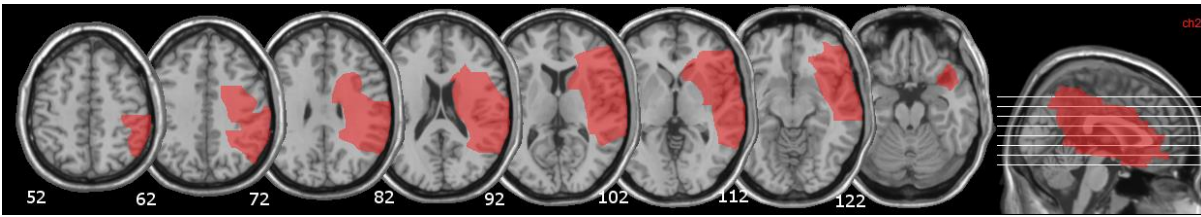
Figure 4.9 – Reconstruction of the brain lesion of V.S.

VS performance between experiments

Experiment 1 (Grasp to Move) and Experiment 2 (Grasp to Use). An independent samples *t*-test found that the difference between the two eye movement conditions was not significant for any of the kinematic parameters for Experiment 1 or 2 considered independently. The difference between tasks was significant for RT (t (61) = 2.3, $p<0.05$), which were longer when she grasped to move (831 ms) than to use (612ms) the objects, and for nTMGA (t (60) = -2.1, p<0.05), which was longer in grasping to use (82%) than to move (72%).

Experiment 3 (Reach) and Experiment 4 (Grasp). In Experiment 1, an independent samples *t*-test found that the difference between the two eye movement conditions was significant for RT (t(11) = 3.4, $p<0.01$), which were faster when looking at the objects (358ms) rather than when fixating the LED (578ms).

VS performance against LBD controls

Means and SEM of left brain damaged patients (control sample) without apraxia and VS are reported in Table 4.13. A Crawford modified t-test (Crawford and Howell, 1998) was carried out in order to explore possible dissociation in performance of VS and controls. The analysis showed that VS reached the time to peak speed slightly later than the other patients in Experiment 1 (grasp to move) when she was free to look at the objects (t(6)= 1.9, one tailed $p=0.056$). Most importantly, she was faster than LBD controls (t(6)= -3.02, p<0.05) in reaching the objects in order to use them when fixating the LED. Interestingly, a similar behavior was observed in Experiment 3: although it did not reach significance, VS took less time to reach the objects than the LBD controls when asked to keep fixation on the LED [t= -1.8, one tailed $p=0.065$]. Finally, in Experiment 4, VS reached the maximum grip aperture earlier in the movements than controls [t (6)= -2.1, one tailed $p=0.04$].

Table 4.13 – Performance of VS and LBD patients in Experiments 1, 2, 3 and 4. In bold, significant effects of Crawford's modified t-test (2 tailed); in bold-underlined trends toward statistical significance

Experiment 1 – Grasp to move		RT	MT	nTPV	MGA	Ntmga
Fixed	Mean (LBD)	725.62	1089.89	33.24	84.45	77.20
	SEM (LBD)	213.63	202.20	2.58	7.76	5.52
	Mean (VS)	831.25	841.25	31.7698	78.35	73.36
Free	Mean (LBD)	777.51	984.62	34.53	78.69	76.63
	SEM (LBD)	200.87	172.30	1.42	7.71	4.71
	Mean (VS)	831.25	838.13	***37.48***	71.76	71.31
Experiment 2 – Grasp to use		RT	MT	nTPV	MGA	nTMGA
Fixed	Mean (LBD)	725.70	1032.06	33.19	85.66	74.38
	SEM (LBD)	265.00	78.92	6.350	8.53	7.76
	Mean (VS)	710.67	**774**	34.69	82.83	80.93
Free	Mean (LBD)	660.55	977.46	31.53	80.86	74.47
	SEM (LBD)	182.24	113.19	8.206	8.36	8.58
	Mean (VS)	520	838.75	37.89	74.34	82.80
Experiment 3– Reach		RT	MT	nTPV		
Fixed	Mean (LBD)	569.61	792.20	36.44		
	SEM (LBD)	182.81	89.40	6.06		
	Mean (VS)	578	***618***	31.45		
Free	Mean (LBD)	671.28	739.76	33.54		
	SEM (LBD)	242.46	116.33	3.73		
	Mean (VS)	358.75	633.75	38.10		
Experiment 4 – Grasp		RT	MT	nTPV		
Fixed	Mean (LBD)	627.14	738.83	31.87		
	SEM (LBD)	117.27	77.25	13.30		
	Mean (VS)	442.5	727.5	39.33		
Free	Mean (LBD)	671	739.5	35.90		
	SEM (LBD)	158.75	96.32	7.46		
	Mean (VS)	504.67	790	34.56		

A post hoc assessment of the video showed that the patient was unable to mimic the use of the object during the experiment, as in the screening task she placed the object in the correct orientation

near the starting point, but she was not using it afterward. None of the other patients showed this tendency consistently across trials. This behavior was not due to her language difficulties, since the examiner explained the task several times and performed the task with her for a few trials to ensure she understood the instructions. Furthermore, VS exhibited wrong grips, as she often grasped small objects with power grips and big objects with precision grips. These behaviors were observed equally often when fixating the LED and looking at the objects when grasping to use, while it was only observed in the fixed eye movements condition when grasping to move (Table 4.14). VS routinely grasped objects from their 'head' (the points of the forks) to move them , but only when she looked at the objects, while other LBD displayed this behavior (Table 4.14, t(6)=6.84, *p*<0.001) less frequently, while in grasping to use she awkwardly rotated her wrist to grasp the object more frequently than controls (Table 4.14, t(6)=4.99, *p*<0.005).

Table 4.14 – Accuracy of VS and LBD patients in Experiments 1 and 2. In bold, significant effects of Crawford's modified t-test (2 tailed); in bold-underlined trends toward statistical significance. WR: Wrist rotation, OM: Object manipulation, WG: Wrong Grip , T: Unconfortable grasp at the end of the handle of the object, H: Uncomfortable on the end of the object opposite to T; EP: perplexities in movement execution.

Experiment 1 – Grasp to move		WR	OM	WG	T	H	EP
Fixed	Mean (LBD)	16,92	29,38	44,43	3,97	10,11	71,44
	SEM (LBD)	15,49	12,74	10,43	5,45	14,97	42,37
	Mean (VS)	30,00	35,00	60,00	0,00	10,00	80,00
Free	Mean (LBD)	10,67	24,67	41,45	2,11	6,93	45,59
	SEM (LBD)	14,89	7,92	17,53	4,71	10,45	44,82
	Mean (VS)	23,53	29,41	16,65	0,00	**82,35**	77.77
Experiment 2 – Grasp to use		WR	OM	WG	T	H	EP
Fixed	Mean (LBD)	30,94	33,64	42,81	1,85	1,59	32,23
	SEM (LBD)	17,78	16,81	10,58	4,54	3,89	47,87
	Mean (VS)	26,32	36,84	52,63	0,00	0,00	0,00
Free	Mean (LBD)	16,52	28,99	31,27	0,93	6,35	42,32
	SEM (LBD)	6,27	22,84	20,22	2,27	8,20	47,29
	Mean (VS)	**50,00**	16,67	44,44	0,00	0,00	0,00

Comments

VS was a patient with left brain damage and mild ideomotor apraxia as assessed by the preliminary tool use task. She was tested in all four tasks composing our study (reach, grasp, grasp to move and grasp to use). With the exception of Experiment 2 (grasp to use), VS could comply with the instructions and execute the requested motor acts.

In Experiment 2, however, VS did not mimic the use of the tools and rather remained with her hand still in mid-air after having performed the prehension movement and brought back the objects near the starting point. This peculiar behavior could be responsible for the differences in movement times between VS and the other patients with LBD, as the movements VS executed were similar to the one expected in Experiment 1 (grasp to move): I can therefore argue that the simple motor plan enacted could be executed faster than the more complex grasping to use.

In both Experiment 1 and 2, VS often used the wrong grip to take hold of the objects (whole hand grip for small objects or precision grip for big objects). This is a behavior similar to the one reported in Sirigu et al. (1995). While in Experiment 1 participants were free to take the objects in the way they preferred, as the only requirement of the task was the transport of the objects back near the starting point, in Experiment 2 participants were explicitly asked to grasp the object to use them. As VS did not significantly differ in the percentage of wrong grips from group of LBD patients, I can argue that errors in grip selection and/or hand posture are not a specific deficit of VS, but represent a component of movement that can be impaired by left brain damage

4.4 General discussion

The present study aimed at exploring the possible differences between brain damaged patients and healthy controls in a wide range of motor tasks: reaching and grasping, grasping to move and grasping to use. In addition, a key manipulation was the presentation of the targets in the central or in the peripheral visual field. In particular, in one experimental condition participants were asked to execute the movements towards the objects while keeping eye fixation on a central LED, while in the other condition participants could look at the objects they were reaching (see Fisk & Goodale, 1988 for a similar experimental design).

The present results showed that LBD patients' performance differed from controls in some kinematic characteristics of grasping movements. In particular, LBD patients showed a similar performance to controls when the actions were executed while looking at the objects, while their performance decreased when they grasped or reached objects while keeping fixation on the central LED. Furthermore, while healthy controls modulated their movements according to the characteristics of the task, LBD patients showed less flexibility. This evidence can be explained with the reference to the hypothesis of different contributions of the left and right brain hemispheres to motor control. In particular, it has been proposed (Haaland & Harrington, 1994, Winstein & Pohl, 1995) that the left hemisphere could be involved in planning and execution of open-loop movements, while visuospatial integration and online feedback processing would be lateralized in the right hemisphere (Hermsdöfer et al., 1999; Hermsdöfer et al., 1999b). This theoretical framework could account for the differences between healthy controls and LBD patients observed in the present study, as in the fixed eye movement condition participants were executing the movements keeping fixation on the LED, a condition in which the visual information about the position of the target was not fully available, and therefore participants relied more on proprioceptive and kinaestetic feedback and on pre-planned ballistic movements. The present results are in line with the description of the left hemisphere as being more involved in the planning and execution of open loop movements (Winstein & Pohl, 1995). A study (Triteluxana, Gordon & Winstein, 2008) analyzed reach-to-grasp movements executed by healthy subjects with their left or right hand and found evidence for a more specialized role of the right hemisphere for anticipatory grasp pre-shaping. In our experiment, neither LBD nor RBD patients showed differences with the control group with respect to grasp formation variables. This might be due to the different testing conditions, as the different roles of the right and left hemispheres emerged in the work of Triteluxana et al. (2008) only when a screen blocked the vision of the initial position of the hand. Furthermore, in their study the authors did not vary the position of the objects to be grasped, while we found a significant interaction between hand used and position of the objects in the space: it is therefore possible that their finding cannot generalize to our experiment.

It has been shown (Winstein & Pohl, 1995) that in a reciprocal aiming task, requiring alternating tapping on two different targets, LBD patients were particularly impaired when the targets were larger. The authors interpreted these results as further evidence in support of the hypothesis that LBD patients would show a selective impairment in open-loop conditions and ballistic movements. However, in our study the interaction between groups (LBD versus control) and size of the objects was not significant in any of the tasks, suggesting that LBD patients were not specifically impaired in reaching for big rather than small objects. This evidence might be due to the nature of the task, such as in grasp to move the accuracy requirements of the big and small objects could be less demanding than in grasp to use as objects could be grasped in different ways without compromising the outcome of the trial, or of the stimuli as the difference in size were not as marked as in other studies (i.e. Hermsdöfer et al., 2003). It is worth noting that not all the previous studies found that LBD patients are more impaired when executing reaching movement towards big target than towards small ones. For instance, in Hermsdöfer et al. (2003), the authors found that LBD patients were more impaired when executing reaching movements towards small targets than towards big ones.

I also noted that LBD patients of the present study did not modulate the kinematic parameters of their movements according to the task. This result emerged when comparing Experiments 1 and 2, but also when comparing Experiments 3 and 4. I propose as possible interpretation of this evidence that LBD patients might be less able to modulate their movements according to the task, probably because of a reduction in cognitive flexibility caused by left brain damage (Tessari et al., 2009). In particular, the performance of LBD patients' was similar to the healthy controls in grasping to use but not when grasping to move experiment. It is therefore possible that patients were not able to take advantage, as much as controls, of the reduced requirements of the grasp to move as compared to grasp to use task. In this light, it might be argued that LBD patients adopted a conservative strategy similar to the one used by older subjects (see Chapter 3 and Welsh et al., 2007). However, further studies are required to confirm this interpretative hypothesis.

Comparing the performance of control subjects with patients with RBD, I did not notice the same effects observed for LBD. This could be expected, since it has often been observed that RBD patients are only slightly impaired (if distinguishable at from control subjects) in tasks such as reaching, pointing and grasping (Hermsdöfer and Goldenberg, 2002, Haaland & Harrington, 1994, Weiss et al., 2001). In the present study, I was not able to detect any significant difference between RBD patients and healthy controls in terms of movement times or on the relative length of acceleration phases, in contrast with some previous studies (Hermsdöfer et al., 1999b; Winstein & Pohl, 1995). In particular, the absence of longer deceleration phases in the RBD group could be interpreted as an argument against the role

played by the right hemisphere in the control of movements, but the small sample size of the group makes hard to draw definitive conclusions about the motor behavior of patients with unilateral RBD.

Finally, I analyzed the performance of a single patient with left brain damage and limb apraxia, VS. In the preliminary testing phase VS was able to use and denominate the objects she was presented with, and during the experimental tasks there were only a few differences between VS and the LBD group: most notably, she was slightly faster than LBD controls in the grasp to use task in when fixating the LED and had longer acceleration phases in grasp to move when fixating the objects. In Experiment 2 (grasp to use) VS did not make more errors in grasping the objects than LBD patients, but she did not show object use when required to do so (Experiment 2). Therefore, the difference in speed could be explained by hypothesizing that VS executed the trials of Experiment 2 as if she was simply grasping the objects and moving them. All considered, the results do not fully support the hypothesis of difference in kinematics between LBD patients without apraxia and apraxic patients which were found in some studies (Haaland et al., 1999) but not confirmed in others (Hermsdöfer et al, 1996). However, it should also be noted that VS showed only mild apraxia. Future studies will be address in order to increase in the number of patients with LBD and apraxia in order to explore this preliminary evidence.

In conclusion, the results of the present study seem to support the hypothesis that the left hemisphere contributes more to the planning of open-loop than of closed-loop, visual-guided movements. On the other hand, I did not found any specific impairment of RBD patients in reaching and grasping movements on which they could use to a greater extent online visual feedback. Further work would be required to increase the sample of RBD and LBD patients, and to fully explore the different contributions of right and left brain hemispheres in motor control.

Chapter 5

5.1 Summary

Humans master a wide range of motor skills, from simple skills, such as reaching and grasping, to complex skills, such as in the case of imitation or tool use. While reaching and grasping tasks have been largely explored both quantitatively and qualitatively (see Castiello, 2006, for a review), imitation and production of complex movements have been more often investigated using qualitative measures, even if some recent studies (Hermsdörfer et al., 2012; Hermsdörfer et al., 2013) analysed the kinematics of complex gestures such as tool use or pantomimes.

In my PhD thesis I aimed at exploring different aspects of the human movements, by adopting a quantitative approach. I used an imitation task to assess, using parameters such as scale, orientation and shape similarity, how faithful to the model was participants' imitation and the relationship between eye and arm movements (Chapter 2); I also investigated the kinematics of reaching and grasping (Chapters 3 and 4) in a variety of tasks, posing different degrees of complexity and carrying out different purposes. What all studies have in common is the interplay between action and perception as well as the role played by the task. While in Chapter 2 I looked at whether participants changed their fixation behaviour during imitation of meaningless gestures, in Chapters 3 and 4 I assessed the performance of young and older adults (Chapter 3), and of patients with unilateral brain damage and healthy controls (Chapter 4) during reaching and grasping tasks. While the results of Chapters 3 and 4 showed the effect of perceptual factors on the motor task and, in particular, that the levels of visual feedback had a different effect on performance depending the group participants belonged to, in Chapter 2 I observed the effect of the motor task on perceptual processes, with the eye fixation of participants varying as a function of the repetitions of the task and of learning effect in the motor task itself.

In Chapter 2, I investigated imitation by analysing both the perceptual component and the motor component. In particular, I was interested in exploring whether the nature of the task and the effect of learning could influence the way in which participants look at the stimuli before imitating them. In order to do so, I had participants watch videos showing a dot moving following a biological kinematics along a path, and reproduce the corresponding gesture just after the end of the movie. I then analysed the spatial pattern of fixations, and distinguished between participants' fixations along the stimulus' path or on other areas of the screen, paying particular attention to the preference of the visual

system for extrema of curvature. Motor performance, on the other hand, was analysed using the Procrustes' distance, a measure of global similarity to the model derived from the statistical shape analysis, and on the basis of features such as movement duration, size and orientation of the reproduced gestures.

I interpreted the results of the study reported in Chapter 2 in terms of action and perception sharing the same representation. In particular, I confirmed the relevance of high-curvature parts of the trajectory of the movement model to be reproduced. This evidence is in line with the observation that extrema in curvature are highly salient for visual processes in different types of task, such as driving along a road (Land & Tatler, 2001), tracing a shape in space (Reina & Schwartz, 2003), but also parsing complex shapes (Singh et al., 1999). In the study I described in Chapter 2, participants changed the focus of their fixation across trials: while in the first trials they were looking at the movement of the dot which traced the gesture to be reproduced on the screen, in subsequent trials participants looked more often at the centre of the screen, irrespective of the shape displayed on the screen or the motion of the dot. This effect developed in parallel with participants' learning the motor task, as demonstrated by participants' stark improvements in parameters such as the size and the angle of the reproduced gesture and by a more gradual speeding up of movement execution. The main finding of this study is the co-occurrence of the change in participants' gazing behaviour, with a ceiling effect in learning the motor tasks. This latter result was interpreted as evidence for a coupling in these tasks between action and perception, and is consistent with recent studies that show how expertise about the task at hand can affect our visual processes (Land, 2009; Crespi et al., 2012). Participants did not improve the quality of their imitation as assessed by the Procrustes' distance in later trials. While this might be due to the experimental design (stimuli presented in random order rather than in blocks), it is interesting to note that previous studies (Agam et al., 2010; Maryott et al., 2011) found a correlation between the precision of the eye movements when tracking the stimulus and the quality of the reproduction. Another interesting finding is that participants improved the quality of their motor performance according to some parameters (especially orientation and size of the gesture), therefore showing a dissociation between the learning of global and local features of the stimulus.

In Chapters 3 and 4 I used a different approach to explore the relationship between visual perception and action. In these studies, participants were presented with common objects placed in different positions and were asked to reach for them, to execute a grasping movement towards them, to grasp the objects in order to move them back to the starting point or to grasp the objects to use them on a predefined target. This set up was first used to explore the differences in kinematics parameters between young adults and elderly participants (Chapter 3). While elderly participants were faster than young adults in terms of movement times when grasping to use, this effect was reversed in less

ecological tasks such as grasping meaningless objects. This result supports the idea that the differences between young adults and elderly people might be reduced in motor tasks closer to everyday life actions that have a specific purpose (Bennett & Castiello, 1994). However, to the best of our knowledge, this is the first study showing this effect in aging. For instance, Carnahan et al. (1998) showed that older adults were faster than young ones in a grasping task, but they did not compare tasks with varying ecological value. On the other hand, Bock and Steinberg (2012) analysed the performance of young and older adults in two computer-based tasks, one of which was characterized as being purposeless, repetitive and attention-attracting, and the other one as being purposeful, little attended and spontaneously initiated. These authors found that the elderly participants' performance was slower and more stereotyped than that of young adults, and that these differences were particularly stronger in the 'ecological' task. However, Bock and Steinberg noted that both the 'ecological' and the 'laboratory' experiment were easier for young subjects than for elderly participants, with youngsters being more used to video games and electronic devices. Thus, their result is not necessarily extendable also to everyday actions. Interestingly, in Chapter 3 we found that young adults were faster and more accurate in their movements when they were free to look at the objects rather than when they were asked to fix the LED while performing the action, while the same result was not found for elderly participants. In fact, we observed an inverse effect, present in all four experiments: elderly participants were faster in the condition in which they were moving while keeping fixation on the LED, regardless of the task.

In Chapter 4, I used a similar experimental setup to analyse the kinematics of reaching and grasping in patients with unilateral brain damage. As in Chapter 3, the key manipulations were the different task goals (reaching, grasping, grasping to move and grasping to use), and the eye movements (i.e., looking at the objects versus keeping fixation on the LED).

Some authors (Haaland & Harrington, 1994; Winstein & Pohl, 1995) proposed that left and right hemispheres might play a different role in motor control of skilled goal-directed movements. While the left hemisphere has been proposed to be more involved in planning and execution of open loop and ballistic movements, the right hemisphere might be more involved in the control of closed-loop, visually driven movements. The contribution of the left hemisphere in open loop movement control (that is, a kind of control that only relies on its current state and model of the system, but not on feedback or external inputs), has not been univocally recognized. For instance, Ietswaart et al. (2001) found no impairment in the kinematics of pointing movements in patients with left brain damage and apraxia, even when they were asked to execute the movement from memory or without visual the feedback of the target. Similarly, Hermsdörfer et al. (2003) found that while patients with LBD were slower than controls in a reaching task, they exhibited longer approach phases. However, the severity of this impairment was dependent on the task complexity, but it did not specifically affect the open loop

component of movement. Furthermore, different manipulations can be used to vary the degree of open loop conditions, by simply modifying the level of feedbacks related to the position of the target and to the position of the hand of the participants. In their study, Haaland et al. (1999) found that removing the information relative to the position of the hand produced a greater impairment in apraxic patients' performance than removing the information relative of the spatial position of the target.

In the studies I have conducted, movements executed while keeping fixation on the LED could be less dependent on the online visual feedback and more on the tactile and kinaesthetic feedbacks. The hemispheric specialization of motor control hypothesis (Haaland & Harrington, 1994; Winstein & Pohl, 1995) predicts that patients with unilateral left brain damage would be more impaired in this condition rather than when looking at the object to be grasped, and that the opposite pattern could be observed for patients with right brain damage. Our results partially confirmed this prediction: LBD patients performed worse than healthy controls when they grasped the objects while fixating the LED, supporting the hypothesis that the left brain hemisphere contributes to the planning and execution of open loop movements. In line with the literature (Halland & Harrington, 1989; Hermsdorfer et al., 2003; Hermsdorfer et al., 2012), I also found that RBD patients had a performance similar to the healthy controls. However, we did not confirm a longer approach phases in RBD patients, as shown in previous studies (Hermsdorfer et al., 1999; Laimgruber et al., 2005), a result which would have reinforced the hypothesis of a specific involvement of the right hemisphere in the control of closed loop movements. Neither LBD nor RBD patients did not differ from healthy controls when considering grasp formation (maximum grip aperture and time to maximum grip aperture). This finding is in agreement with Hermsdorfer et al. (1999B) and does support the hypothesis of specific roles played by the left or right hemisphere, as proposed for instance by Tretriluxana et al. (2008) on the basis of healthy subjects' performance on a grasping task. As discussed in Chapter 4, the small size of our patients' sample (especially in the case of RBD patients) is a shortcoming of this study which should be taken into consideration and that might be responsible for failing to observe an effect for the RBD group.

Finally, we found that the difference between LBD patients and controls emerged in less ecological tasks compared with more complex actions: LBD differed from controls only in grasping to move (but not in grasping to use) and in reaching (but not grasping). Compared with controls, patients performed both tasks in a similar manner. The objects might trigger a use of a specific strategy which is then applied consistently across tasks even when tasks differed in the actual goal as a consequence of a reduced cognitive flexibility due to brain damage (Tessari et al., 2007). In support of this interpretation, qualitative post hoc analysis of the grasping movements of LBD patients showed that they often grasped the objects in the same way, regardless of the task (move them or show their use).

Furthermore, indirect support of this hypothesis comes from the evidence that in our sample of LBD, besides language impairments, executive functions were also compromised, as 5 out of 6 LBD patients were below the cut-off score in at least one of the executive function tests. Therefore, I speculate that reduced cognitive flexibility might be responsible of some changes in motor control processes in normal aging but especially, and to a greater degree, after brain damage.

5.2 Shortcomings and future directions

Far from providing definite answers, the present work taps into the relationship between perception and action, by offering further evidence about the dynamics relationship between these two systems, and indicating some directions for futures studies.

In the interaction between perception and action learning during an imitation task described in Chapter 2, the stimuli I used were not biological (moving dots) but presented biological kinematics complying with the 2/3 power law. As the nature of the movement to be reproduced (i.e. human versus non-human)has been shown to have an effect on imitation, with biological motion is processed differently than non-biological motion, in future studies it would be interesting to compare imitation of complex gestures moving with biological kinematics with the imitation of stimuli moving with perturbed kinematics. This comparison would allow to explore the relationship between geometrical and kinematical aspects of the movement model.

Furthermore, even if the paths of the stimuli to be imitated used in Chapter 2 were similar to the ones used in previous studies (for instance, Bennequin et al., 2009), we found notable differences between the trefoil, on the one side, and the egg-curve and limaçon, on the other. As the trefoil was reproduced less accurately than the other shapes, future studies should aim at disentangling the general complexity of the task from the specific shape of the model, by using a wider range of shapes with a similar perceived difficulty and/or complexity.

As a last remark, while the correspondence between the gestures produced by participants and the models provided a description of the motor performance along different dimensions (time, general similitude to the model and differences in size or in the orientation), the measure of similarity used in this study (Procrustes' Distance) does not necessarily correspond to human assessment of the accuracy and of the quality of the gesture. Future study should explore the relationship between a qualitative assessment of the accuracy of the gesture and the qualitative measure of the performance.

In Chapters 3 and 4 I showed that both elderly people and LBD patients in particular, might manifest a decrease in modulation of the motor behaviour according to the goals and requirements of the task. I interpreted the effect in terms of a loss of cognitive flexibility in brain damaged patients. To

confirm this hypothesis, in future studies a greater temporal distance between tasks could be used, by, for instance testing participants in different days, using only one task in each day. In these conditions, the reduced modulation of kinematic parameters in different tasks could not be imputed to a loss in cognitive flexibility due to the presentation of different tasks in a short temporal interval. Adding time limits to the performance of each task (i.e.: more time allowed for grasp to use, less for grasp to move) would force participants to speed up movement planning and execution when grasping to move. If unable to do so, the slowing down of movements showed by LBD patients in the grasping to move task should be interpreted as a sign of a general impairment of their motor processes (Hermsdofer et al., 2003).

In our set of experiments the perceptual aspect of the task was manipulated by presenting the objects in the central and peripheral visual field. This manipulation was discussed in the light of the posited specialization of left and right hemispheres in action controls (see Chapter 4). Although, using this manipulation the visual feedback of the hand and target were somehow degraded when the objects were presented in the peripheral visual field, causing an increase in demand of proprioceptive feedbacks, further study could be devoted at exploring the effect of open and closed loop condition on grasping to use and move task more directly.

In particular, the specific assessment of patients with alleged optic ataxia or limb apraxia using this paradigm could allow bringing to the surface dissociations between these two syndromes. Indeed, while optic ataxia and ideational apraxia have been studied for long time and possible dissociations in performance have been logically hypothesized, none of the extant studies has carefully evaluated these two neuropsychological patterns within the same sample of patients.

Furthermore, while the number of LBD patients might be considered sufficient to draw some conclusions, the size of the RBD group is too small for anything but preliminary results. Only one patient with LBD and apraxia was tested using this paradigm: without doubt more apraxic patients are required to describe possible differences with the patients with LBD but without apraxia.

Finally, in my thesis I showed that the differences between groups are reduced in tasks more similar to everyday life. Based on this one can develop motor tasks differing in complexity and ecological value, and thus able to detect even subtle motor deficits and to guide rehabilitation of brain damaged patients.

Appendix A

A.1 Kinematic and geometrical characteristics of the stimuli used in Chapter 2

In this appendix are reported the characteristics of the stimuli used in the imitation experiment described in Chapter 2: time plot of x and y coordinates for the three shapes (Figure A.1) and speed and curvature profiles (Figure A.2). Furthermore, at the end of the appendix are shown sample trials of participants' eye and arm data
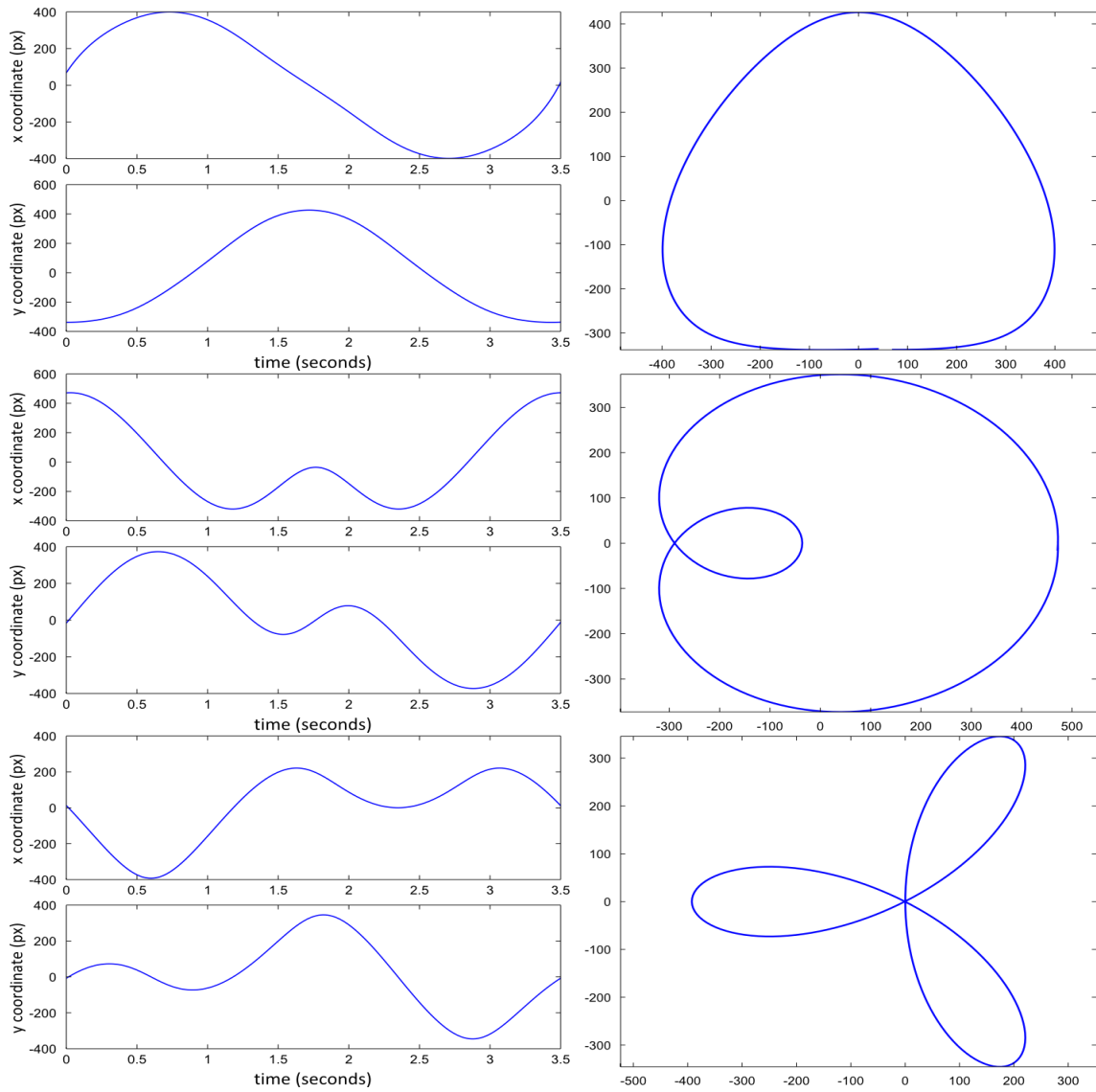
Figure A.1 – Complete path and time plot of x and y coordinates of the egg curve (top), limaçon (middle) and trefoil (bottom row)

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As shown in figure A.2, all the stimuli were compliant with a power law. For the egg-shaped curve the exponent, beta, was exactly as postulated by the 2/3 power law (β=0.333), while the betas of the limaçon (β=0.318), and of the trefoil (β=0.320) are slightly lower, an effect due to numerical approximation in their generation. Still, in all three cases the linear regression between the logarithms of speed and curvature is almost perfect (corrected R squared >0.99 in all cases) .
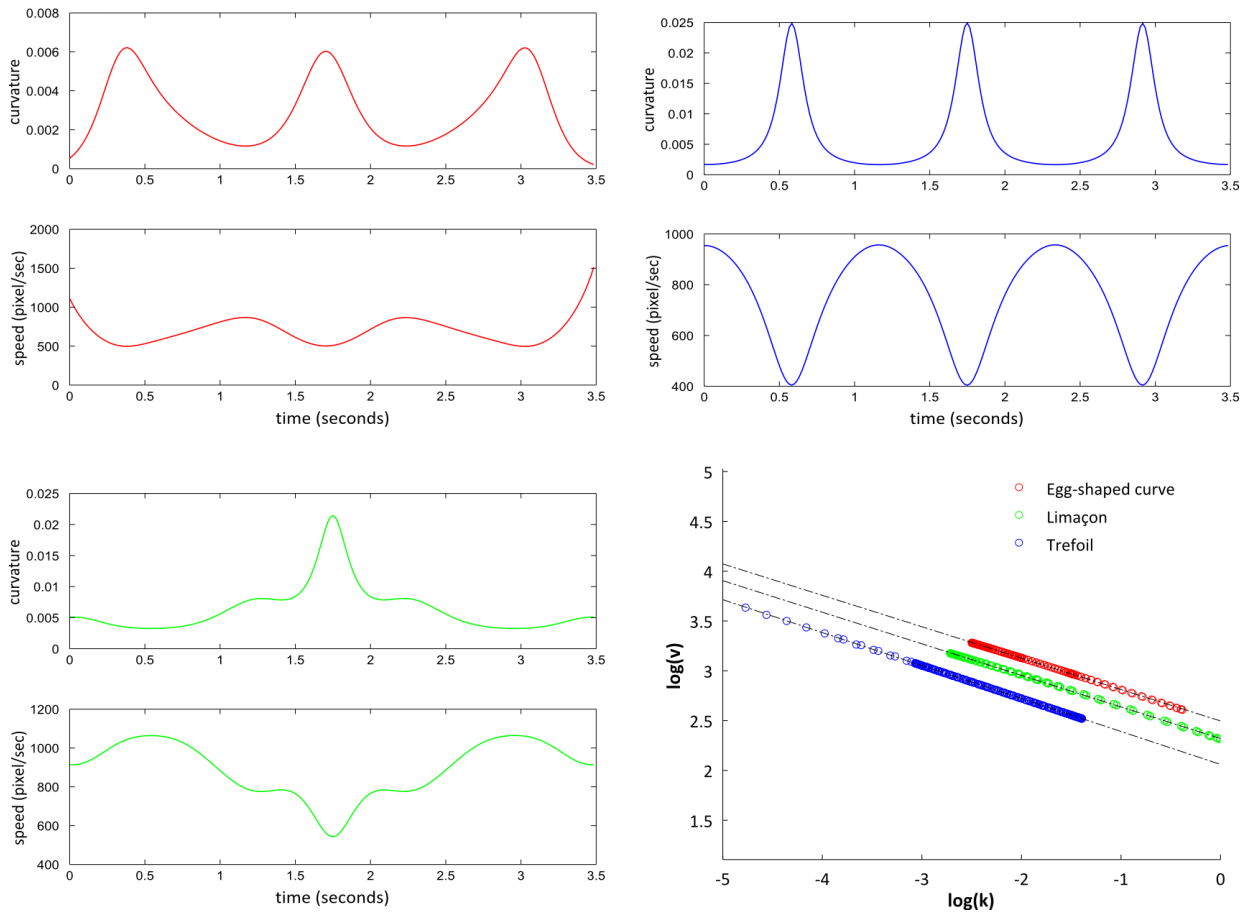

Figure A.2 – Speed and curvature of the three stimuli (egg curve in red, limacon in green, trefoil in blue). At the bottom right, relationship between speed and curvature for the three stimuli).

A.2 Sample plots of eye movements - Experiment 2
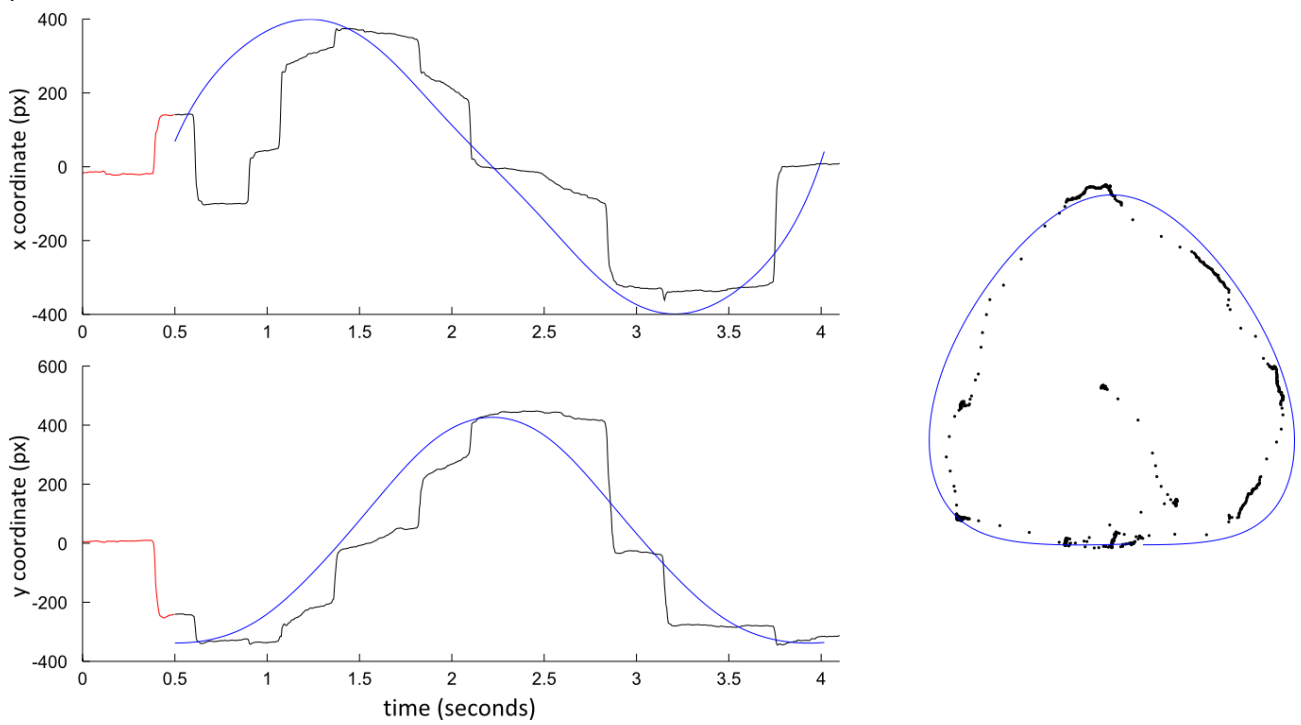
Eye movements - Behavior A

Figure A.3 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Egg-shaped curve, Subject YM, repetition 2.
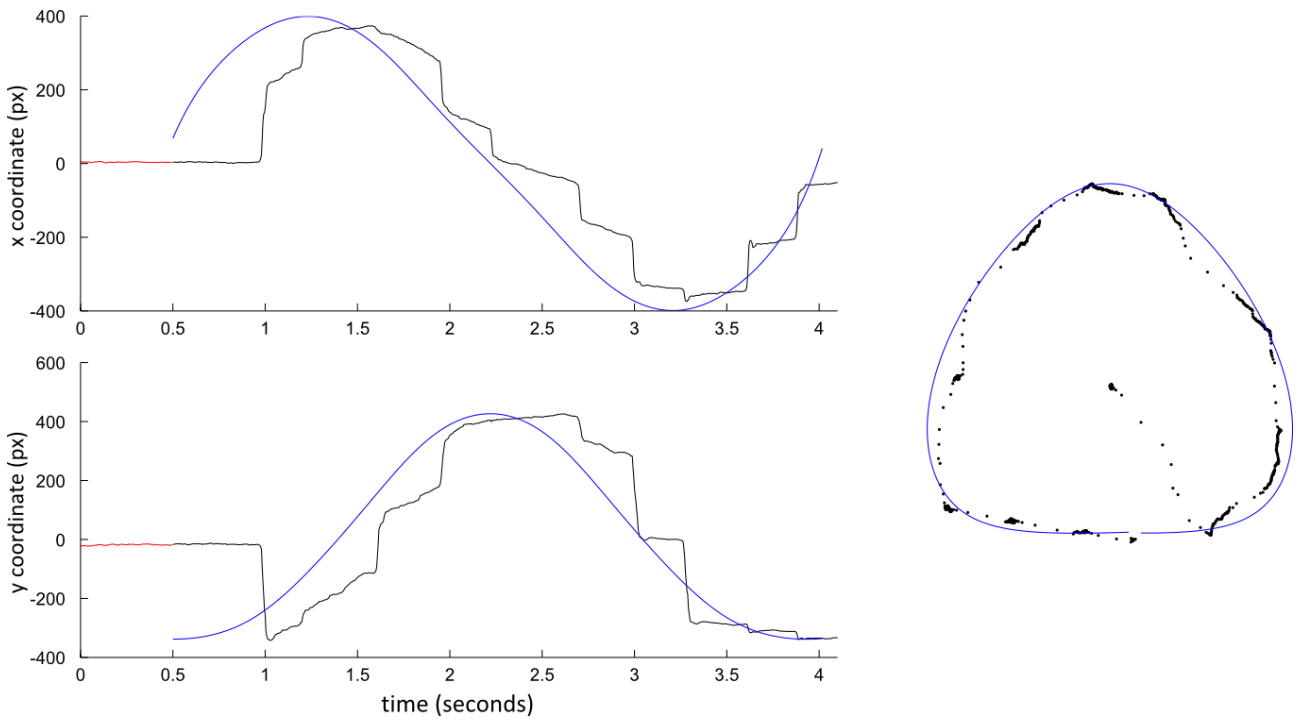
Figure A.4 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Egg-shaped curve, Subject SP, repetition 1.
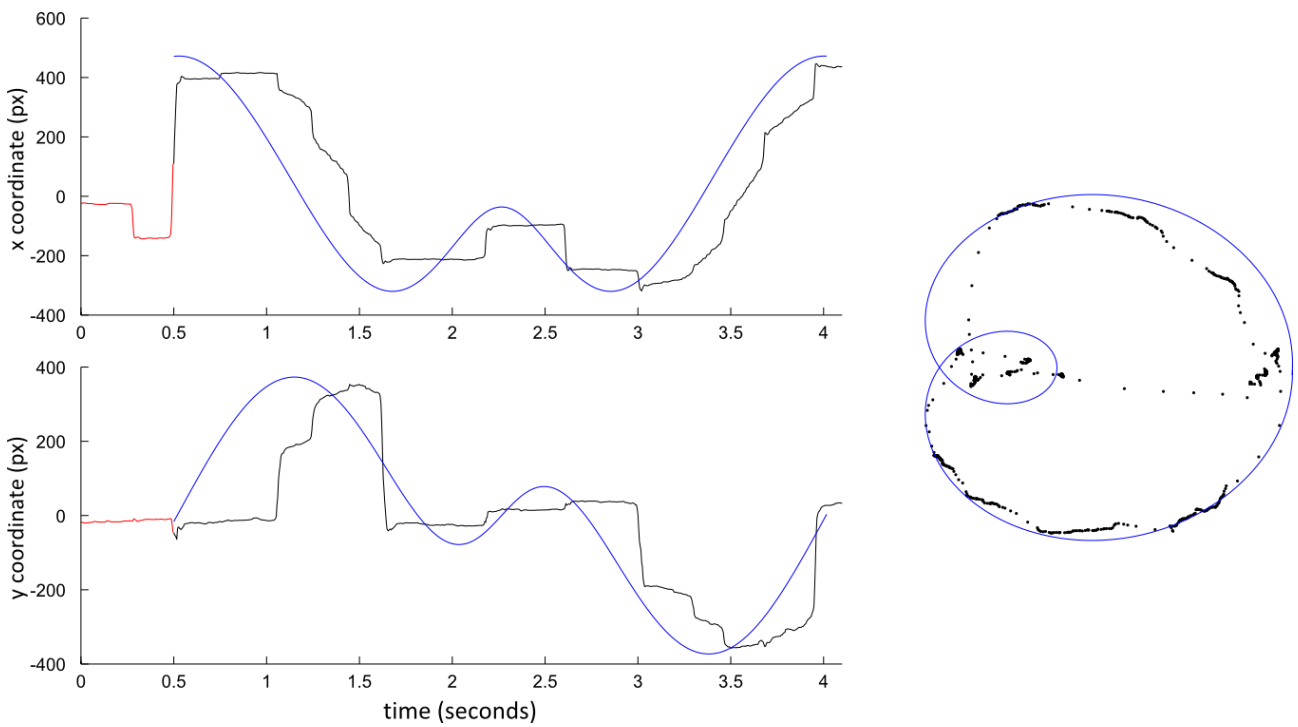

Figure A.5 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Limaçon, Subject FC, repetition 1.
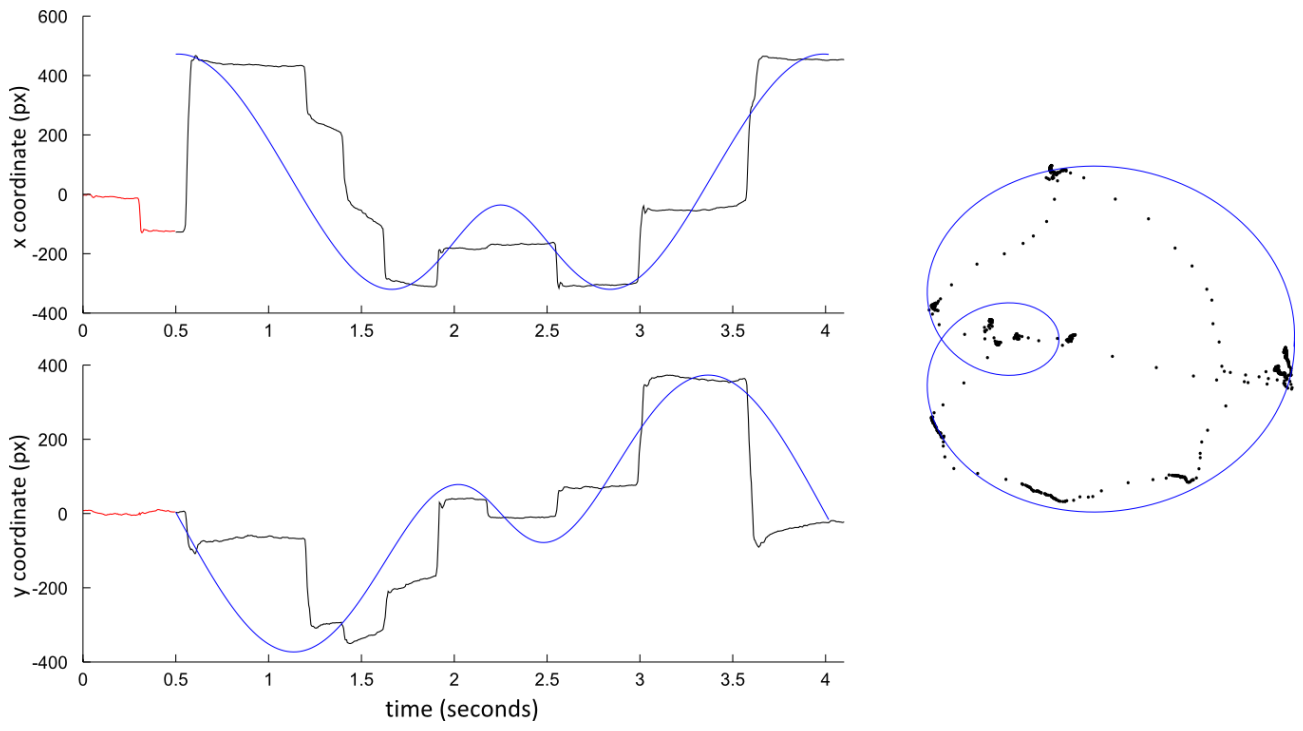
Figure A.6 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Limaçon, Subject YM, repetition 3

Figure A.7 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Trefoil, Subject MK, repetition 1
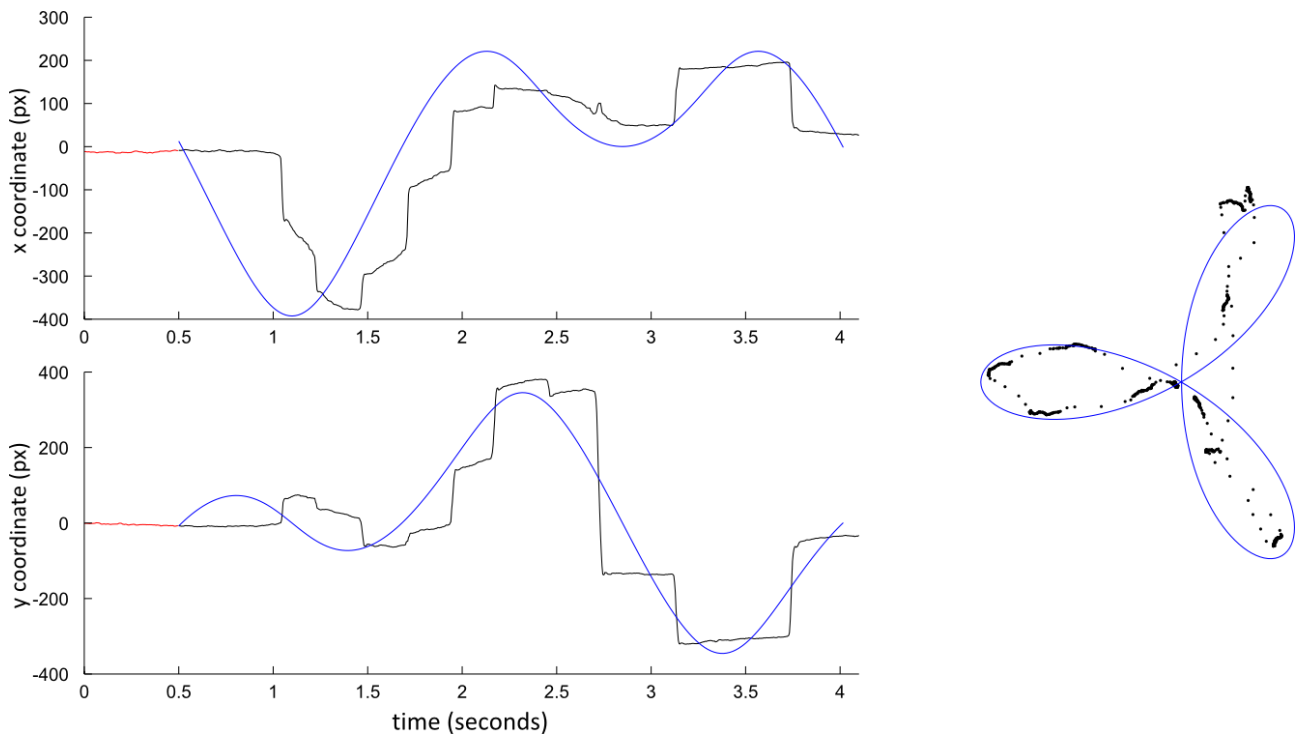
Figure A.8 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Trefoil, Subject SO, repetition 2

Figure A.9 – Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Egg curve, Subject YZ, repetition 8

Figure A.10– Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Limaçon, Subject CC, repetition 6

Figure A.11– Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Limaçon, Subject MK, repetition 8
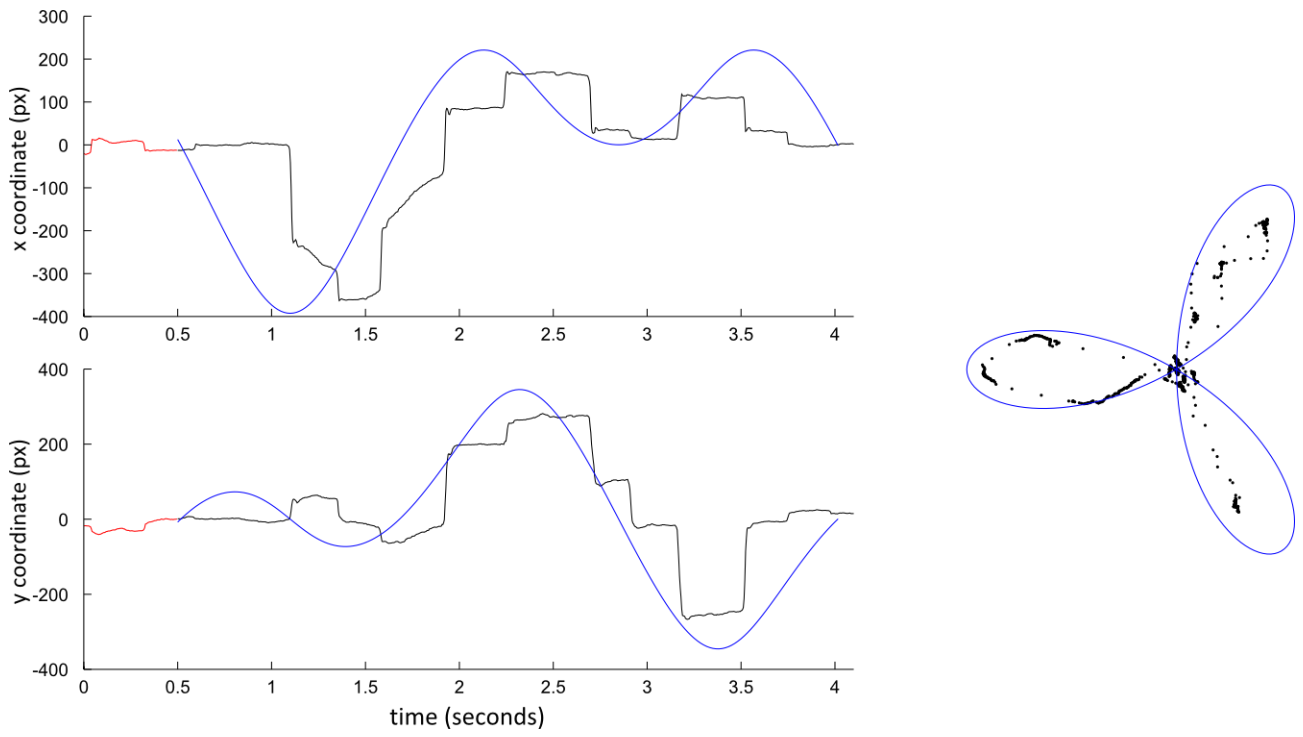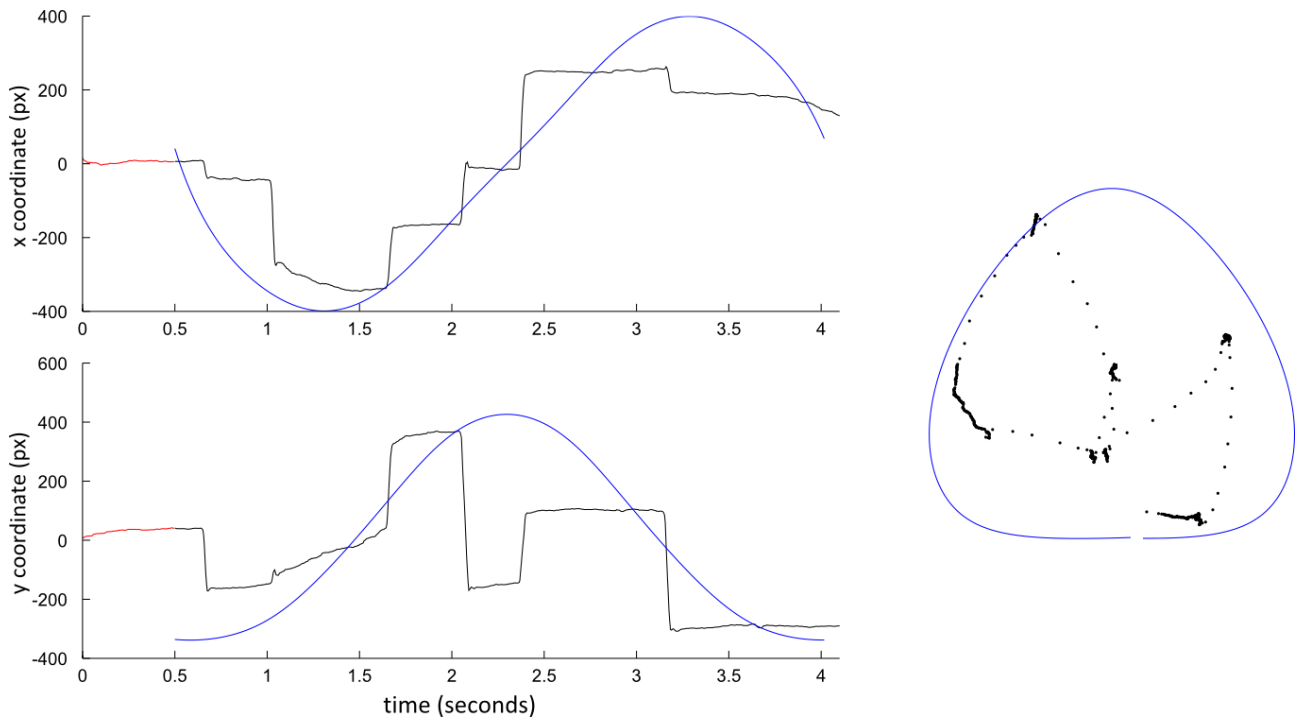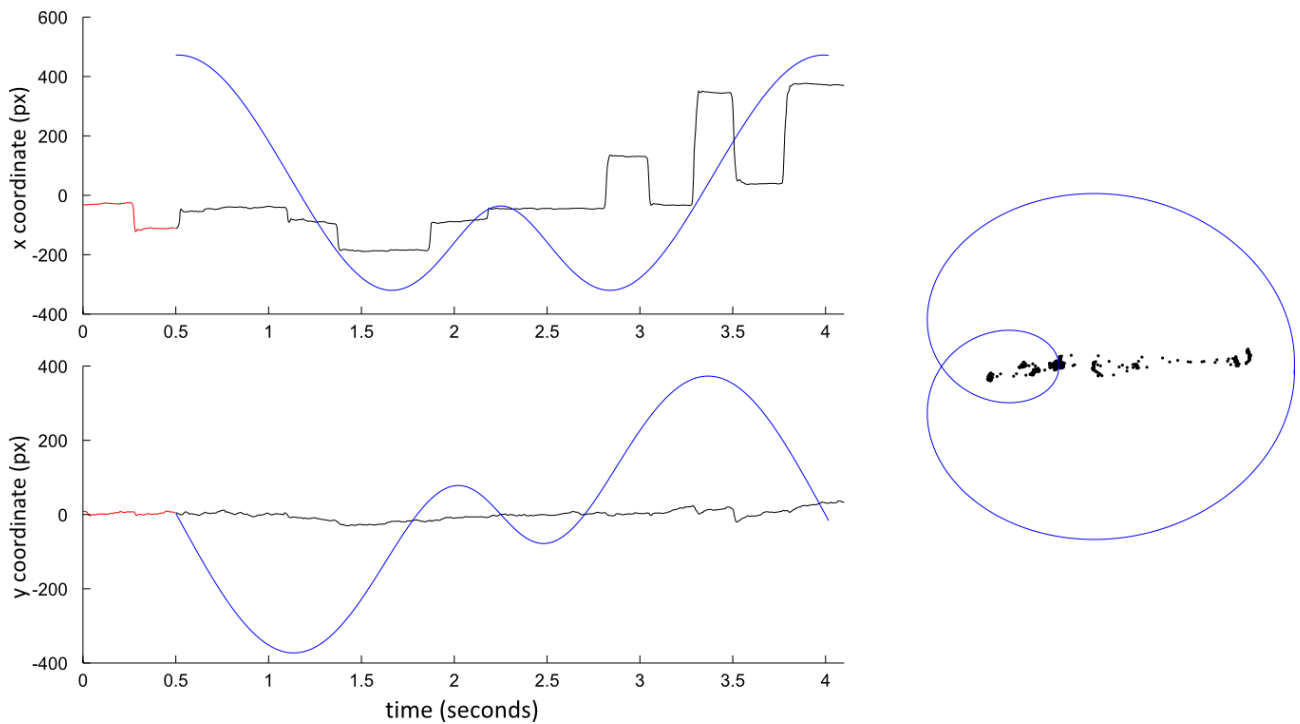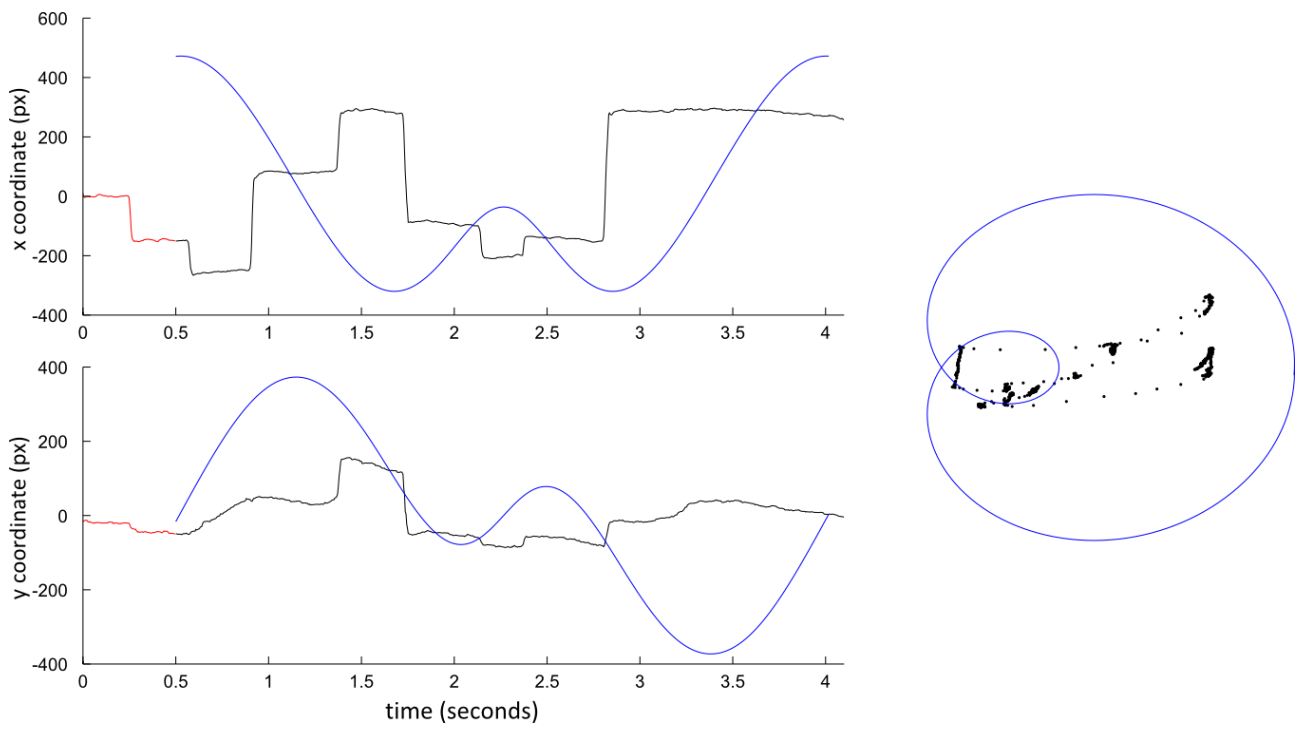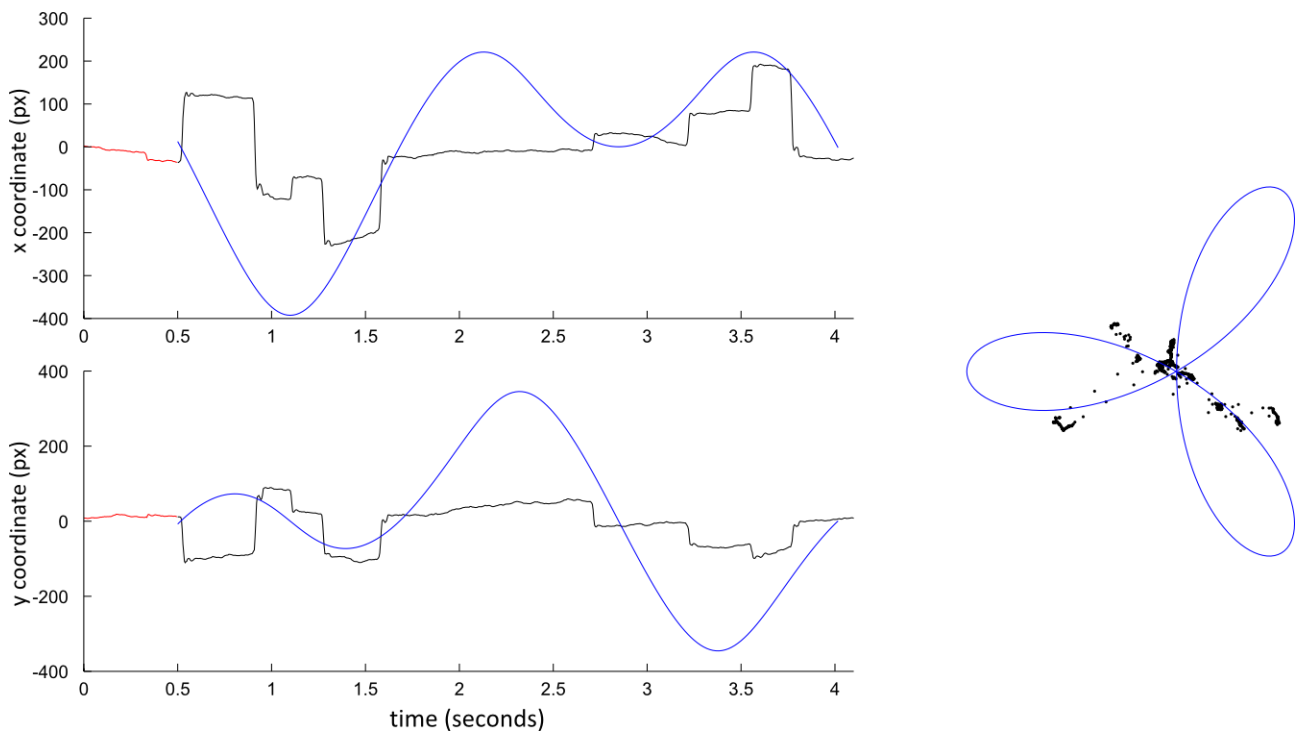

Figure A.12– Plot of x and y components of eye movement data (left) and path of eye movements (right) compared with the stimulus (blue). Trefoil, Subject SO, repetition 8

Sample plots of arm movements - Experiment 2

Here are presented the paths of the arm movements of one subject (LS) as an example of the gesture reproduced by the participants. Figure A.13 shows all the repetitions of the clockwise egg curve, Figure A.14 all the repetitions of the clockwise limaçon and figure A.15 all the repetitions of the clockwise trefoil. The shape presented here are plotted from the filtered data, and the model has not been superimposed on the plots for sake of readability. Repetition number 1 is at the top left, number 2 at the top middle, number 4 at the middle left and so on. Participant LS had a poor performance in reproducing the trefoil shape, but represents well the average participant.

Figure A.13– Arm movements – clockwise egg curves. Repetitions 1-9, participant LS.

Figure A.14– Arm movements – clockwise limaçons. Repetitions 1-9, participant LS.

Figure A.13– Arm movements – clockwise trefoils. Repetitions 1-9, participant LS.

Appendix B

In this appendix I will report the complete neuropsychological screening of LBD patients taking part in the experiment described in Chapter 4 (Table B.1) and the full analysis of reach to grasp movements performed on control subjects.
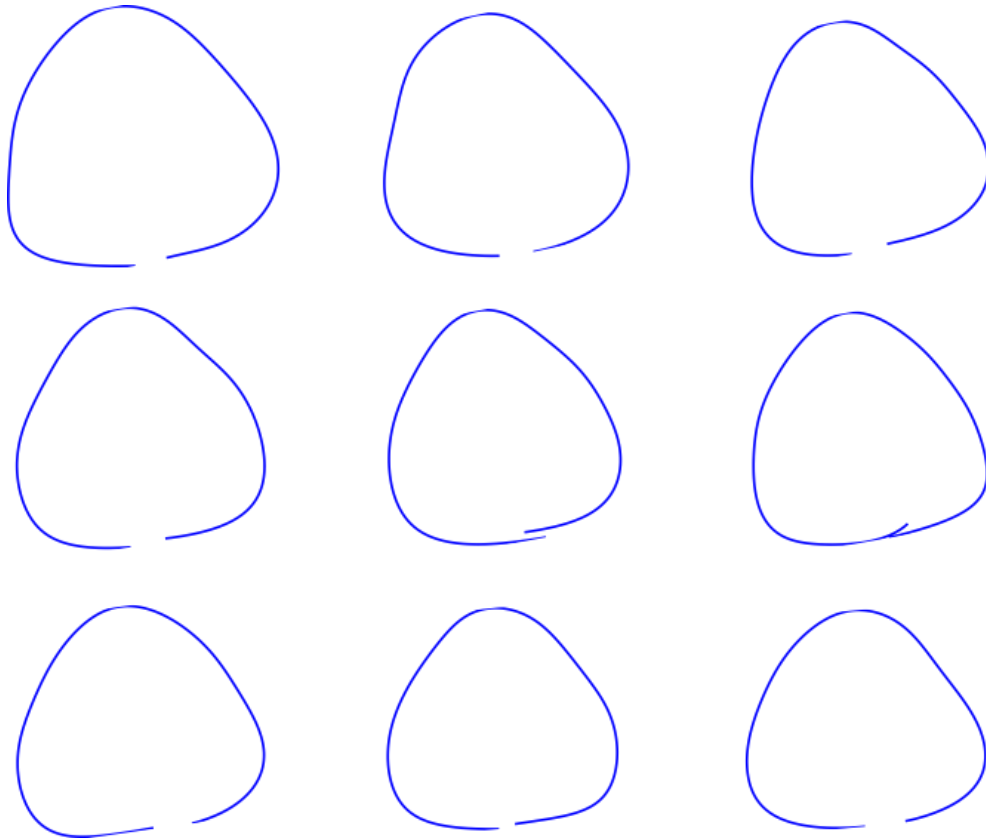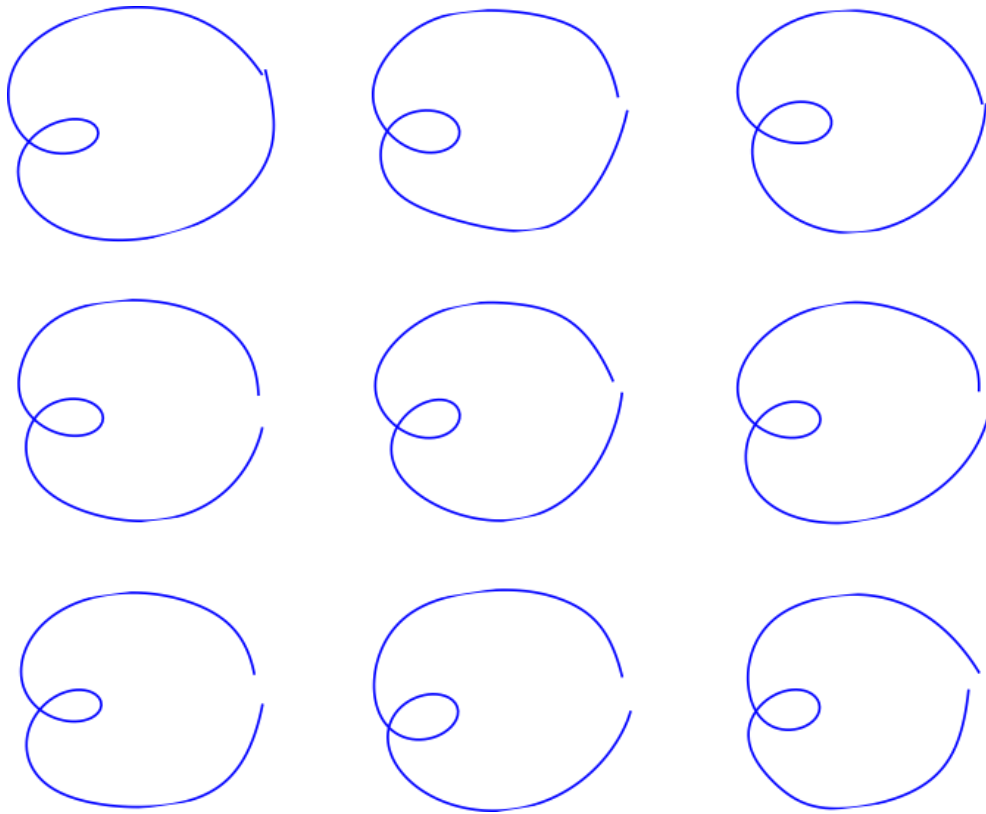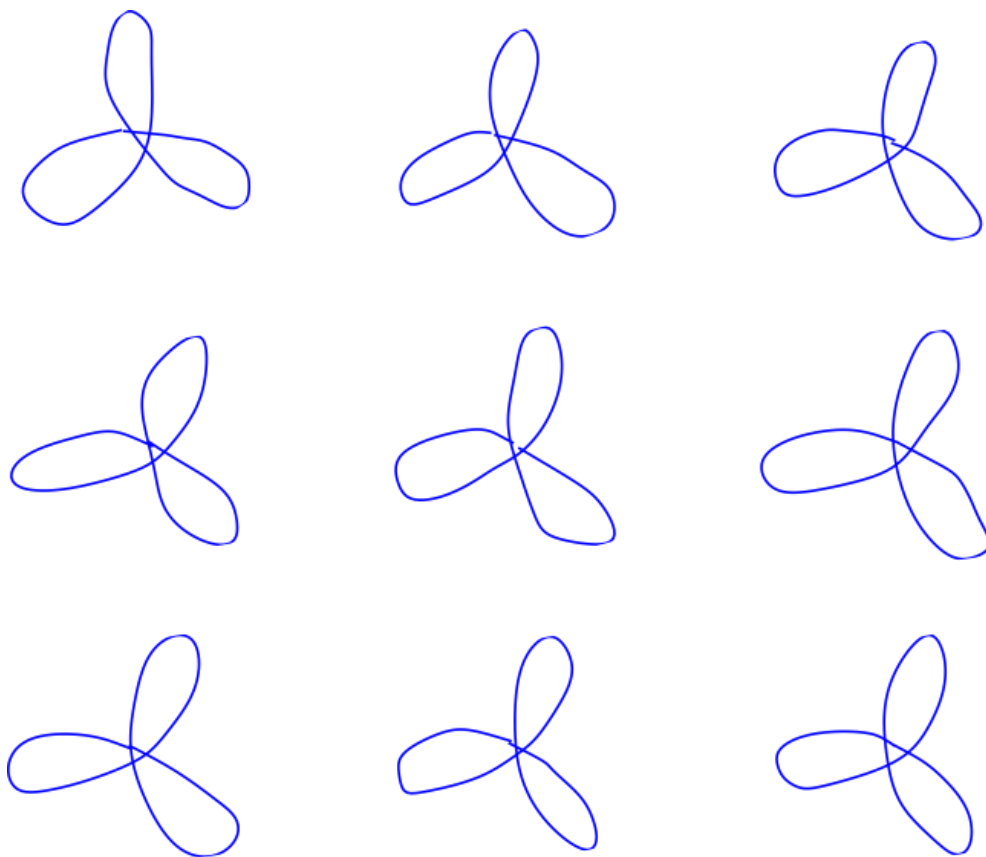
B.1 Neuropsicological Screening of LBD patients

Table B.1 – Neuropsychological testing of LBD patients, Chapter 4. Pathological performances in a test are indicated in bold-italic

Patient	EL	EV	MA	SA	GR	PO
Preliminary Object Use	*6*	*6*	*6*	*6*	*6*	*6*
Preliminary Object Naming	*6*	*5*	*6*	*6*	*5*	*5*
Ideomotor Apraxia (De Renzi et al., 1980; Tessari et al., 2011)	*59/72*	*58/72*	*56/72*	*62/72*	*68/72*	*32/36 ML 30/36 MF*
Buccofacial Apraxia (De Renzi et al., 1980)	*24/24*	*24/24*	***17/24***	***9/24***	*24/24*	*24/24*
AAT (Luzzatti et Al., 1996)						
Tokens	***32***	***21***	***13***	***14***	***35***	***36***
Repetitions	*131*	***94***	*134*	***127***	*86*	***128***
Written	*76*	***60***	*75*	*85*	***35***	***64***
Naming	*97*	***80***	*93*	*94*	***50***	***54***
Comprehension	*105*	*106*	*98*	*109*	*96*	*99*
Raven Matrices (max 36)	*-*	*33*	*24*	*-*	*35*	*34*
Attentional Matrices (max 60)	***27***	***25***	*31*	*-*	*41*	***38***
Stroop Error	*8*	*-*	*-*	*-*	*-*	*-*
Fonemic Fluency (Carlesimo et al, 1995)	*-*	***11***	*-*	*-*	*-*	*-*
Semantic Fluency (Novelli et al., 1986)	*-*	***21***	*-*	*-*	*-*	*-*
Weigl (max 15; Spinnler and Tognoni, 1987)	*11*	*-*	*5*	*-*	*12*	*5*
Digit Span Forward (Orsini et al., 1987)	*-*	***4***	*5*	*-*	***3***	*4*
Digit Span Backwards	*-*	*4*	*3*	*-*	***2***	*-*
Spatial Span (Corsi Cubes) (Spinnler and Tognoni, 1987)	*5*	*4*	*4*	*-*	*6*	*4*
Supraspan learning (Corsi Cubes)	*-*	*10*	*7*	*-*	*-*	*-*
Rey's Figures - Immediate Recall (Caffarra et al., 2002)	*-*	*-*	*-*	*-*	*32*	*-*
Rey's Figures - Differed Recall	*-*	*-*	*-*	*-*	*17*	*-*
Trail Making Test A	*-*	*-*	*-*	*-*	*40*	*49*
Trail Making Test B	*-*	*-*	*-*	*-*	*191*	***376***

B.2 Analysis of movements performed by control subjects

Experiments 1 and 2: Grasp to Move and Grasp to Use.

Main effect of the hand. The hand used by the control subjects had an influence on most of the parameters taken into account. As shown on Table 4.4, participants were faster in initiating the movement with the left hand (**RT** $F_{1,676}$=13.47 p<0.001) but had shorter movement times with the right hand (**MT** $F_{1,676}$=49.45 p<0.001). The maximum grip aperture was wider and the time to reach it was longer when control subjects used the right hand (**MGA** $F_{1,676}$=4.22 p<0.05; **nTMGA** $F_{1,676}$=7.29 p<0.01)

Main effect of the task. Also the task influenced most of the grasping parameters:, control subject were faster when grasping to use than in grasping to use in terms of both reaction times (**RT** $F_{1,676}$=7.96 p=0.005) and movement times **MT** $F_{1,676}$=9.58 p<0.005), adopted a wider grip (**MGA** $F_{1,676}$=30.71 p<0.001) and longer acceleration phase(**nTPV** $F_{1,676}$=5.94 p<0.05).

Main effect of the eye movements. Control subjects had shorter movement times (**MT** $F_{1,676}$=44.85 p<0.001), longer acceleration phases (**nTPV** $F_{1,676}$=21.01 p<0.001) and larger grip apertures (**MGA** $F_{1,676}$=48.76 p<0.001) if they were grasping the objects while fixating the LED rather than looking at the objects themselves.

Main effect of the side. The main effect of the side (left or right half of the board) was not significant for any parameters.

Main effect of the size. Control subjects were faster in initiating the movement and adopted a larger grip when grasping big rather than small objects (**RT** $F_{1,676}$=3.77 p=0.05; **MGA** $F_{1,676}$=1842.22 p<0.001)

Main effect of the orientation. The orientation of the objects was found to have a significant effect on the movement times of the control subjects (**MT** $F_{1,676}$=9.81 p<0.005), as participants were faster when the object were placed in congruent orientations. However, participants adopted larger grip (**MGA** $F_{1,676}$=4.37 p<0.05), shorter acceleration phases and times to maximum grip apertures (**nTMGA** $F_{1,676}$=10.21 p<0.001; **nTPV** $F_{1,676}$=3.38 p=0.066*, trend*) when grasping the objects placed in congruent orientation.

Table B.2 - Means and SD of the kinematic parameters referred to the main effects (grasp to move and grasp to use)

	Mean	SD	Mean	SD
Hand	*Left*		*Right*	
RT	*565.28 ms*	*177.40*	*651.10 ms*	*204.31*
MT	*952.23 ms*	*169.20*	*879.21 ms*	*159.03*
MGA	*78.54 mm*	*17.26*	*80.00 mm*	*18.31*
Task	*Move*		*Use*	
RT	*570.08 ms*	*187.84*	*609.41 ms*	*195.59*
MT	*899.24 ms*	*163.87*	*932.99 ms*	*170.88*
MGA	*81.07 mm*	*18.77*	*77.46 mm*	*16.59*
nTPV	*32.64%*	*8.27*	*31.30%*	*9.05*
nTMGA	*73.90%*	*11.04*	*72.40%*	*12.19*
Eye movements	*Fixed*		*Free*	
MT	*899.24 ms*	*163.87*	*932.99 ms*	*170.89*
MGA	*81.07 mm*	*18.77*	*77.46 mm*	*16.59*
nTPV	*32.64%*	*8.27*	*31.30%*	*9.05*
Size	*Small*		*Big*	
RT	*603.16 ms*	*189.86*	*576.41 ms*	*194.77*
MGA	*65.30 mm*	*9.29*	*93.37 mm*	*12.36*
Orientation	*Down*		*Up*	
MT	*932.38 ms*	*175.17*	*899.94 ms*	*159.41*
MGA	*78.67 mm*	*17.48*	*79.85 mm*	*18.10*
nTPV	*32.40%*	*9.06*	*31.53%*	*8.29*
nTMGA	*74.37%*	*11.63*	*71.92%*	*11.56*

The interaction *hand by task* was significant for different parameters: reaction times (**RT** $F_{1,676}=10.12$ $p<0.005$), movement times (**MT** $F_{1,676}=16.32$ $p<0.001$), normalized times to peak velocity (**nTPV** $F_{1,676}=7.78$ $p=0.005$) and maximum grip aperture (**MGA** $F_{1,676}=3.36$ $p=0.056$). Reaction times were shorter when participants grasped to move than to use, but only on the left hand ($p<0.001$), while the effect was not significant for the right hand. No difference was found between the two sides when participants were grasping to use, but the left hand was faster in grasping to move ($p<0.001$). Movement times were faster in grasping to move than in grasping to use task, but only with the left hand ($p<0.001$). Furthermore, MT were faster with the right than with the left hand, but only when

grasping to use ($p<0.001$). Acceleration phases were longer in grasping to move than in grasping to use task, but only with the right hand ($p<0.001$); and were also longer with the right than with the left hand, but only when grasping to use ($p<0.001$). Finally, the maximum grip aperture was wider when grasping to move than when grasping to use with both right ($p<0.05$) and left ($p<0.005$) hand, and it was wider with the right than with the left hand only when participants grasped to use ($p<0.005$).

The interaction *hand by side* was significant for movement times (**MT** $F_{1,676}=116.90$ $p<0.001$), normalized times to peak velocity (**nTPV** $F_{1,676}=47.81$ $p<0.001$), maximum grip apertures (**MGA** $F_{1,676}=13.45$ $p<0.001$) and normalized times to maximum grip aperture (**nTMGA** $F_{1,676}=21.35$ $p<0.001$). Movement times were shorter with the right than with the left hand when the objects were placed on the right ($p<0.001$), and the opposite (left hand faster than the right) was true when the objects were on the left ($p<0.001$). Using the right hand, movements were faster on the right than on the left ($p<0.001$). On the contrary, hand movements were faster performing the action with the left had on the left rather than on the right side of the space ($p<0.001$). Likewise, acceleration phases were longer on the right side when using the left hand ($p<0.001$) and on the left side when using the right hand ($p<0.001$). On the left side, acceleration phases were longer with the right hand than whit the left ($p<0.001$), while on the right acceleration phases were longer with the left hand ($p<0.001$). Maximum grip aperture was bigger when the objects were placed on the left than on the right side, but only when participants used the right hand ($p<0.01$). When the objects were placed on the left, participants adopted a wider grip with the right than with the left hand ($p<0.001$). In a similar way, normalized times to maximum grip aperture were longer with the right than with the left hand when the objects were placed to the left side ($p<0.01$) and with the left hand when objects were placed to the right hemispace ($p<0.001$)

The interaction *task by orientation* was significant for movement times (**MT**($_{1,676}=12.49$ $p<0.001$). The difference between orientations was significant only when participants grasped to use, as they were faster when the objects were in congruent rather than in incongruent orientation ($p<0.001$). When the objects were placed in incongruent orientation, movement times were longer for grasping to use than for grasping to move ($p<0.001$).

The interaction *hand by size* was significant for **nTMGA**($F_{1,676}=44.85$ $p<0.001$): when participants used the left hand, the normalized time to maximum grip aperture was longer for big rather for small objects ($p<0.001$), but no effect was found for the right hand.

The interaction *orientation by side* was significant for the **nTMGA**($F_{1,676}=5.34$ $p<0.05$) and for the **nTPV**($F_{1,676}=4.37$ $p<0.05$). When participants grasped objects in incongruent positions, the normalized time to maximum grip aperture was longer if the objects were placed on the left rather than on the right ($p=0.05$), but no effect was found for objects in congruent orientation. Only when objects were placed

on the left side, acceleration phases were longer when the objects were placed in incongruent rather than congruent orientation ($p<0.05$),

The interaction *orientation by* size was significant for the **nTMGA**($F_{1,676}$=5.17 $p<0.05$): When participants grasped objects in incongruent positions the normalized time to maximum grip aperture was longer for big than for small objects ($p=0.012$) , but no effect was found for objects in congruent orientation. When grasping big objects, the time to maximum grip aperture was longer when grasping objects in incompatible rather than compatible orientation ($p<0.01$), but no effect was found for small objects.

Experiments 3 and 4: Reach and Grasp

Main effect of the hand. The main effect of the hand was significant for some transport parameters (see Table 4.5), as participants were faster to react when using the left hand (**RT** $F_{1,306}$=21.92 $p<0.001$) but had shorter movement times with the right hand (**MT** $F_{1,306}$=18.67 $p<0.001$).

Main effect of the task. The main effect of the hand was significant for the movement times (**MT** $F_{1,306}$=81.83 $p<0.001$), as participants were faster when reaching than when grasping, and in the duration of acceleration phases (**nTPV** $F_{1,306}$=10.36 $p=0.001$), that were longer when participants were reaching than when grasping.

Main effect of the eye movements. The main effect of the eye movements was significant for the movement times (**MT** $F_{1,306}$=17.31 $p<0.001$), as participants had faster movements when looking at the objects rather than at the LED.

Main effect of the side. The main effect of the side (left or right half of the board) was not significant for any parameters.

Main effect of the size. The main effect of the size was found to be significant for some transport parameters, as participant were faster both in terms of reaction times and movement times when presented with bigger objects (**RT** $F_{1,306}$=4.75 $p<0.005$; **MT** $F_{1,306}$=8.09 $p=0.005$)

Main effect of the distance. The main effect of the distance was significant for all transport parameters, as participants were slower to react, had longer movement times and longer acceleration phases when the objects were placed in the far rather than in the near positions (**RT** $F_{1,306}$=7.44 $p<0.01$; **MT** $F_{1,306}$=462.98 $p<0.001$; **nTPV** $F_{1,306}$=4.17 $p<0.05$).

Table B.3 - Means and SD of the kinematic parameters referred to the main effects (grasp to move and grasp to use)

	Mean	SD	Mean	SD
Hand	*Left*		*Right*	
RT	*532.80 ms*	*171.16*	*608.17 ms*	*168.29*
MT	*741.38 ms*	*196.77*	*689.46 ms*	*177.64*
Task	*Reach*		*Grasp*	
MT	*661.34 ms*	*185.54*	*769.20 ms*	*182.440*
nTPV	*34.98%*	*15.68*	*30.37%*	*177.135*
Eye movements	*Fix*		*Free*	
MT	*741.51 ms*	*209.66*	*690.16 ms*	*162.92*
Size	*Small*		*Big*	
RT	*588.18 ms*	*188.92*	*552.29 ms*	*155.48*
MT	*733.58 ms*	*198.65*	*697.77 ms*	*177.77*
Distance	*Near*		*Far*	
RT	*549.15 ms*	*173.71*	*591.56 ms*	*171.45*
MT	*592.12 ms*	*129.28*	*841.13 ms*	*154.40*
nTPV	*31.21%*	*16.56*	*34.15%*	*9.78*

The interaction *hands by side* was found to be significant for the **MT** ($F_{1,306}=47.30$ $p<0.001$), as movement times were shorter with the right hand than with the left hand when the object were placed on the right ($p<0.001$), but when the objects were placed on the left, MTs were shorter with the left hand ($p<0.001$). As well, the right hand movements were faster on the right than on the left ($p<0.001$) and left hand movements were faster on the left than on the right ($p<0.001$).

The interaction *task by hand* was significant for the normalized duration of acceleration phases (**nTPV** $F_{1,306}=4.56$ $p<0.05$). When participants were using the left hand there was no difference between the tasks, but with the right hand participants had longer acceleration phase when reaching than grasping ($p<0.001$). Furthermore, there was no significant difference between the hands when participants reached for the objects, but they showed longer acceleration phases with the right rather than with the left hand when grasping ($p<0.005$).

The interaction *eye movements by distance* was significant for the **MT** ($F_{1,306}=4.15$ $p<0.05$). Movement times were shorter when objects were placed in the near position both in the fix ($p<0.001$) and in the free ($p<0.001$) conditions, but while there was no effect of the location of eye movements

for objects placed in the near positions, for objects placed in the far positions participants were faster when they could look at the object rather than fixating the LED ($p<0.001$)

Comments

We performed this preliminary analysis only on control subjects in order to assess the differences in performing the tasks using the right or the left hand. As our control group was composed solely of right-handed participants, we expected that they would perform better (faster and more accurately) with the right hand than with the left. Furthermore, we expected an interaction between hand and side, as it is known (Fisk and Goodale, 1985, Simon and Reeve, 1990) that right-handers show a facilitation effect using the right hand in the right hemispace. Indeed, we found that participants had shorter MT and using the right hand. However the main effect of the hand is not so clear-cut (for instance, RTs are shorter with the left and), and the interaction hand by side was significant for all variables except for reaction times. In general, of the present results confirm the preference of the right hand for moving in the right hemispace and of the left hand to move in the left one.

The interaction between task and orientation of the objects confirmed the importance of role of the task goal for grasping movements, as the initial (and final) orientations of the objects were not significant when participants were asked to grasp to move, a task in which arguably the orientation of the objects was not relevant. Orientation, however, was important in the grasp to use task, and in this task it was revealed to have a statistically significant effect on several grasping parameters (MT, MGA and nTPV), as movements were faster, with longer acceleration phases and with a narrower grip when the objects were placed in congruent condition.

In general, this first comparison allowed us to better define our control group, especially with regard to the effect of the location of the eye movements: even if our participants are middle-aged, their performance resembles the one of older adults in Chapter 3, as in grasp to move and in grasp to use control subject exhibited shorter movement times, wider maximum grip aperture and longer normalized acceleration phases when executing the movement while fixating the LED than when looking at the objects.

However, this effect was only found for Experiments 1 and 2, as in Experiment 3 and 4 control subjects movements took more time while fixating the LED than when looking at the objects. Furthermore, no effect of the eye movement conditions was found for the other variables taken into consideration in those movement. Therefore, this experimental factor might not be as relevant to simpler tasks such as reaching as it is for tasks such as grasping to use.

Bibliography

Abend, W., Bizzi, E., Morasso, P., & others. (1982). Human arm trajectory formation. *Brain: a journal of neurology*, *105*(Pt 2), 331.

Agam, Y., & Sekuler, R. (2008). Geometric Structure and Chunking in Reproduction of Motion Sequences. *Journal of Vision*, *8*(1). doi:10.1167/8.1.11

Ansuini, C., Santello, M., Massaccesi, S., & Castiello, U. (2006). Effects of end-goal on hand shaping. *Journal of neurophysiology*, *95*(4), 2456–2465.

Ansuini, Caterina, Giosa, L., Turella, L., Altoè, G., & Castiello, U. (2008). An object for an action, the same object for other actions: effects on hand shaping. *Experimental Brain Research*, *185*(1), 111–119. doi:10.1007/s00221-007-1136-4

Barclay, C. D., Cutting, J. E., & Kozlowski, L. T. (1978). Temporal and spatial factors in gait perception that influence gender recognition. *Attention, Perception, & Psychophysics*, *23*(2), 145–152.

Bauer, D. W., & Miller, J. (1982). Stimulus-response compatibility and the motor system. *The Quarterly Journal of Experimental Psychology Section A*, *34*(3), 367–380. doi:10.1080/14640748208400849

Ben-Itzhak, S., & Karniel, A. (2008). Minimum acceleration criterion with constraints implies bang-bang control as an underlying principle for optimal trajectories of arm reaching movements. *Neural computation*, *20*(3), 779–812.

Bennett, K. M. B., & Castiello, U. (1994). Reach to Grasp: Changes With Age. *Journal of Gerontology*, *49*(1), P1–P7. doi:10.1093/geronj/49.1.P1

Bennequin, D., Fuchs, R., Berthoz, A., & Flash, T. (2009). Movement Timing and Invariance Arise from Several Geometries. *PLoS Comput Biol*, *5*(7), e1000426. doi:10.1371/journal.pcbi.1000426

Bernshteĭn, N. A. (1967). *The co-ordination and regulation of movements*. Pergamon Press.

Bock, O., Steinberg, F., (2012). Age-related deficits of manual grasping in a laboratory versus in an everyday-like setting. *Ageing Research*, 3(1).

Brown, L., Halpert, B., Goodale, M. (2005). Peripheral vision for perception and action. *Exp Brain Res (2005) 165: 97–106*

Bookstein, F. L. (1997). *Morphometric Tools for Landmark Data: Geometry and Biology*. Cambridge University Press.

Brown, L. E., Halpert, B. A., & Goodale, M. A. (2005). Peripheral vision for perception and action. *Experimental brain research*, *165*(1), 97–106.

Brownlow, S., Dixon, A. R., Egbert, C. A., & Radcliffe, R. D. (1997). Perception of movement and dancer characteristics from point-light displays of dance. *Psychological Record*, *47*, 411–422.

Carmeli, E., Patish, H., & Coleman, R. (2003). The Aging Hand. *The Journals of Gerontology Series A: Biological Sciences and Medical Sciences*, *58*(2), M146–M152. doi:10.1093/gerona/58.2.M146

Casile, A., Dayan, E., Caggiano, V., Hendler, T., Flash, T., & Giese, M. A. (2010). Neuronal encoding of human kinematic invariants during action observation. *Cerebral cortex (New York, N.Y.: 1991)*, *20*(7), 1647–1655. doi:10.1093/cercor/bhp229

Chua, R., & Elliott, D. (1993). Visual regulation of manual aiming. *Human Movement Science*, *12*(4), 365–401.

Crespi, S., Robino, C., Silva, O., de'Sperati, C (2012) Spotting expertise in the eyes: Billiards knowledge as revealed by gaze shifts in a dynamic visual prediction task. *Journal of Vision 12(11):30, 1-19*

Coen-Cagli, R., Coraggio, P., Napoletano, P., Schwartz, O., Ferraro, M., & Boccignone, G. (2009). Visuomotor characterization of eye movements in a drawing task. *Vision research*, *49*(8), 810–818. doi:10.1016/j.visres.2009.02.016

D' Avella, A., Saltiel, P., & Bizzi, E. (2003). Combinations of muscle synergies in the construction of a natural motor behavior. *Nature Neuroscience*, *6*(3), 300–308. doi:10.1038/nn1010

Dayan, E., Casile, A., Levit-Binnun, N., Giese, M. A., Hendler, T., & Flash, T. (2007). Neural representations of kinematic laws of motion: evidence for action-perception coupling. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(51), 20582–20587. doi:10.1073/pnas.0710033104

Dayan, E., Inzelberg, R., & Flash, T. (2012). Altered Perceptual Sensitivity to Kinematic Invariants in Parkinson's Disease. *PLoS ONE*, *7*(2). doi:10.1371/journal.pone.0030369

De' Sperati, C., & Viviani, P. (1997). The Relationship between Curvature and Velocity in Two-Dimensional Smooth Pursuit Eye Movements. *The Journal of Neuroscience*, *17*(10), 3932–3945.

Dingwell, J. B., Mah, C. D., & Mussa-Ivaldi, F. A. (2004). Experimentally confirmed mathematical model for human control of a non-rigid object. *Journal of neurophysiology*, *91*(3), 1158–1170. doi:10.1152/jn.00704.2003

Dittrich, W. H., Troscianko, T., Lea, S. E. G., Morgan, D., & others. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception-London*, *25*(6), 727–738.

Edelman, S., & Flash, T. (1987). A model of handwriting. *Biological Cybernetics*, *57*(1), 25–36.

Elliott, D., Hansen, S., Grierson, L. E. M., Lyons, J., Bennett, S. J., & Hayes, S. J. (2010). Goal-directed aiming: Two components but multiple processes. *Psychological bulletin*, *136*(6), 1023.

Errol, R.H. (1991). A comparison of hand and foot movement times. *Ergonomics*, *34*(4), 397–406.

Farnè, A., Roy, A. C., Paulignan, Y., Rode, G., Rossetti, Y., Boisson, D., & Jeannerod, M. (2003). Visuo-motor control of the ipsilateral hand: evidence from right brain-damaged patients. *Neuropsychologia*, *41*(6), 739-757.

Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research*, *60*(1), 159–178.

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of experimental psychology*, *47*(6), 381.

Flash, T., & Handzel, A. A. (2007). Affine differential geometry analysis of human arm movements. *Biological cybernetics*, *96*(6), 577–601.

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *5*(7), 1688–1703.

Georgopoulos, A. P., Kalaska, J. F., & Massey, J. T. (1981). Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty, and change in target location. *Journal of Neurophysiology*, *46*(4), 725–743.

Gentilucci, M., Negrotti, A., & Gangitano, M. (1997). Planning an action. *Experimental Brain Research*, *115*(1), 116–128. doi:10.1007/PL00005671

Grosjean, M., Shiffrar, M., & Knoblich, G. (2007). Fitts's Law Holds for Action Perception. *Psychological Science*, *18*(2), 95–99. doi:10.1111/j.1467-9280.2007.01854.x

Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, *35*(6), 1167–1175.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, *12*(5), 711–720.

Haaland, K. Y., & Harrington, D. (1989). The role of the hemispheres in closed loop movements. *Brain and cognition*, *9*(2), 158-180.

Haaland, K. Y., Harrington, D. L., & Knight, R. T. (1999). Spatial deficits in ideomotor limb apraxia A kinematic analysis of aiming movements. *Brain*, *122*(6), 1169-1182.

Haaland, K. Y., Prestopnik, J. L., Knight, R. T., & Lee, R. R. (2004). Hemispheric asymmetries for kinematic and positional aspects of reaching. *Brain*, *127*(5), 1145-1158.

Harada, T., Miyai, I., Suzuki, M., & Kubota, K. (2009). Gait capacity affects cortical activation patterns related to speed control in the elderly. *Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale*, *193*(3), 445–454. doi:10.1007/s00221-008-1643-y

Hermsdörfer, J., Laimgruber, K., Kerkhoff, G., Mai, N., & Goldenberg, G. (1999). Effects of unilateral brain damage on grip selection, coordination, and kinematics of ipsilesional prehension. *Experimental brain research*, *128*(1), 41-51.

Hermsdörfer, J., Ulrich, S., Marquardt, C., Goldenberg, G., & Mai, N. (1999). Prehension with the ipsilesional hand after unilateral brain damage. *Cortex*, *35*(2), 139-161.

Hermsdörfer, J., & Goldenberg, G. (2002). Ipsilesional deficits during fast diadochokinetic hand movements following unilateral brain damage. *Neuropsychologia*, *40*(12), 2100.

Hermsdörfer, J., Blankenfeld, H., & Goldenberg, G. (2003). The dependence of ipsilesional aiming deficits on task demands, lesioned hemisphere, and apraxia. *Neuropsychologia*, *41*(12), 1628-1643.

Henderson, J. M. (2003). Human gaze control during real-world scene perception. *Trends in cognitive sciences*, *7*(11), 498–504.

Heuninckx, S., Wenderoth, N., Debaere, F., Peeters, R. & Swinnen, S.P. Neural Basis of Aging: The Penetration of Cognition into Action Control *The Journal of Neuroscience, 20 July 2005, 25(29)*

Hoffman, D.D.; Richards, W.A. (1984). Parts of Recognition. *Cognition.*

Hutchinson, S., Kobayashi, M., Horkan, C. M., Pascual-Leone, A., Alexander, M. P., & Schlaug, G. (2002). Age-related differences in movement representation. *NeuroImage*, *17*(4), 1720–1728.

Ietswaart, M., Carey, D. P., Sala, S. D., & Dijkhuizen, R. S. (2001). Memory-driven movements in limb apraxia: is there evidence for impaired communication between the dorsal and the ventral streams?. *Neuropsychologia*, *39*(9), 950-961.

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature reviews. Neuroscience*, *2*(3), 194–203. doi:10.1038/35058500

Ivanenko, Y. P., Poppele, R. E., & Lacquaniti, F. (2004). Five basic muscle activation patterns account for muscle activity during human locomotion. *The Journal of Physiology*, *556*(1), 267–282. doi:10.1113/jphysiol.2003.057174

Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. *Canadian Journal of Psychology/Revue canadienne de psychologie*, *41*(3), 365–378. doi:10.1037/h0084157

Kaminski, T. R., Bock, C., & Gentile, A. M. (1995). The coordination between trunk and arm motion during pointing movements. *Experimental brain research*, *106*(3), 457–466.

Kang, N., Shinohara, M., Zatsiorsky, V. M., & Latash, M. L. (2004). Learning multi-finger synergies: an uncontrolled manifold analysis. *Experimental Brain Research*, *157*(3), 336–350.

Kawato, M., Maeda, Y., Uno, Y., & Suzuki, R. (1990). Trajectory formation of arm movement by cascade neural network model based on minimum torque-change criterion. *Biological Cybernetics*, *62*(4), 275–288.

Ketcham, C. J., Dounskaia, N. V., & Stelmach, G. E. (2006). The Role of Vision in the Control of Continuous Multijoint Movements. *Journal of Motor Behavior*, *38*(1), 29–44. doi:10.3200/JMBR.38.1.29-44

Ketcham, C. J., Seidler, R. D., Van Gemmert, A. W. A., & Stelmach, G. E. (2002). Age-related kinematic differences as influenced by task difficulty, target size, and movement amplitude. *The journals of gerontology. Series B, Psychological sciences and social sciences*, *57*(1), P54–64.

Kozlowski, L. T., & Cutting, J. E. (1978). Recognizing the gender of walkers from point-lights mounted on ankles: Some second thoughts. *Attention, Perception, & Psychophysics*, *23*(5), 459–459.

Krishnamoorthy, V., Latash, M. L., Scholz, J. P., & Zatsiorsky, V. M. (2004). Muscle modes during shifts of the center of pressure by standing persons: effect of instability and additional support. *Experimental brain research*, *157*(1), 18–31.

Kurz, M. J., & Stergiou, N. (2003). The aging humans neuromuscular system expresses less certainty for selecting joint kinematics during gait. *Neuroscience Letters*, *348*(3), 155–158. doi:10.1016/S0304-3940(03)00736-5

Kutch, J. J., Kuo, A. D., Bloch, A. M., & Rymer, W. Z. (2008). Endpoint force fluctuations reveal flexible rather than synergistic patterns of muscle cooperation. *Journal of neurophysiology*, *100*(5), 2455–2471. doi:10.1152/jn.90274.2008

Lacquaniti, F., & Soechting, J. F. (1982). Coordination of arm and wrist motion during a reaching task. *The Journal of Neuroscience*, *2*(4), 399–408.

Lacquaniti, F., Terzuolo, C., & Viviani, P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta psychologica*, *54*(1-3), 115–130.

Land, M. F., Lee, D. N., & others. (1994). Where we look when we steer. *Nature*, *369*(6483), 742–744.

Land, Michael F, & Tatler, B. W. (2001). Steering with the head: The visual strategy of a racing driver. *Current Biology*, *11*(15), 1215–1220. doi:10.1016/S0960-9822(01)00351-7

Latash, M. L. (2008). *Synergy*. Oxford University Press.

Latash, M. L., & Zatsiorsky, V. M. (2001). *Classics in Movement Science*. Human Kinetics.

Lee, W. A. (1984). Neuromotor synergies as a basis for coordinated intentional action. *Journal of motor behavior*, *16*(2), 135–170.

Liepmann, H. (1908). Drei Aufsätze aus dem Apraxiegebiet. *Karger, Berlin*

Maoz, U., Berthoz, A., & Flash, T. (2009). Complex unconstrained three-dimensional hand movement and constant equi-affine speed. *Journal of neurophysiology*, *101*(2), 1002–1015.

Maryott, J., Noyce, A., & Sekuler, R. (2011). Eye movements and imitation learning: intentional disruption of expectation. *Journal of vision*, *11*(1), 7. doi:10.1167/11.1.7

Marteniuk, R. G., & Bertram, C. P. (1999). On achieving strong inference in prehension research. *Motor Control*, *3*(3), 237–71.

Mattay, V. S., Fera, F., Tessitore, A., Hariri, A. R., Das, S., Callicott, J. H., & Weinberger, D. R. (2002). Neurophysiological correlates of age-related changes in human motor function. *Neurology*, *58*(4), 630–635.

Marchetti, C., & Sala, S. D. (1997). On crossed apraxia. Description of a right-handed apraxic patient with right supplementary motor area damage. *Cortex*, *33*(2), 341-354.

Nelson, W. L. (1983). Physical principles for economies of skilled movements. *Biological cybernetics*, *46*(2), 135–147.

Petreska, B., Adriani, M., Blanke, O., & Billard, A. G. (2007). Apraxia: a review. *Progress in brain research*, *164*, 61-83.

Polcyn, A. F., Lipsitz, L. A., Kerrigan, D. C., & Collins, J. J. (1998). Age-related changes in the initiation of gait: Degradation of central mechanisms for momentum generation. *Archives of Physical Medicine and Rehabilitation*, *79*(12), 1582–1589.

Polyakov, F., Drori, R., Ben-Shaul, Y., Abeles, M., & Flash, T. (2009). A Compact Representation of Drawing Movements with Sequences of Parabolic Primitives. *PLoS Comput Biol*, *5*(7), e1000427. doi:10.1371/journal.pcbi.1000427

Raymer, A. M., Maher, L. M., Foundas, A. L., Heilman, K. M., & Gonzalez Rothi, L. J. (1997). The significance of body part as tool errors in limb apraxia. *Brain and cognition*, *34*(2), 287-292.

Reina, G. A., & Schwartz, A. B. (2003). Eye–hand coupling during closed-loop drawing: Evidence of shared motor planning? *Human Movement Science*, *22*(2), 137–152. doi:10.1016/S0167-9457(02)00156-2

Richardson, M. J. E., & Flash, T. (2002). Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis. *The Journal of neuroscience the official journal of the Society for Neuroscience*, *22*(18), 8201–8211.

Reingold, E. M., Charness, N., Pomplun, M., & Stampe, D. M. (2001). Visual span in expert chess players: Evidence from eye movements. *Psychological Science, 12 (1), 48–55.*

Riecker, A., Gröschel, K., Ackermann, H., Steinbrink, C., Witte, O., & Kastrup, A. (2006). Functional significance of age-related differences in motor activation patterns. *NeuroImage*, *32*(3), 1345–1354. doi:10.1016/j.neuroimage.2006.05.021

Rosenbaum, D. A. (2009). *Human Motor Control.* Academic Press.

Scholz, J. P., & Schöner, G. (1999). The uncontrolled manifold concept: identifying control variables for a functional task. *Experimental brain research*, *126*(3), 289–306.

Schwartz, A. B., & Moran, D. W. (1999). Motor Cortical Activity During Drawing Movements: Population Representation During Lemniscate Tracing. *Journal of Neurophysiology*, *82*(5), 2705–2718.

Shiffman, L. M. (1992). Effects of Aging on Adult Hand Function. *The American Journal of Occupational Therapy*, *46*(9), 785–792. doi:10.5014/ajot.46.9.785

Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences*, *105*(2), 809–813. doi:10.1073/pnas.0707021105

Simon, J. R., & Reeve, T. G. (1990). The effects of an irrelevant directional cue on human information processing, Stimulus-Response compatibility: An integrated perspective, 31–88.

Singh, M., Seyranian, G. D., & Hoffman, D. D. (1999). Parsing silhouettes: The short-cut rule. *Attention, Perception, & Psychophysics*, *61*(4), 636–660.

Sirigu, A., Duhamel, J. R., Cohen, L., Pillon, B., Dubois, B., Agid, Y., & others. (1996). The mental representation of hand movements after parietal cortex damage. *SCIENCE-NEW YORK THEN WASHINGTON-*, 1564–1568.

Schlicht, Erik J., and Paul R. Schrater. "Effects of visual uncertainty on grasping movements." *Experimental Brain Research* 182.1 (2007): 47-57.

Simon, J. R., & Reeve, T. G. (1990). The effects of an irrelevant directional cue on human information processing, Stimulus-Response compatibility: An integrated perspective, 31–88.

Smith, M. W., Sharit, J., & Czaja, S. J. (1999). Aging, Motor Control, and the Performance of Computer Mouse Tasks. *Human Factors: The Journal of the Human Factors and Ergonomics Society*, *41*(3), 389–396. doi:10.1518/001872099779611102

Stein, R. B., Oguztoreli, M. N., & Capaday, C. (1986). What is optimized in muscular movements. *Human muscle power*, 131–150.

Sivak, B., & MacKenzie, C. L. (1990). Integration of visual information and motor output in reaching and grasping: the contributions of peripheral and central vision. *Neuropsychologia*, *28*(10), 1095-1116.

Soechting, J. F., & Lacquaniti, F. (1981). Invariant characteristics of a pointing movement in man. *The Journal of Neuroscience*, *1*(7), 710–720.

Soukoreff, R. W., & MacKenzie, I. S. (2004). Towards a standard for pointing device evaluation, perspectives on 27 years of Fitts' law research in HCI. *International Journal of Human-Computer Studies*, *61*(6), 751–789. doi:10.1016/j.ijhcs.2004.09.001

Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is' mirror'only for biological actions. *Current Biology; Current Biology*. Recuperato da http://psycnet.apa.org/psycinfo/2004-95261-002

Ting, L. H., & McKay, J. L. (2007). Neuromechanics of muscle synergies for posture and movement. *Current opinion in neurobiology*, *17*(6), 622–628. doi:10.1016/j.conb.2008.01.002

Torres-Oviedo, G., & Ting, L. H. (2010). Subject-Specific Muscle Synergies in Human Balance Control Are Consistent Across Different Biomechanical Contexts. *Journal of Neurophysiology*, *103*(6), 3084–3098. doi:10.1152/jn.00960.2009

Tresch, M. C., & Jarc, A. (2009). The case for and against muscle synergies. *Current Opinion in Neurobiology*, *19*(6), 601–607. doi:10.1016/j.conb.2009.09.002

Tretriluxana J., Gordon J., Winstein C.J. Manual asymmetries in grasp pre-shaping and transport-grasp coordination. Exp Brain Res. 2008 Jun;188(2):305-15. doi: 10.1007/s00221-008-1364-2.

Tucker, M., & Ellis, R. (2001). The potentiation of grasp types during visual object categorization. *Visual Cognition*, *8*(6), 769–800. doi:10.1080/13506280042000144

Vallortigara, G., Regolin, L., & Marconato, F. (2005). Visually inexperienced chicks exhibit spontaneous preference for biological motion patterns. *PLoS biology*, *3*(7), e208.

Van de Kamp, C., & Zaal, F. T. J. M. (2007). Prehension is really reaching and grasping. *Experimental Brain Research*, *182*(1), 27–34.

Viviani, P., Burkhard, P., Chiuvé, S., Dell' Acqua, C., & Vindras, P. (2009). Velocity control in Parkinson's disease: a quantitative analysis of isochrony in scribbling movements. *Experimental Brain Research*, *194*(2), 259–283. doi:10.1007/s00221-008-1695-z

Viviani, P., & Cenzato, M. (1985). Segmentation and coupling in complex movements. *Journal of experimental psychology: Human perception and performance*, *11*(6), 828.

Viviani, Paolo, & Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony: converging approaches to movement planning. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(1), 32–53. doi:10.1037/0096-1523.21.1.32

Voorbij, A. I., & Steenbekkers, L. P. (2001). The composition of a graph on the decline of total body strength with age based on pushing, pulling, twisting and gripping force. *Applied ergonomics*, *32*(3), 287–292.

Wada, Y., & Kawato, M. (1995). A theory for cursive handwriting based on the minimization principle. *Biological Cybernetics*, *73*(1), 3–13.

Weiss, P. H., Dohle, C., Binkofski, F., Schnitzler, A., Freund, H. J., & Hefter, H. (2001). Motor impairment in patients with parietal lesions: disturbances of meaningless arm movement sequences. *Neuropsychologia*, *39*(4), 397-405.

Welsh, T. N., Higgins, L., & Elliott, D. (2007). Are there age-related differences in learning to optimize speed, accuracy, and energy expenditure? *Human movement science*, *26*(6), 892–912.

Winstein, C. J., & Pohl, P. S. (1995). Effects of unilateral brain damage on the control of goal-directed hand movements. *Experimental Brain Research*, *105*(1), 163-174.