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Understanding motor planning and action recognition of pantomimed grasps

by

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Declaration

I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other university. This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and Acknowledgements. This dissertation contains fewer than 65,000 words including appendices, bibliography, footnotes, tables and equations and has fewer than 150 figures.

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Abstract

The ability to manipulate objects with considerable skill is one of the defining features of primates. In both humans and non-human primates, grasping is typically directed toward a visible object and results in contact with the object. Humans - and perhaps some other species - are also capable of grasping imaginary objects in a pantomimed prehension. Pantomimed grasps are well studied, both for theoretical and clinical interests, to explore the double function of human hands, as instrumental as well as communicative devices.

The present thesis aims to investigate both aspects of pantomimed grasps in terms of motor control, action understanding and neural activation during action observation. The first experiment explored whether the way pantomimed grasps are executed can convey weight information of imaginary objects. The second experiment tested whether observers can exploit movement kinematics to discriminate between real (i.e., movements directed toward a physically present object) and pantomimed grasps. The third study investigated if perception of real and pantomimed grasps might automatically drive object representation. The fourth experiment inspected whether having a motor expertise on pantomimed grasp execution impacts pantomimed grasp processing. The fifth experiment shed new insights on the neural underpinnings of action understanding mechanisms by exploring electroencephalography (EEG) signals during real and pantomimed grasp observation.

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GENERAL INTRODUCTION

Imagine being in a theatre: an actor is pantomiming to grasp an imaginary object from thin air; then, he turns to an actress and stabs her in the chest.

Although it is clear that the weapon does not exist, that the action is merely pantomimed, and the actor does not really act, observers recognize in that gesture a precise intention, that of killing. This is possible, because that gesture, acted by nothing, reveals that what the actor is pretending to grasp is a knife. In this way, the action seems real. How do you act towards an object that is not there? How do you understand that a grasp is directed toward an imaginary knife? Can pantomimed grasp reveal object properties by the way it is performed? Can observers infer if an agent is grasping an existent or an imaginary object by only looking at the hand motion? How is this possible?

The current dissertation will investigate these questions by exploring motor control strategies in performing pantomimed grasps and action understanding abilities at behavioural level as well as at neuronal level.

1. Definition of pantomimed action

In cognitive neuroscience, there is no common definition of pantomimed action. The two most used definitions are:

- *an action performed in the absence of a physical tool and/or object* (Jazi et al., 2015).
- *an execution of the relevant motor sequence in the absence of its instrumental goal, and in the absence of its object for transitive actions* (Żywiczyński, Wacewicz, & Sibierska, 2016).

To note, pantomimed actions should not be confused with gestures representing intransitive actions (e.g., hitchhiking or saying goodbye), which are more dependent on social-cultural information, or symbolic descriptions of objects, which are mostly performed by using body parts as object representations (e.g., moving the index and the middle finger to represent scissors).

In motor control research, specifically in grasping literature, the term "pantomimed action" mostly refers to *pantomimed grasp*. In experimental settings, an object is usually displaced from a target position and participants are required to pantomime a reach-to-grasp movement toward the target position as if the object is still there (Goodale et al., 1994; Westwood et al., 2000; Cavina-Pratesi et al. 2011; Holmes et al. 2013; Whitwell et al. 2015; Jazi & Heath 2016; Ansuini et al. 2016).

2. Pantomimed action: clinical background

Historically, pantomimed action was first used by Hugo Liepmann (1905-1980) to explore apraxic motor deficits (i.e., impairments in gesture production) following stroke. Patients were required to manually pantomime the common use of familiar objects (e.g. cutting with scissors or hammering a nail). Liepmann believed that performing an action in the absence of cues from real objects was a more direct way - compared to real object use - to test the translation from the mental image of a movement (in his term, the *motor formula*) into the required motor program. The basic assumption was that the inability to pantomime object use - reported by some patients - underlined a loss of retrieval or a destruction of the stored action representation of real object use (Bartolo et al.,2003; Osiurak et al. 2012; Worthington, 2016; Goldenberg, 2017).

The general inability to use objects/tools, as a disorder of skilled voluntary behaviors in the absence of any motor, sensory, perceptual or attentive impairments, has been described with the term *apraxia* (De Renzi, 1985; Roth & Heilman, 1984; Osiurak et al., 2012). Since the preliminary research of Liepmann, several studies have reported patients with apraxia making gross spatiotemporal errors on hand coordination when performing real object use. Of interest, in some cases, impairments were more pronounced in pantomiming than in real object use (De Renzi, 1985; Rothi et al., 1986; Heilman & Watson, 2008; Hoeren et al., 2014;

Valyear et al., 2017). Despite the absence of a unified accepted theory, extensive research on defective pantomimed action helped to build a taxonomy of different type of apraxia and several models on how human brain deals with action execution (for reviews, see Wheaton & Hallett 2007; Osiurak & Gall 2012).

Nowadays, research on pantomimed action is a long-standing element of cognitive neuropsychology, with pantomimed action being not only a standard diagnostic tool for apraxia (De Renzi, 1985; Rothi et al., 1986; Wheaton & Hallett, 2007; Heilman & Watson, 2008; Niessen et al., 2014; Goldenberg, 2016), but also a way to test imitation deficit and dyspraxia in Autism Spectrum Disorder (Rogers et al., 1996; Dowell et al., 2009; Ham et al., 2011; Ewen et al., 2016), asymbolia and communication impairments in aphasia (Varney & Benton, 1982; Goldenberg et al., 2003; Rose et al., 2016; van Nispen et al., 2018;), impaired gesture production and recognition in schizophrenia (Stegmayer et al., 2016; Viher et al., 2018).

Finally, some studies have proposed rehabilitation therapies based on the reproduction of simple gesture and pantomimed actions to improve word recovery in aphasia, for instance the Gesture+Verbal Training (GVT) (Raymer et al., 2006) and the Visual Action Therapy (VAT) (Helm et al., 1982).

3. Pantomimed action: theoretical background

3.1. Motor control in action execution

Scientific interest in pantomimed actions is not limited to the clinical field, but is a rich source of insights for motor control theories of grasping movements. In particular, the physical features of movements (i.e., kinematics) are well investigated.

Several experiments have shown that the kinematics of pantomimed grasps differs distinctively from the kinematics of real grasps. For instance, pantomimed grasps consistently reach lower peak velocities, tend to last longer, follow more curvilinear trajectories, and undershot target position, compared to real grasps. Moreover, the maximum grip aperture of pantomimed grasps is smaller with respect to grip aperture of real grasps (Goodale et al.1994; Westwood et al., 2000; Cavina-Pratesi et al. 2011; Jazi et al. 2015).

There is not an agreement on which loss of information causes these kinematic differences. In fact, during real grasp, the object is physically present and allows the motor system to access visual, haptic and tactile information. Contrariwise, during pantomimed grasp, because of the absence of the object, these sources of information are not available and the motor system has to recall an internal motor representation to perform the action. Some authors claimed that pantomimed grasp is mostly influenced by the absence of absolute visual feedback (Fukui & Inui, 2013; Holmes et al., 2013; Whitwell et al., 2014), meanwhile other authors pointed out the relevance of haptic feedback deprivation (Schenk, 2012; Jazi et al., 2015; Jazi & Heath, 2016, 2017).

Nonetheless, the difference in the way real and pantomimed actions are performed has cast doubts on the traditional assumption that pantomimed actions are executed by replicating the very same motor programs of real actions (Króliczak et al., 2007; Finkel et al. 2018). A more plausible view considers pantomimed actions as gestures with a double nature in that they involve the repetition of real movements, without acting on an object, as a way of communicating something about the imaginary object or the action itself (Goldenberg, 2013, 2017; Finkel et al., 2018;). Recently, this perspective has taken hold specifically in grasping (Utz et al. 2015; Ansuini et al. 2016) as well as in action observation literature (Podda et al. 2017).

3.2. Mirror neurons in action observation

The investigation of pantomimed grasp execution is promising because it allows to explore *how human brain controls the dual functions of hands as instrumental and communicative devices* (Goldenberg et al., 2007). On the other hand, the exploration of pantomimed grasps in action observation studies can provide new insights for the discussion around humans' ability to understand others' action. Of interest, action execution and action observation seem to be two sides of the same coin and are mostly questioned together.

It has been claimed that *there is analogy at the cortical level between the mechanisms that mediate action observation and those involved in action execution* (Rizzolatti et al., 2001). The core of this speculation came from the discovery of a particular class of neurons in non-human primates' brain that fired not only when a monkey performed an action, but also when a monkey observed another individual performing the same action (di Pellegrino et al., 1992; Gallese et al., 1996). These neurons have been called *mirror neurons* and are supposed to play a role in action understanding via action perception. Several investigations demonstrated the existence of mirror neurons also in humans (for reviews, see Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010; Rizzolatti & Fogassi, 2014; Rizzolatti and Sinigaglia 2016).

Different models and interpretations have been proposed to explain mirror neurons' mechanism (for a review, see Michael, 2011). In particular, some authors claimed that action perception exploits the same mechanisms that is necessary for action execution, as if observers were performing (i.e., simulating) in their brain the same action they were observing. This simulation has been called *action/motor simulation* (Rizzolatti & Craighero, 2004). Thus, mirror neurons seem to match the observation of an action with the motor program that would be required for the observer to execute that action.

Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Thus, the mirror system transforms visual information into knowledge (Rizzolatti and Craighero 2004)

Mirror neurons' mechanism is supposed to be crucial not only for action perception, but also for speech comprehension, language evolution, gesture imitation, empathy and emotions recognition, and intention understanding (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004; Iacoboni, 2009; Friedemann & Fadiga, 2010; Ocampo & Kritikos, 2011; Rizzolatti & Sinigaglia, 2016; Becchio et al., 2017). Despite these intriguing speculations, an accordance on *what* mirror neurons response actually reflects has still to be found. In particular, an open question is present about the relative contribution of hand motion features (i.e., movement kinematics) and goal information to action observation. Since there is not a goal-object toward which pantomimed grasps are directed, many authors exploited pantomimed grasps to tackle this issue.

For instance, a well-known study by Umiltà and colleagues (Umiltà et al., 2001) showed that a subset of mirror neurons - recorded in primates' premotor cortex – fired when the monkeys observed a grasp only when movements were directed toward an object, but they did not fire when the grasp was pantomimed (i.e., the object was absent). The authors concluded that it is not movement kinematics, but rather goal information, that drives mirror neurons' response during action observation. This evidence has been replicated in humans by mean of transcranial magnetic stimulation (TMS) technique (Villiger et al., 2011).

Both studies lacked a fine-grained kinematics quantification of the hand. Therefore, conclusions on mirror neurons' activity might be questioned. Indeed, at least from a behavioural point of view, converging evidence revealed that humans are able to use movement kinematics to predict the outcome or the goal of an observed movement in the absence of any other contextual cues (Abernethy & Zawi, 2007; Abernethy et al., 2008; Aglioti et al., 2008; Stapel et al., 2012; Ansuini et al., 2015; Cavallo et al., 2016). In addition, Kraskov and colleagues (Kraskov et al., 2009), reported that in the same brain region reported by Umiltà and colleagues, mirror neurons fired - to a lesser extent than real grasps - when monkeys observed pantomimed grasps. This evidence has been replicated in humans by using functional magnetic resonance imaging (fMRI) (Turella et al., 2012). Finally, in the past studies, goal information and movement kinematics always matched in the observed action stimuli, leading to confounding effects.

In summary, the lack of knowledge regarding the relative contribution of movement kinematics and goal information to action perception highlights the need of a systematic investigation on pantomimed grasp, in terms of execution, perception and neural activation during action observation.

4. Aims of the research

The aims of the present research are to:

a. investigate *how* real and pantomimed grasps are executed and to inspect *whether* and *when* they differ in terms of their kinematics profile over time;
b. inspect if real and pantomimed kinematics retain *enough information* to allow action discrimination;

c. understand *whether* and *when* real and pantomimed grasps can be correctly recognized, and investigate *which factors* modulate pantomimed grasp observation;
d. explore the *neural underpinnings* of *action observation* by exploiting real and pantomimed grasp perception.

Considering the lack of kinematics quantification in action observation studies, the current research pursued a methodological approach divided in two phases:

1. *Action execution phase*: where kinematics features of movement are measured and quantified during real and pantomimed grasp execution (Chapter 1).
2. *Action observation phase*: where, using video clips of the same movements performed in the execution phase, action understanding abilities (Chapter 2) and neural underpinnings of action observation (Chapter 3) are probed.

This approach will reinforce our knowledge about the relationship between movement kinematics and object properties and has the power to shed new light on the quantity and the quality of information available in the kinematics of a reach-to-grasp movement over time. This might have important implications for our understanding of the action-perception coupling mechanism.

CHAPTER 1

REAL AND PANTOMIMED GRASPS EXECUTION

Experiment 1: Are we real when we fake?

Attunement to object weight in natural and pantomimed grasping movements.

Published paper (Ansuini et al., 2016)

1. Introduction

The double nature of pantomimed grasp – both instrumental and communicative at the same time - is reflected in the differential use that real and pantomimed grasps make of object knowledge. In real grasps, knowledge about objects and their manipulation is used to conform the hand gradually to the properties of the object to be grasped. For example, when grasping a glass, scaling of grip width to the width of the glass is achieved by first opening the hand in proportion to, but wider than the visually perceived width of the glass, and then closing it around the glass, ensuring a safety margin for grasping the object securely (Smeets & Brenner, 1999).

In contrast, in pantomimed grasps, knowledge about objects is converted into actions that *demonstrate* the perceptual distinctive features of the pretended objects (Goldenberg et al., 2007). This conversion necessitates the selection of some features of the actual grasp, while permitting one to neglect others, i.e., those features that adapt the hand to the material object. Thus, when pantomiming, for instance, participants do not show grip 'overshoot', but open the hand to the approximate width of the pretended object 'to depict' its width (Goodale et al., 1994). One particular difficulty of pantomimed grasp tasks relates, therefore, to the transformation of object features into a non-routine movement sequence that *demonstrates the perceptual features of the pretended object* (Goldenberg et al., 2003).

Although previous research indicates that pantomimed grasp incorporates spatial features of a pretended target, such as its actual (Goodale et al., 1994; Cavina-Pratesi et al. 2011) or visually perceived size (Westwood et al., 2000), it is questionable whether pantomimed grasp can also demonstrate non-spatial features of the target. Specification of object size requires selecting a simple spatial characteristic of the object (e.g., the width of the object) and converting it into a spatial relationship between a limited set of discrete body parts (e.g., the distance between thumb and index). Arguably, depicting a non-spatial characteristic of the object, such as its weight or fragility, might be more complicated as no simple perceptual matching is possible for transforming the representation of the weight or the fragility of an object into a distinctive grasping pattern.

Here we set out to examine the representational reach of pantomime by asking whether pantomimed grasping can transmit information about the weight of a pretended object.

1.1 Influence of object weight on action planning and control

Object weight has been shown to influence visuo-motor planning and control of real grasps (Brouwer et al., 2006; Eastough & Edwards, 2007). For example, Eastough and Edwards (2007) observed that heavy compared to light objects caused greater peak grip aperture and the opposing placement of the index finger and thumb. This effect of weight on grasping kinematics has been proposed to directly reflect the requirements for a stable grasp (Smeets & Brenner, 1999). When grasping heavy objects, to reduce the chances of object rotation and slippage, fingers should be positioned accurately enough so that the grip position passes through the centre of mass of the object to be grasped. It is perhaps not surprising, therefore, that weight influences pre-contact kinematics of real grasp movements.

In contrast to real grasps, however, pantomimed grasps entail no preparation for a stable final grip placement on the object. After all, the pretended target is *weightless* and there is no risk of slippage or rotation. The influence of object weight on pantomimed grasps, if any, would thus reflect the pure effort to *depict* the weight of the imagined object by translating a non-spatial property of the object into distinctive features of a motor act.

To determine whether (and to what extent) kinematics of a pantomimed grasp can reveal the weight of the pretended target, in the present study, we first recorded the kinematics of real grasping and pantomimed grasping movements towards differently weighted objects. Using linear discriminant analysis, we then proceeded to classify the weight of the target – either real or pretended – on the basis of the recorded movement patterns. This innovative approach combining kinematics with classification methods allowed us to obtain a measure of weight-related information transmitted by the hand movements over time.

2. Methods

2.1. Participants

Fifteen participants took part in the study. They had a mean age of 26.8 years (SD: 2.2; range: 24-32 years old; 5 males) and were all right handed, with normal or corrected-to-normal vision, and with no history of either psychiatric or neurological disorders. The experimental procedures were approved by the local ethical committee (ASL 3 Genovese) and were carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Association, 2013). Each participant provided written informed consent and was paid in return for participation.

2.2. Apparatus and procedures

Participants were seated on a height-adjustable chair with the right elbow and wrist resting on a table, the forearm pronated, the arm oriented in the parasagittal plane passing through the shoulder, and the right hand in a semi-pronated position, with the tips of the thumb and index finger placed, in gentle opposition, on a tape-marked point. This posture as well as the angular orientation of the wrist were controlled so as to guarantee the consistency of the start position across participants. The working space was set on the surface of a table (wide = 140 cm; length = 70 cm; see Figure 1A) covered with a black cloth. A glass (height = 11 cm; diameter = 8 cm) was presented on each trial. Depending on the condition, the glass could be empty (i.e., light object; weight = 139 g; see Figure 1B) or filled with iron screws (i.e., heavy object; weight = 838 g; see Figure 1B).

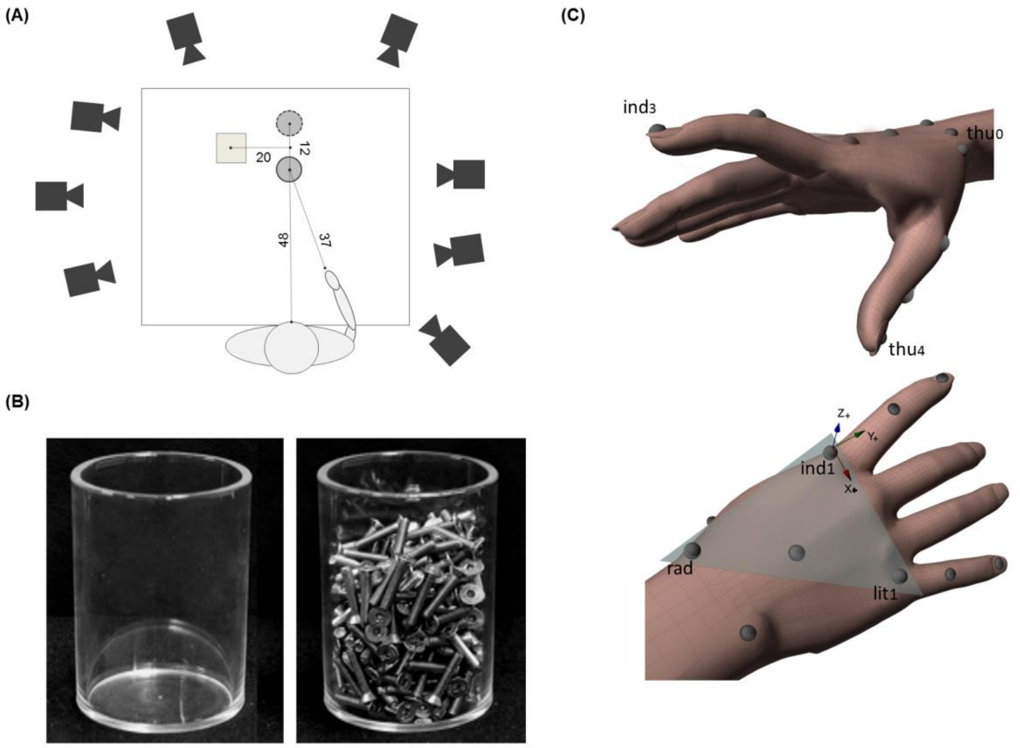


Figure 1. *Experimental set-up and hand models for kinematics parameters computation.* **(A)** A schematic representation of the top view of the experimental set-up (not to scale). The position of the object in real grasp task and in pantomimed grasp task is indicated with a filled and a dashed line circle, respectively. Distances are provided in centimetres. **(B)** A picture of light and heavy object used as target objects. **(C)** The hand model used to compute kinematics parameters together with a graphical representation of the local frame of reference (*Flocal*). *Flocal* had its origin in the marker placed at the metacarpo-phalangeal joint of the index (see *ind1*). Vectors (*ind1 - lit1*) and (*ind1 - rad*) defined the metacarpal plane of the hand (shaded triangle). In this frame of reference, the x-axis had the direction of the vector (*ind1 - lit1;* refer to the red arrow) and pointed ulnarly, the z-axis was normal to the metacarpal-phalangeal plane, pointing dorsally (refer to the blue arrow), while the y-axis was calculated as the cross-product of z- and x-axes, pointing distally (refer to the green arrow).

In the ‘real grasp’ task, participants were requested to reach towards, grasp, pick up either the empty or filled glass, and place it on a platform (height = 7 cm; width = 9 cm; length = 9 cm), located to the left of the target; see Figure 1A). The glass was positioned at a distance of about 48 cm from the participant’s body midline with which it was aligned. The angle between the sagittal plane passing through the object and the hand start position was equal to about 35° (see Figure 1A).

In the ‘pantomimed grasp’ task, the glass, either empty or filled, was positioned at a displaced location (see Figure 1A; dashed line circle). Participants were instructed to imagine that an identical glass was positioned at the target position and were asked to pretend to perform the very same action sequence towards the imagined glass (for a similar paradigm, see Goodale et al., 1994)).

In both real and pantomimed grasp tasks, participants started the reach-to-grasp movement after a verbal signal from the experimenter. They were instructed to return to the start position and resume hand posture once they were finished placing the glass (or the pretended glass) over the platform. Then, the experimenter returned the glass (if any) to the target position. To ensure that the position of the target object did not vary from trial to trial, for both tasks the glass was placed in between two short pegs that were fixed at the table, the distance between the centre of the glass in the real and the pantomimed grasp task being equal to 12 cm (see Figure 1A).

In each experimental session, a total of 96 trials were administered in 8 separate blocks of 12 trials, i.e., two for each type of movement by object weight combination. Blocks were presented in a fixed order. For each object weight, participants performed the real grasp task followed by the pantomimed grasp task. This was done to allow actual experience with object weight and to prevent spurious weight crossover effects when transitioning from the real grasp to the pantomimed grasp task. The order of presentation of object weight was counterbalanced across participants. On average, the time between trials was 15 s and that between the blocks was 90 s.

At the beginning of each block, the position of the glass (either target or displaced) signalled participants the type of action to be performed (real vs. pantomimed grasp, respectively). Before the experimental session, participants completed 12 practice trials (in 4 blocks of 3 trials for each object weight and type of action combination). Block order within the practice session was the same as that adopted during the experimental session. A 2-minute pause was allowed between the practice and experimental session. The entire experiment lasted about 60 minutes.

2.3. Movement recordings and kinematics parameters

To track the kinematics of the hand, we used a near-infrared camera motion capture system (frame rate: 100 Hz; Vicon System). Eight cameras were placed at a distance of 1.5 – 2 m from the table on which the object was placed. Each participant was outfitted with 13 light-weight retro-reflective hemispheric markers (4 mm in diameter) to create a hand model for kinematics analysis. Markers were placed on the dorsal aspect of the hand and the radial and the ulnar aspect of the wrist. Additional markers were placed at the tip, the metacarpo-phalangeal joint, the phalangeal-phalangeal joint of thumb, the index finger and the little finger, and on the trapezium bone of the thumb (Figure 1C).

After data collection, each trial was individually inspected for correct marker identification and then run through a low-pass Butterworth filter with a 6 Hz cutoff. We used a custom software (Matlab; MathWorks, Natick, MA) to obtain the following kinematics parameters:

a. *grip aperture,* defined as the distance between the marker placed on thumb tip and that placed on the tip of the index finger (mm) (see Figure 1C);
b. *wrist velocity,* defined as the module of the velocity of the wrist marker (mm/sec; see *rad* in Figure 1C);
c. *wrist height*, defined as the z-component of the wrist marker (mm).

All these variables were expressed with respect to the original frame of reference (i.e., the frame of reference of the motion capture system, termed as global frame of reference; *Fglobal*). In addition, the trajectory of the index and thumb finger were computed within a local frame of reference centred on the hand (i.e., *Flocal*; see (Carpinella et al., 2006; Carpinella et al., 2011; Ansuini et al., 2015) for a similar method). *Flocal* had its origin in the marker placed at the metacarpo-phalangeal joint of the index finger (see *ind1* in Figure 1C). Vectors (*ind1 - lit1*) and (*ind1 - rad*) defined the metacarpal plane of the hand (refer to the shaded triangle in Figure 1C). In this frame of reference, the x-axis had the direction of the vector (*ind1 - lit1*) and pointed ulnarly, the z-axis was normal to the metacarpal plane, pointing dorsally, while the y-axis was calculated as the cross-product of z- and x-axes, pointing distally (see Figure 1C). Within this *Flocal,* we computed the following parameters:

c. *x-, y-, and z-thumb,* defined as x-, y- and z-coordinates for the marker placed on the tip of the thumb (mm);
d. *x-, y-, and z-index,* defined as x-, y- and z-coordinates for the marker placed on the tip of the index finger (mm);

All these kinematics variables were expressed with respect to normalized (%) rather than absolute (ms) movement durations. To this aim, we first computed time of *reach onset* (i.e., the first time point at which the wrist velocity crossed a 20 mm/sec threshold and remained above it for longer than 100 ms) and time of *reach offset* (i.e., the time at which the wrist velocity dropped below a 20 mm/sec threshold) to calculate movement duration (i.e., the time interval between *reach onset* and *offset*;). In line with previous evidence (Goodale et al., 1994; Cavina-Pratesi et al. 2011b), analyses revealed that pantomimed movement were longer than real movements (average ± SE: 944 ± 55 vs. 889 ± 42 ms; $p < .05$). Moreover, heavy compared to light target elicited longer movement durations (average ± SE: 946 ± 52 ms vs. 887 ± 44; $p < .05$). Of interest, the effect of weight was identical in both real and pantomimed grasps (average ± SE: 910 ± 51 vs. 978 ± 59 ms and 864 ± 39 vs. 914 ± 47 ms for light vs. heavy object in pantomimed and real movements, respectively; $p > .05$ for 'Weight' by 'Condition' interaction). After normalizing the duration of each grasping movement, the data were resampled at intervals of 0.1 of the normalized reaching duration (resulting in decile increments of normalized reach duration).

To control for outliers, we z-transformed normalized data for each condition. Data points with *z-scores* less than -2.5 or greater than 2.5 were classified as statistical outliers and removed. Missing and outlier values (<1.5%) were then replaced using Matlab File Exchange submission inpaint_nans. This procedure interpolates and extrapolates based on sparse linear algebra and Partial Differential Equations (PDE) discretization. A default method was used to solve approximations to PDEs using least squares approach in case of interpolation, while a linear behaviour was applied for extrapolation (for a similar procedure, see Ansuini et al., 2015).

2.4. Statistical analyses

2.4.1. Principal Component Analysis of kinematic parameters

To perform dimensionality reduction while retaining the maximum variation present in the original dataset and handling data collinearity (Næs & Mevik, 2001), we performed a Principal Component Analysis (*PCA*) on the set of 90 variables, comprising the 9 spatial features (i.e., *grip aperture*, *wrist velocity*, *wrist height*, *x-*, *y-*, *z-thumb*, and *x-*, *y-*, *z-index*) across the 10 equally spaced temporal steps of the normalized reaching duration, for 1380 movements (60 over 1440 trials were discarded due to problems related to data recording). Principal Components (PCs) were extracted from a dataset where participants' data were pooled together rather than separated, thus applying the rule of thumb of higher observations per observed variable ratios in order to get more stable estimates (Leonard, 2010). Furthermore, Bartlett's test of sphericity and Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy were used to test for factorability (Bartlett, 1950; Kaiser, 1974). Both tests indicated that the sample was adequate for *PCA* (Bartlett's test: χ^2 = 410925,33; d.f. = 4005; $P < .001$ and KMO = .828).

Mathematically, PCA consists of an orthogonal transformation which converts a set of p variables $X = x_1, x_2,.... x_p$ (in our case, the kinematics variables in a time normalized domain sampled at each 10% from 10% up to 100% of the movement duration) into p new uncorrelated PCs, $Z = z_1, z_2,.... z_p$. The PCs obtained are mutually uncorrelated in the sample and are arranged in decreasing order of their explained sample variances. The PC model is $Z = U^tX$, where the columns of $U = u_1, u_2,.... u_p$ are the loading vectors, that is, the eigenvectors of the correlation matrix and X is the 1380 by 90 matrix with observations/trials arranged in row and observed features over time arranged in column. To simplify data interpretation, we applied a varimax rotation to Principal Component axes to maximize the sum of the variances of the squared coefficients within each eigenvector (Kaiser, 1958). Kaiser's eigenvalue larger-than-one rule was applied to determine the number of significant components (Kaiser, 1960). The *PCA* led to the selection of the first 13 PCs as significant based on the selection of eigenvalues above 1. To obtain the lower dimension matrix based on the significant PCs, we generated component scores. Component scores are transformed variable values based on the constituent variables and their relative importance for a particular PC.

Mathematically, let i=1…, N index the rows (observations) and j=1,…, M index the columns (variables), then component score for a principal component k for observation row i, ($Z_{k,i}$) can be represented as:

$$Z_{k,i} = u_{i1}*X_{i1} + u_{i2}*X_{i2} + \ldots\ldots u_{iM}*X_{iM}$$

The component scores, thus, are a linear combination of the optimally-weighted observed variables (Harman, 1976). This allowed us to obtain a lower dimension data set of component scores for all the PCs, with as many rows as original observations (i.e., 1380) and as many columns as the number of significant *PCs* (i.e., 13 *PCs*).

2.4.2. Analysis of PCA data using Linear Discriminant Analysis

To determine the extent to which *PCA* data supported discrimination between the different movement categories, we submitted the output of the *PCA* to a linear discriminant analysis (LDA) (see Calder, Burton, Miller, & Young, 2001) for a similar procedure). Discriminant functions maximize the ratio of the between group variance (**B**) to the within group variance (**W**), in our instance, the groups being each of the four types of movements (i.e., real grasp_light object, real grasp_heavy object, pantomimed grasp_light object, pantomimed grasp_heavy object). The discriminant functions y_i are computed from the eigenvectors l_i of the ratio $\mathbf{W}^{-1}\mathbf{B}$ of the between group covariance matrix (**B**) to the within group covariance matrix (**W**):

$$y_i = l_i\, v$$

where v is the thirteen-dimensional vector of component scores. The relative size of each eigenvalue (l_i) indicates the relative importance of each of the discriminant functions; rank-ordered according to the size of l_i. The standardized canonical discriminant function coefficients that can be obtained from the eigenvectors express the contribution of each dependent variable to the different discriminant function (Field, 2013). Canonical R^2 (obtained by squaring canonical correlation for each discriminant function) was used as a variance-accounted measure for effect size (Field, 2013).

In *LDA*, the knowledge of the data class labels is used to find a low-dimensional representation that preserves the class differences, so that a classifier can be designed in the feature domain (Nenadic, 2007).

For each of the four groups, we determined the location of the point representing the mean for all variables in the multivariate space defined by the variables in the model (i.e., centroids) and then computed the Mahalanobis distances (of the respective case) from each of the group centroids. Therefore, each case was classified as belonging to the group to which it was closest (i.e., where the Mahalanobis distance was smallest). A leave-one-out cross-validation method was applied to evaluate the performance of the *LDA* model (Efron, 1982). In each round of this procedure, one case is held out from the dataset and assigned as a test for the classifier developed by using the remaining cases assigned as training set. This process is repeated until all the withheld cases in the dataset are validated and allows us to calculate the overall diagnostic accuracy of the *LDA* model. To investigate whether allocation distributions differed between expected (i.e., prior probabilities) and observed distributions (i.e., actual group membership), we applied *Chi-squared* test. Finally, to test whether classification scores significantly exceeded chance level, we randomly permuted the class labels and recomputed classification performance and a 95% confidence interval (Good, 2005; Tritchler, 1984) (as implemented by an in-house R package) (R Core Team; 2015). All analyses (except permutation testing) were performed using SPSS statistical software (version 21.0).

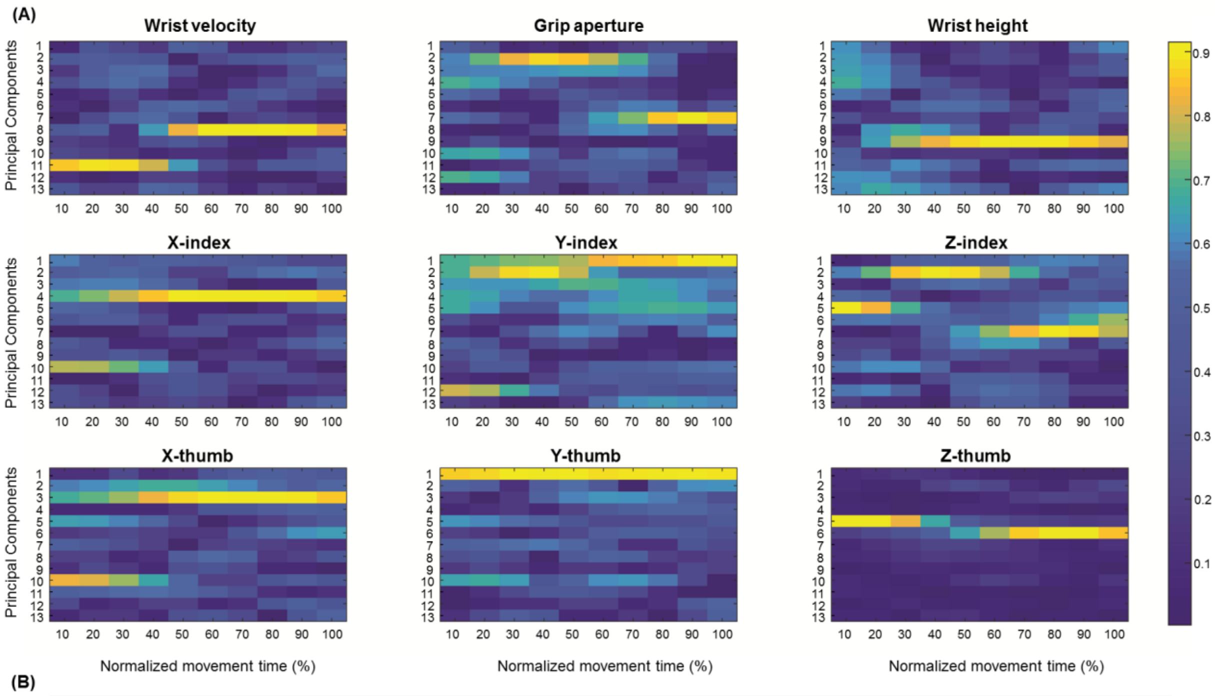
3. Results

3.1. Extracting Principal Components

Thirteen *PCs* having eigenvalues above 1.00 accounted for 92% of the variance and all had communalities (i.e., amount of variances each component has in common with the set of all components; Field, 2013) greater than 0.70 (Dunteman, 1989; Stevens, 1996). It is a general rule to interpret variables with larger factor loadings as representative of the component (Hair et al., 1998). Here we followed this rule and consider factor loadings greater than 0.8 to load significantly on the component. Moreover, if the same variable loaded significantly onto more than one component, we considered the highest factor loading for interpreting the variable contribution on the corresponding component. A graphical representation (heat map) of all factor loadings (i.e., the factor loadings across all trials from all participants) for each variable is reported in Figure 2.

As can be seen, for the first seven PCs, high loadings (>0.8) were found only for grip aperture and finger coordinates, suggesting that these PCs were related mainly to the distal aspect of the movement. In particular, the main contribution to PC1 originated from y-thumb (from 10% to 100% of normalized reaching duration) and y-index (from 60% to 100% of reaching duration). Grip aperture between 20% and 60% of movement duration, z-index between 30% and 60% of movement duration, and y-index between 20% and 50% of movement duration loaded significantly on PC2, while x-thumb from 30% up to 100% of movement duration contributed significantly to PC3. For PC4, PC5, and PC6, higher factor loadings were found for x-index between 30% and 100%, z-thumb, and z-index finger at the beginning of the movement (i.e., from 10% up to 40%), and for z-thumb from 50% up to 100% (Figure 2). Grip aperture between 70%

and 100%, and z-index within the same temporal interval loaded significantly on PC7. In contrast, kinematics parameters related to more proximal aspects of the movement were found to load significantly onto PC8, PC9 and PC11 (see Figure 2). In particular, wrist velocity from 10% up to 40% and from 50% up to the end of the movement contributed to PC11 and PC8, respectively, and wrist height from 30% up to the end of the movement loaded on PC9. Finally, an inspection of the factor loadings of *PC10* and *PC12*, revealed large loadings of x-thumb and x-index at 10% and 20% of movement duration on PC10, grip aperture and y-index finger at 10% on PC12, and wrist height at 20% on *PC13*, suggesting that these components were associated mainly with the earliest phases of the movement.



(B)

PCs	PC1		PC2			PC3	PC4	PC5		PC6	PC7		PC8	PC9	PC10		PC11	PC12		PC13
Kinematics Variables	Y-thumb	Y-index	Grip aperture	Z-index	Y-index	X-thumb	X-index	Z-thumb	Z-index	Z-thumb	Grip aperture	Z-index	Wrist velocity	Wrist height	X-thumb	X-index	Wrist velocity	Grip aperture	Y-index finger	Wrist height
Time window (%)	10 - 100	60 - 100	20 - 60	30 - 60	20 - 50	30 - 100	30 - 100	10 - 40		50 - 100	70 - 100		50 - 100	30 - 100	10	20	10 - 40	10		20

Figure 2. *Factor Loadings for significant Principal Components.* **(A)** Graphical representation of factor loadings across all trials from all participants (heat maps) for the 13 Principal Components (PCs) for each kinematics variable (i.e., wrist velocity, grip aperture, wrist weight, x-, y-, and z-coordinate for both index finger and thumb) over normalized reaching duration (from 10% up to 100% in ten step of 10%). Note that factor loadings greater than 0.8 are considered to load significantly on the component. **(B)** A table summarizing the kinematic parameters encoded by each of the 13 Principal Components (PCs), together with the time window in which they are mainly involved.

3.2. Identifying the discriminant functions for different movement categories

The LDA revealed that the first function accounted for 92.2% of the discriminating ability of the discriminating factors (eigenvalue equal to 2.085; canonical R^2 = 0.68), the second function for 7.1% (eigenvalue equal to .162; canonical R^2 = 0.14), and the third function for the remaining 0.7% (eigenvalue equal to .016; canonical R^2 = 0.02). As indicated by the *chi-square tests* performed on Wilk's lambda values (λ value = .275; for 1st to 3th function, 2nd to 3th function, and 3th function, respectively), the combination of the three functions provided a significant discriminative power ($p < .05$). A similar result was also found when considering the combination of the second and the third function as well as the contribution of the third function alone (λ value = .847; and .984; $p_s < .05$). Figure 3A represents the canonical discriminant function scores for each observation, grouped according to the experimental condition to which that observation belonged. This graph, together with the values of the centroids, provides an intuitive visualization of how each function discriminates groups (Field, 2013). As apparent from this figure (refer to x-axis), the first discriminant function mainly separated real and pantomimed grasping movements. The examination of the canonical discriminant function coefficients suggests that this function was most dependent on *PC7*, *PC5*, and *PC9* (refer to Table 1).

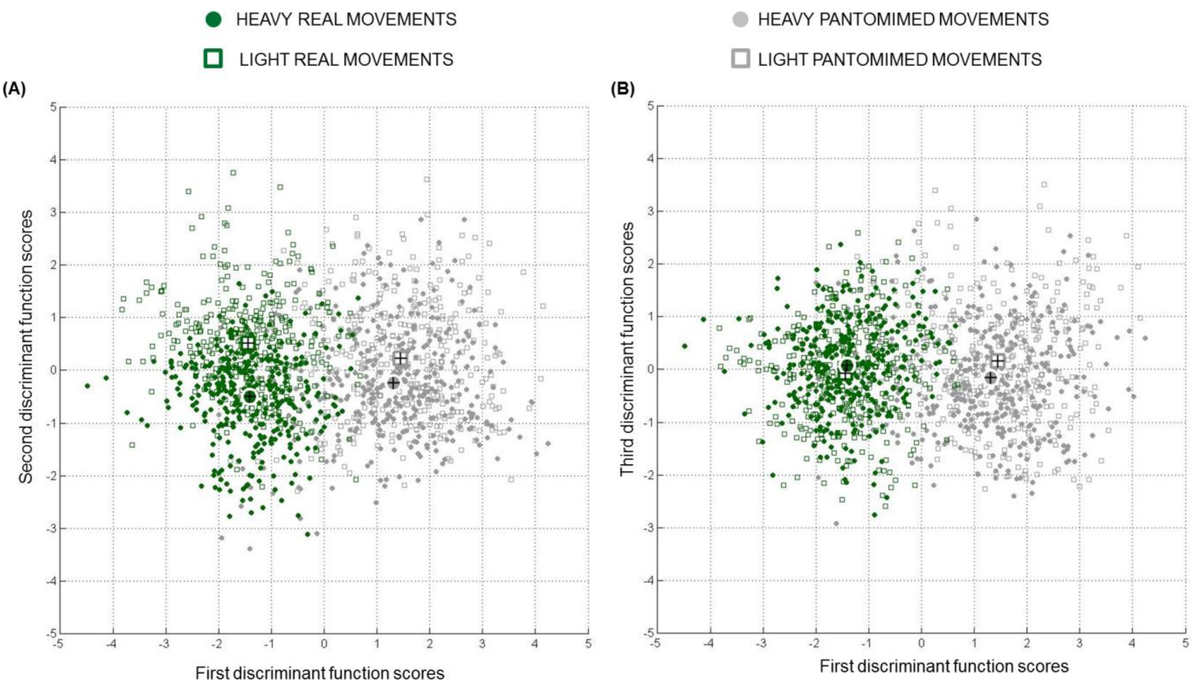


Figure 3. *Combined-group plots for centroids and canonical discriminant function scores*. Group centroids (bigger circles and squares) and individual scores (smaller circles and squares) for **(A)** the first vs. second discriminative functions, and **(B)** the first vs. third discriminative functions are represented. The x-axis shows that the first function separated real vs. pantomimed grasps, whereas the y-axis shows that the second and the third functions separated the movements towards heavy and light object. Note that cases near a centroid are predicted as belonging to that group. Data for all participants in the sample are presented.

Table 1. Canonical discriminant function coefficients for the three discriminant functions together with information related to the original kinematics variables that contributed the most to each Principal Component (PC).

Original Features Contributing to Principal Component (PC)	*PC number*	*1st Function*	*2nd Function*	*3th Function*
Y-thumb (from 10% up to 100%) and y-index (from 60% up to 100%)	***PC1***	-,479	-,240	**,889**
Grip aperture (from 20% to 60%), z-index (from 30% to 60%), and y-index (from 20% to 50%)	***PC2***	3,878	**,279**	-,763
X-thumb (from 30% up to 100%)	***PC3***	-1,067	**,878**	-,478
X-index (from 30% to 100%)	***PC4***	-1,726	-,692	**1,177**
Z-thumb and z-index finger (from 10% up to 40%)	***PC5***	**1,561**	-,988	-,785
Z-thumb (from 50% up to 100%)	***PC6***	1,735	**2,094**	1,251
Grip aperture and z-index (from 70% to 100%)	***PC7***	**-3,594**	1,077	-1,011
Wrist velocity (from 50% up to100%)	***PC8***	4,062	1,557	**,544**
Wrist height (from 30% up to 100%)	***PC9***	**,325**	,260	,301
X-thumb (at 10%) and x-index (at 20%)	***PC10***	3,740	**,452**	-,714
Wrist velocity (from 10% up to 40%)	***PC11***	,220	**,342**	2,247
Grip aperture and y-index finger (at 10%)	***PC12***	,736	1,480	-1,746
Wrist height (at 20%)	***PC13***	,140	-,668	**1,481**

Note. Values in bold refer to dependent variables for which a significant canonical function correlation coefficient was found. Dependent variables with high canonical function correlations are usually interpreted as contributing the most to group separation (Bargman, 1970).

As evident from table in Figure 2 and Figure 3, the z-coordinate for index and thumb posture, wrist height, and grip aperture contributed at the most to PC7, PC5, and PC9 so that these kinematics parameters were relatively more important than others for classifying the *reality* of the movement. It is worth noticing, however, that it is difficult to determine which kinematics behaviour a PC is coding by simply inspecting the visual representation of its loadings. To complement this visual inspection of kinematics parameters across conditions over time, comparisons of interest were further explored by means of post hoc tests (with Bonferroni's correction). As shown in Figure 4A, for what concerns the first discriminant function, grip aperture was greater for real than for pantomimed grasping movement between 80% and 100% of normalized reaching duration (*PC7*). Moreover, the index finger was less extended in the palmar direction (i.e., z-index) in real than in the pantomimed movements from 70% up to 90% of normalized reaching duration (*PC7*) (Figure 4B). From 70% up to 90% of the reach-to-grasp movement, the wrist was higher when the movement was pantomimed rather than when it was real (*PC9*) (Figure 4C). Finally, during the first part of the reaching movement (i.e., from 10% up to 40% of normalized reaching duration), the thumb extended more dorsally (i.e., z-thumb) when the movement was real than when it was pantomimed (*PC5*) (Figure 4D).

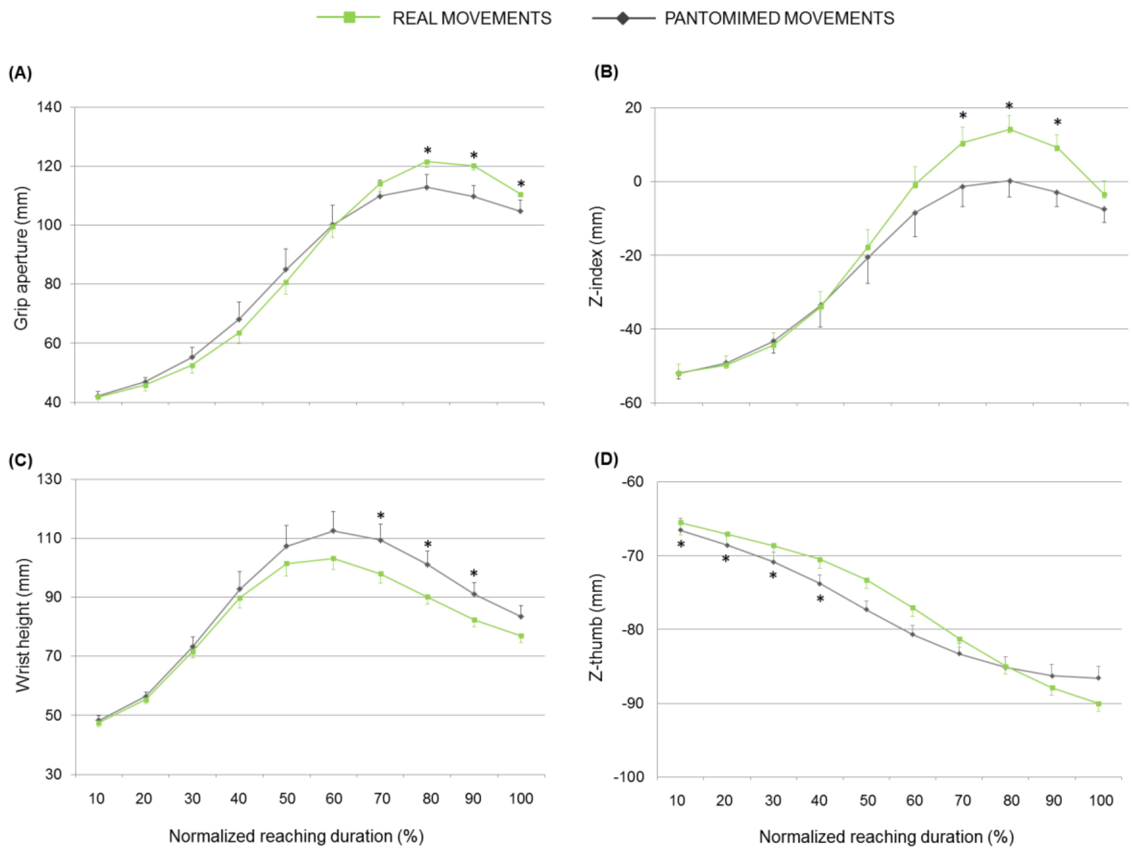


Figure 4. *Hand kinematics of real and pantomimed grasping movements.* **(A)** Grip aperture, **(B)** z-index finger, **(C)** wrist height, and **(D)** z-thumb over time for real (green lines) and pantomimed (grey lines) grasping movements. Data are averaged across trials and participants. Bars represent standard error of the mean. Asterisks refer to statistical significance ($p < 0.05$).

As illustrated in Figure 3A, the second discriminant function was more related to weight, supporting separation between real grasp movements performed towards heavy and light objects and, to a less extent, separation between pantomimed movements towards pretended heavy and light targets (refer to y-axis in Figure 3A). The *PC6*, *PC3*, *PC10*, *PC11*, and *PC2* correlated significantly with this second function (refer to Table 1 for canonical discriminant function coefficients). Examining the kinematics parameters coded by these components (see Figure 2) revealed that, for both real and pantomimed movements, the thumb extended more dorsally (z-thumb*; PC6*) during the second phase of the movement when the target was heavy than when it was light (see Panel A in Figures 5 and 6, respectively). Moreover, at about half of the reach-to-grasp movement, the grip aperture was smaller when the target was light than when it was heavy (*PC2*; see Figures 5B and 6B). Other variables only expressed weight-related differences for real grasps. For example, wrist velocity between 10% and 40% of normalized reaching duration was greater for the heavy than for the light object for real but not for pantomimed movements (*PC11*; refer to Figure 5C). Similarly, for real grasps but not for pantomimed grasps, the index finger was less extended in palmar direction and pointed more distally (z-index and y-index; *PC2)*, and the thumb pointed more radially (x-thumb*; PC3*), for the heavy object than for the light object Figures 5D-F and Figure 6D-F, respectively). Finally, since the x-coordinate of index finger (*PC10*) did not express significant weight-related differences in either pantomimed or real movements ($p_s > .05$), no clear interpretation for corresponding component was possible.

For what concerns the third discriminative function, the inspection of Figure 3B suggests that this function separated cases based on the weight of the target object. Interestingly, the inspection of centroids suggests that the separation along this function was more pronounced for pantomimed grasps than for real grasps (‘real grasp’ = -.070 and -.078 for light object and heavy object, respectively and ‘pantomimed grasp’ = .154 and -.167 for light object and heavy object, respectively; see Figure 3B). This function, however, accounted for only a marginal portion of 0.7% of the total variance. Caution is therefore needed when interpreting the kinematics parameters coded by the correlated *PCs* (*PC12, PC4, PC13, PC1*, and *PC8;* refer to Table 1 for canonical discriminant function coefficients).

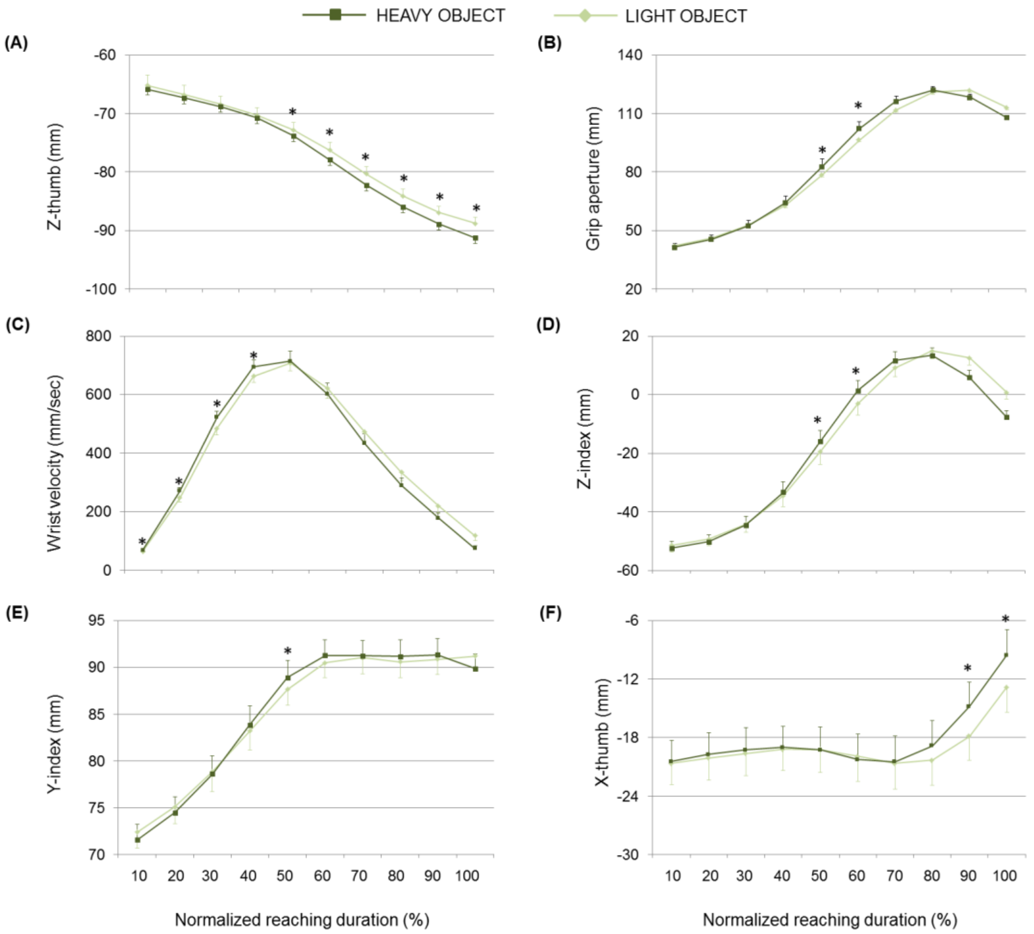


Figure 5. *Hand kinematics of real grasping movements towards light and heavy objects.* **(A)** z-thumb, **(B)** grip aperture, **(C)** wrist velocity, **(D)** z- and **(E)** y-index, finger **(F)** x-thumb over time for movements towards heavy and light object (dark and light green lines, respectively). Data are averaged across trials and participants. Bars represent standard error of the mean. Asterisks refer to statistical significance ($p < 0.05$).

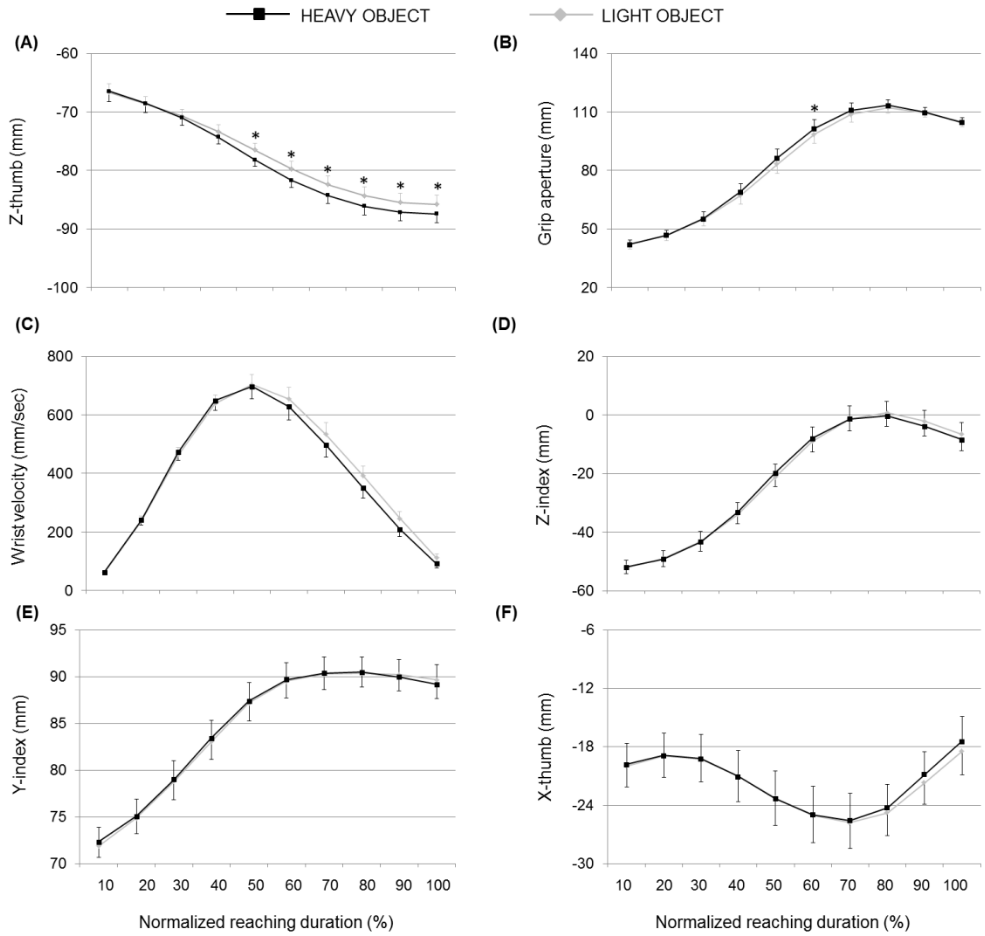


Figure 6. *Hand kinematics of pantomimed grasping movements towards pretended light and heavy objects.* **(A)** z-thumb, **(B)** grip aperture, **(C)** wrist velocity, **(D)** z- and **(E)** y-index, finger **(F)** x-thumb over time for movements towards heavy and light object (black and light grey lines, respectively). Data are averaged across trials and participants. Bars represent standard error of the mean. Asterisks refer to statistical significance ($p < 0.05$).

3.3. Classification of object weight

Table 2A reports the confusion matrix for the linear discriminant analysis (LDA) model from the set of *PCA* data. As can be seen, in each of the four categories, reach-to-grasp movements were classified with above chance accuracy ($\chi^2_{(9)}$ = 1.207,8; P <.05 with an *a priori* probability equal to 25%). In particular, for real grasps, movements towards light and heavy objects were correctly classified on 68% and 67% of cases, respectively, whereas for pantomimed grasps, correct classification of movements towards pretended light and heavy objects occurred in 53% and 49% of cases, respectively.

However, since the probability of light vs. heavy classification interacts with the probability of real vs. pantomimed classification, these results might overstate the effect of object weight. In order to adopt a more conservative approach to quantify the impact of weight, we therefore proceeded to perform two separate

LDAs for real and pantomimed grasps. Table 2B reports the confusion matrices for these analyses. Although the overall proportion of correct classification suffered, classification of object weight was still significantly above chance level for both real and pantomimed grasps. To further support this conclusion, we also performed permutation tests to assess whether correct classification scores were significantly above chance level. By randomly permuting the class labels and re-computing classification performance, we confirmed that the classification scores were indeed significant [(p_s<0.001), 95% Confidence Intervals: All four movements (0%,27%); Light/Heavy for real movements (0%,54%); Light/Heavy for pantomimed movements (0%,53%) (Good, 2005; Tritchler, 1984)].

Table 2. Confusion matrix from linear discriminant analyses for **(A)** the four movement type by object weight categories and **(B)** the two object weight categories for real and pantomimed movements separately, applied to the sets of PCA data (i.e., 13 Principal Components). Note that the grey diagonal highlights cross-validated grouped cases correctly classified. Actual number of observations is shown in parentheses.

(A)		*Real*		*Pantomimed*		*Total*
		Light	*Heavy*	*Light*	*Heavy*	
Real	Light	68% (231)	27% (91)	3% (9)	2% (6)	100% (337)
	Heavy	29% (99)	67% (231)	2% (6)	2% (7)	100% (343)
Pantomimed	Light	5% (19)	5% (17)	53% (188)	37% (130)	100% (354)
	Heavy	4% (15)	10% (36)	37% (127)	49% (168)	100% (346)

(B)		*Real*		*Pantomimed*		*Total*
		Light	*Heavy*	*Light*	*Heavy*	
Real	Light	74% (249)	26% (88)			100% (337)
	Heavy	26% (90)	74% (253)			100% (343)
Pantomimed	Light			60% (212)	40% (142)	100% (354)
	Heavy			42% (145)	58% (201)	100% (346)

4. Discussion

Previous research on the relationship between reach-to-grasp movement and the properties of the to-be-grasped object indicates that object weight influences pre-contact kinematics in preparation for a stable final grip placement on the object (Weir et al., 1991; Brouwer et al., 2006; Eastough & Edwards, 2007). Heavy compared to light objects cause increased peak grip aperture, a final finger and thumb placement on the object that more closely passes through the centre of mass of the object, and a reduced peak lift velocity (Eastough & Edwards, 2007). Our results confirm and extend these findings by showing that early on in the movement, hand kinematics of real grasps is already scaled to the weight of the to-be-grasped object. As shown in Figure 5, the thumb extended more dorsally when the target was heavy than when it was light. Moreover, early on in the reach, grip aperture was larger and wrist velocity was higher for heavy than for light objects. As shown by LDA, prior-to-contact kinematics conveyed indeed enough information to discriminate between real grasp movements aimed at heavy and light objects.

Remarkably, when we examined pantomimed grasp, we found that classification accuracy for heavy vs. light object was lower, but still significantly above the chance level. As for real grasp movements, in the last part of the reach-to-grasp movement, the thumb extended more dorsally (z-thumb) when the pretended target was heavy than when it was light. Other kinematics parameters sensitive to object weight for real grasp movements, however, showed no similar weight-attunement for pantomimed grasp. For example, whereas the thumb pointed more ulnarly and the index finger pointed more radially for real grasps aimed at a heavy object, no similar modulation was observed for pantomimed movements. In the following, we examine in some details three factors that may have contributed to the differential modulatory effect of weight on real and pantomimed grasps.

A first factor to consider is the removal of the physical object *per se*. During real grasps, the mechanical properties of the object (such as its weight) are critical for motor control. During pantomime, in contrast, the participant’s hand does not come into contact with a material object, but only with ‘thin air’. Without actual interaction between the hand and the target, there are no obvious consequences for an inaccurate grasping (e.g., the slippage or the roll of the object), permitting one to neglect motor programs that adapt the hand to the material object. This could explain the reduced attunement to weight for pantomimed in comparison to real grasps.

A second factor – causally related to first – refers to the specific role of haptic-based information in sensorimotor transformations supporting prehensile actions. Interestingly, whereas haptic feedback is *per se* not sufficient to evoke motor programs for correct tool use (Goldenberg et al., 2004), there is evidence that removing haptic feedback shifts the response mode from a real one towards a pantomimed one. Even when the movements are directed towards a visible virtual target (viewed in a mirror), removing haptic feedback has been shown to influence grasp kinematics such that grasps without haptic feedback are statistically indistinguishable from pantomimed grasps (Whitwell et al., 2015). The fundamental role of haptic feedback in hand tuning is further supported by evidence from DF, a patient who suffered from visual form agnosia (Schenk, 2012). By using a mirror-apparatus to dissociate the image of an object from its physical presence, it was shown that, without haptic feedback, DF's grasping performance was not better than her (poor) performance in the manual estimation task (i.e., matching the distance between the thumb and the index finger to the size of the object). Crucially, when intermittent haptic feedback was provided, DF's performance improved (Schenk, 2012). On this account, the patterning of pantomimed grasp would thus reflect the absence of haptic-based object information.

Removal of the physical object or, more specifically, absence of tactile feedback, however, may be not enough to explain the differential features of pantomimed grasps. Pantomime neglects features of the object that are important for manipulation but have little value for discriminating the object, whereas it specifies features that in actual use are determined by the manipulated object.

A third factor to consider relates thus to the deliberate process of demonstrating the properties of the pretended target (Goldenberg et al., 2003). We speculate that the kinematics of pantomimed actions may retain information about the symbolic motor representation of the pretended weight (Goldenberg et al., 2003; Laimgruber et al., 2005). However, we wish to emphasize that these considerations are of a very speculative nature because participants in our study were not explicitly instructed to communicate the weight of the object. An interesting prediction for future studies is that explicitly instructing participants to communicate object weight to another person should increase weight discriminability for pantomimed grasp.

Related to this, it will be interesting to investigate to what extent observers watching a pantomimed grasp are able to infer the properties of the pretended object. Some behavioural studies already indicate that the weight of an object (e.g., a box) can be inferred quite accurately when observing another person lifting it (Bingham et al., 1987; Runeson & Frykholm, 1983; Hamilton et al., 2004). Moreover, there is evidence that muscle-specific M1 excitability modulates to the force requirements of observed object lifting (i.e., M1 excitability is considerably higher when observing heavy object lifting compared to light object lifting) and that this modulation is sensitive to the kinematics conveyed by the observed action (Alaerts et al., 2010). To our knowledge, however, no previous study has investigated whether observers are able to read out the weight of a to-be-grasped object from pre-contact kinematics. Moreover, there is no information in the literature regarding observers' ability to infer object weight from pantomimed grasps. The classification results in our study lend some plausibility to this hypothesis by showing that pre-contact kinematics provide a firm informational basis for weight discrimination for real grasps and – albeit to a lesser extent – for pantomimed grasp. In future research, we plan to test whether and to what extent observers are able to make use of this information to discriminate weight and other non-spatial object properties (such as object fragility). Future research should also focus on the extent to which real and pantomimed grasps convey a categorical representation of weight information (i.e., an object is either heavy or light) versus a continuous representation of weight (i.e., changes in activity patterns that directly correspond to changes in object weight) and on the exact time course of weight specification (i.e., how weight information is specified at specific time intervals).

Finally, it will be important to consider these results from the perspective of the neural mechanism involved in extracting object weight when pantomiming a reach-to-grasp movement. Consistent with the proposed division of labour in the visual pathways of the primate cerebral cortex, between a dorsal pathway specialized for action control and a ventral stream dedicated to the perception of the visual world (Milner & Goodale, 1998), processing object features critical for motor control, such as object weight, has been traditionally thought to be in the purview of the dorsal pathway. Recent functional neuroimaging (fMRI) evidence, however, suggests that, in addition to traditional motor-related areas, the lateral occipital cortex (LOC) in the ventral visual stream represents object weight when preparing to lift an object (Gallivan et al., 2014). Expanding upon this result, it is tempting to speculate that the LOC representation of object weight may inform and support weight-related pantomime. Functional neuroimaging studies and patient studies may help to clarify the differential contribution of the ventral and the dorsal pathways to object weight processing in preparation of real and pantomimed grasps.

Additional analysis: Are we real when we fake?

Kinematic characterization of real and pantomimed grasps over time.

1. Introduction

As explained in the General Introduction, the aims of the present research are to investigate *how* real and pantomimed grasps are executed and to inspect *whether* and *when* real and pantomimed grasps are different in terms of their kinematics over time.

Previous studies have shown that pantomimed kinematics differ distinctively from real kinematics (Goodale et al., 1994; Cavina-Pratesi et al. 2011). For instance, pantomimed grasps consistently reach lower peak velocities, tend to last longer, follow more curvilinear trajectories and undershot target position, compared to real grasps. Moreover, the maximum grip aperture of pantomimed grasps is smaller with respect to grip aperture of real grasps. Kinematic landmarks like peaks (and their times of occurrence) provide an instantaneous snapshot of movement kinematics at discrete points in time. Despite their usefulness in characterizing some aspects of the reach-to-grasp behavior, they do not allow the shape of kinematic profiles that are functions of time to be compared (Ansuini et al. 2015).

Thus, to investigate how real and pantomimed grasp kinematics varies over time, a within-subject multivariate analysis of variance (MANOVA) was performed on the kinematic variables of movements collected in Experiment 1 (for a similar method, see Ansuini et al. 2015; 2016). In order to avoid confounding effects due to weight modulation, only movements toward the heavy object – being real or pantomimed – were selected (645 out of 1380 movements).

2. Methods

Data from one agent (i.e., a participant of the Experiment 1) were discarded due to technical problems. A within-subject MANOVA was run on the set of 180 dependent variables, comprising the 9 spatial features (i.e., *grip aperture*, *wrist velocity*, *wrist height*, *x*-, *y*-, *z-thumb*, and *x*-, *y*-, *z-index*) across the 10 equally spaced temporal steps of the normalized reaching duration of real and pantomimed movements. All dependent variables were averaged across movements (real, pantomimed) for each agent. The input matrix had 14 rows (i.e., 14 agents) and 180 columns (i.e., 90 dependent variables for real movements and 90 dependent variables for pantomimed movements). Significant differences between '*grasp type*' (2 levels; real vs. pantomimed) and '*time bin*' (10 levels; from 10% to 100%, in 10% steps) were analyzed. The MANOVA was followed by separate ANOVAs on each dependent variables. Main effects were used to explore the means of interest (post-hoc t-test), and Bonferroni's corrections (α level<0.05) were applied. All analyses were performed using SPSS statistical software (version 21.0).

3. Results

MANOVA results revealed a significant main effect of both 'grasp type' [$F_{(9,5)}$ = 7.378; *p* = .20; ges = .930] and 'time bin' [$F_{(81,1053)}$ = 4.943; *p* = 2.09e-35; ges = .275]. Moreover, MANOVA results showed a significant '*grasp type*' by '*time bin*' interaction [$F_{(81,1053)}$ = 3.663; *p* = 2.61e-22; ges = .220]. For the purpose of the analysis, only the exploration of the '*grasp type*' by '*time bin*' interaction is reported here.

Separate ANOVAs revealed a significant '*grasp type*' by '*time bin*' interaction for the following dependent variables: Wrist velocity [$F_{(1,13)}$ = 14.730; p = .002; ges = .531], Grip Aperture [$F_{(1,13)}$ = 16.042; p = .001; ges = .552], x-index [$F_{(1,13)}$ = 11.880; p = .001; ges = .589], z-index [$F_{(1,13)}$ = 16.149; p = .001; ges = .554], x-thumb [$F_{(1,13)}$ = 13.614; p = .003; ges = .512] and z-thumb [$F_{(1,13)}$ = 16.068; p = .001; ges = .553]. Conversely, the following dependent variables did not reach significance: Wrist height [$F_{(1,13)}$ = 4.229; p = .059; ges = .248]; y-index [$F_{(1,13)}$ = 2.419; p = .144; ges = .157]; and y-thumb [$F_{(1,13)}$ = 1.291; p = .276; ges = .090].

Post hoc comparisons using Bonferroni's correction revealed that Wrist Velocity was higher during real compared to pantomimed movements from 10% up to 40% of normalized reaching duration, (*ps* ranging from .006 to .037, Figure 7). In contrast, Wrist Velocity was higher during pantomimed than for real movements from 70% to 80% of the normalized reaching duration (*ps* = .011, Figure 7). Grip Aperture was greater during real compared to pantomimed movements from 80% to 90% of normalized reaching duration (*ps* ranging from .003 to .001). The index finger was wider (x-index) during real compared to pantomimed movements from 60% to 80% of the normalized reaching duration, and at the end of the action (*ps* ranging from.006 to .021). The index finger was extended more dorsally (z-index) during real compared to pantomimed movements from 60% to 90% of the normalized reaching duration (*ps* ranging from .000 to .017). The thumb was significantly wider (x-thumb) during real compared to pantomimed movements from 40% to the end of the action (*ps* ranging from .002 to .023). The thumb was extended more dorsally (z-thumb) during real compared to pantomimed movements from 20% to 60% of the normalized reaching duration. In contrast, it was more extended in the palmar direction during real compared to pantomimed movements from 90% to the end of the action (ps ranging from .000 to .041, Figure 7).

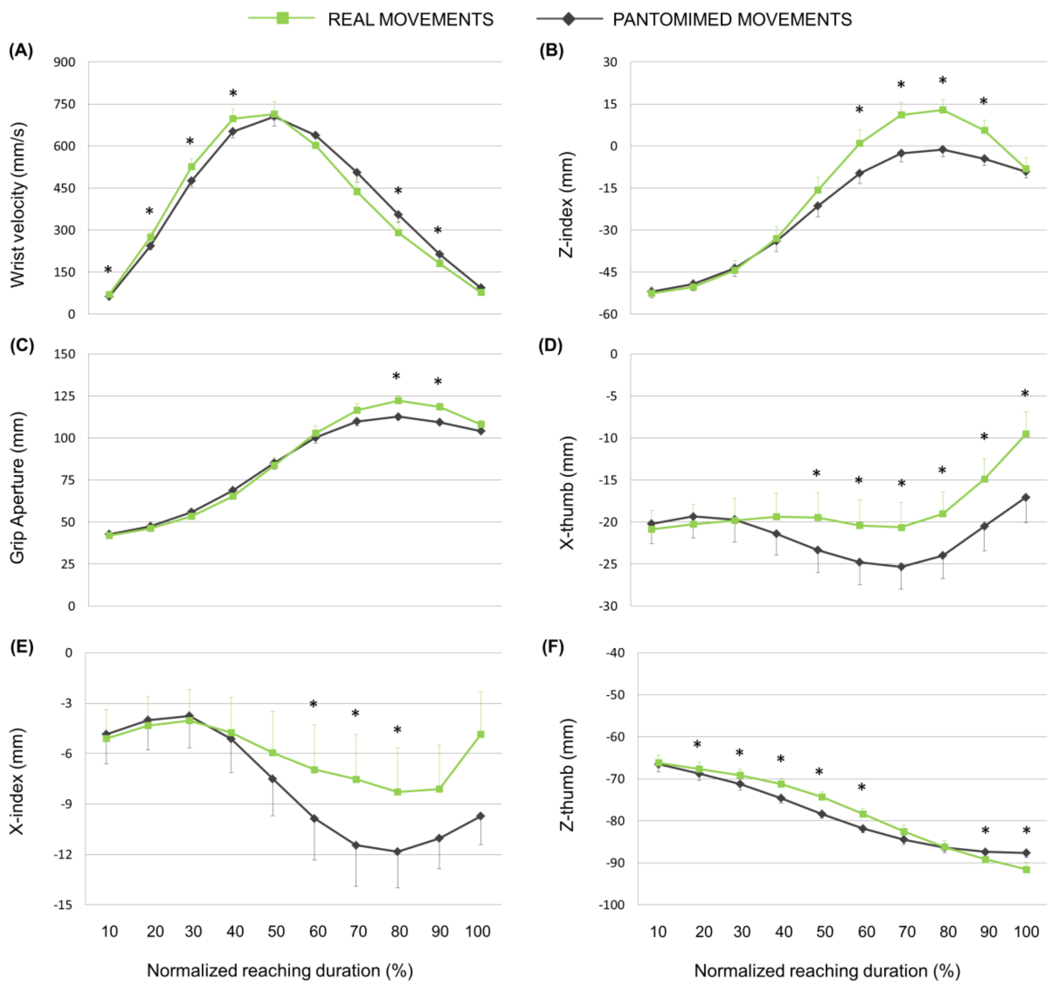


Figure 7. *Hand kinematics of real and pantomimed grasping movements toward the heavy object.* **(A)** wrist velocity, **(B)** z-index finger, **(C)** grip aperture, **(D)** x- thumb, **(E)** x- index finger and **(F)** z- thumb over time for real and pantomimed movements (green and grey lines, respectively). Data are averaged across trials and participants. Bars represent standard error of the mean. Asterisks refer to statistical significance ($p < 0.05$).

4. Discussion

This analysis evidenced that real and pantomimed grasps are differently executed: specifically, they expressed kinematic differences over time. Early on in the movement, real grasps were faster than pantomimed grasps (from 10% up to 40% of normalized reaching duration). An opposite velocity profile has been found within later phases of movements (from 80% up to 90% of normalized reaching duration). Furthermore, the grip aperture was larger for real compared to pantomimed grasps within 80% and 90% of normalized reaching duration, meanwhile the thumb and the index finger were differently displaced in the vertical and the horizontal plane over time.

All in all, these evidence confirm and extend previous knowledge on real and pantomimed grasp execution (Goodale et al., 1994; Cavina-Pratesi et al. 2011) by giving a characterization of their kinematics expressed over time. During real grasp, hand typically opens gradually to the maximum grip aperture scaled to object size (i.e., *preshaping*), to show a subsequent progressive closure around the object. In addition, real grasp velocity usually reflects a bell shape: it increases quickly until a peak, and then decreases to zero at hand-object contact. Hand preshaping and velocity profile are interpreted as motor control strategies to provide hands with a safety-margin to grab the object (Holmes et al., 2013; Rinsma et al., 2017). As described in the General Introduction, the absence of a similar preshaping and the different velocity found during pantomimed grasp execution (compared to real grasps) is interpreted as results of a deprivation of visual and/or haptic feedback provided by the to-be-grasped object (Holmes et al., 2013; Whitwell et al., 2015). However, they might as well be interpreted as a way to communicate something about the object or the action (Goldenberg, 2017).

Regarding these considerations, kinematics information expressed over time may be useful not only to understand the mechanisms subtending execution, but also to investigate human action understanding abilities (Ansuini et al., 2015). In fact, it has been demonstrated that movement execution and movement observation recruit the same set of brain regions (i.e., mirror neurons; Mukamel et al., 2010). The precise timing of this recruitement and its relation to the timing of observed movement kinematics, however, are poorly understood (Ansuini et al., 2015).

Thus, our findings provide the possibility to link movement kinematics and action discrimination performance at specific temporal intervals of the observed movement. This investigation will shed new lights on the action-perception coupling.

CHAPTER 2

THE COUPLING BETWEEN ACTION AND PERCEPTION

Action and perception: Machine learning classification and stimuli selection for action observation experiments.

1. Introduction

In recent years, psychological (Brass et al., 2001; Hommel et al., 2001), neurophysiological (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010) and computational (Wolpert & Kawato, 1998; Wolpert & Ghahramani, 2000) accounts have suggested that action and perception are intrinsically coupled in the human brain. Empirical evidence demonstrated that movement execution and movement observation recruit the same set of brain regions in primate and in human brain (di Pellegrino et al., 1992; Mukamel et al., 2010). Thus, empirical investigation of human perception can not be disentangled by human action research.

As explained in the General Introduction, the aims of the present work are to understand *whether* and *when* real and pantomimed grasps can be correctly recognized by looking at movement kinematics and to investigate *which factors* can modulate pantomimed grasp observation. To pursue this, the same movements of Experiment 1 (refer to the selected movements of Chapter 1 – Additional Analysis) were showed to different groups of participants in a series of action observation studies.

However, before running the observation studies, we inspected whether real and pantomimed kinematics retained *enough information* to allow action discrimination. In other terms, we computed a kinematic quantification of *grasp type information* within the selected movements. All kinematic variables that observers might have exploited to discriminate between grasp types (real, pantomimed) were submitted to a machine learning technique, the Linear Discriminant Analysis (LDA). LDA tested the accuracy performance of movement kinematic variables, used as predictors, in a grasp type classification task (for a similar method, see Koul et al. 2016; Podda et al. 2017; Becchio et al. 2017).

In addition, for each movement, LDA computed the Mahalanobis distance (i.e., the distance of each movement from the mean variate score of each grasp type). This distance was used as a rank to select the *most representative* movements (i.e., the closest movements to their own centroids) for each class (real, pantomimed). Video clips corresponding to the selected movements were displayed as experimental stimuli within the following observation studies (for a similar method, see Koul et al. 2016; Podda et al. 2017; Becchio et al. 2017).

2. Methods

Data from one agent (i.e., a participant of the Experiment 1) were discarded due to technical problems. To note, only real and pantomimed grasps toward the heavy object were exploited (645 out of 1380 movements, see Additional Analysis 1 in Chapter 1).

The set of 90 variables, comprising the 9 spatial features (i.e., *grip aperture*, *wrist velocity*, *wrist height*, *x-*, *y-*, *z-thumb*, and *x-*, *y-*, *z-index*) across the 10 equally spaced temporal steps of the normalized reaching duration, and *movement duration* of 645 movements were submitted as predictors to a linear discriminant analysis (LDA) (see Calder et al. 2001 for a similar procedure).

In LDA, the knowledge of the data class labels is used to find a low-dimensional representation that preserves the class (in this case, the *grasp type*) differences, so that a classifier can be designed in the feature domain (Nenadic, 2007).

For each class (real, pantomimed), LDA determined the location of the point representing the mean for all variables in the multivariate space defined by the variables in the model (i.e., centroids) and then computed the Mahalanobis distances (of the respective case) from each group centroids. Therefore, each case was classified as belonging to the group to which it was closest (i.e., where the Mahalanobis distance was smallest).

A leave-one-trial-out cross-validation method was applied to evaluate the performance of the LDA model (Efron, 1982). In each round of this procedure, one case is held out from the dataset and assigned as a test for the classifier developed by using the remaining cases assigned as training set. This process is repeated until all the withheld cases in the dataset are validated and allows us to calculate the overall diagnostic accuracy of the LDA model. To investigate whether allocation distributions differed between expected (i.e., prior probabilities) and observed distributions (i.e., actual group membership), we applied *Chi-squared* test. All analyses were performed using SPSS statistical software (version 21.0).

2. Results

The resulting discriminant function accounted for 100% of the total variance (Eigen value = 2.583; canonical R^2 = 0.84) and significantly classified movements in real and pantomimed grasps (λ value = 0.27, $\chi^2(43)$ = 793.1, p < 0.001; for a graphical representation of function scores, see Figure 8). Classification analysis using a leave-one-trial-out cross validation (Efron, 1982) revealed an above chance level classification (93.3% of accuracy with an *a priori* probability of 50%, Table 3).

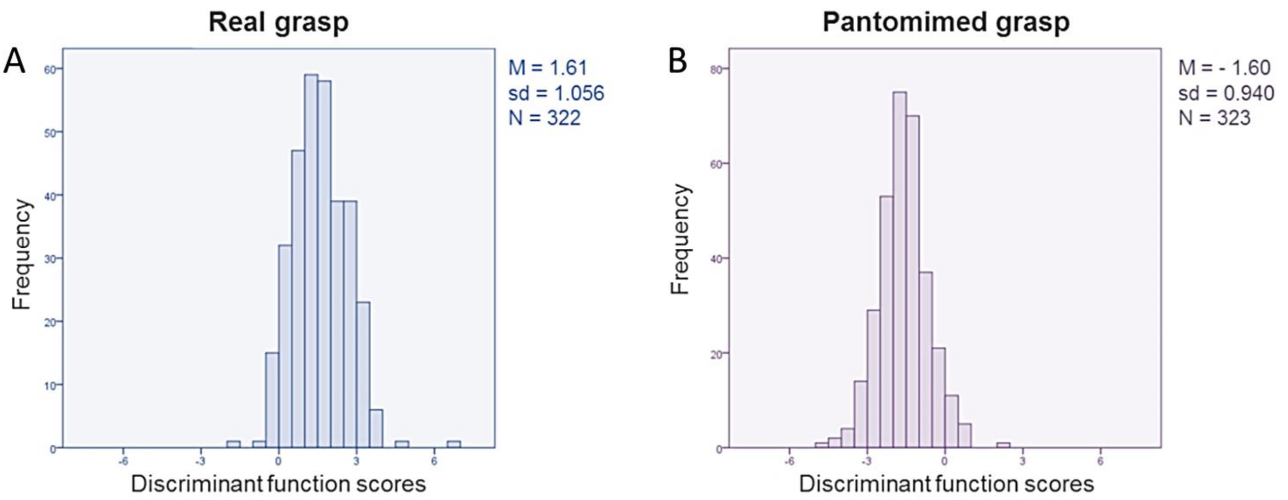


Figure 8. *Frequency distributions of discriminant function scores for* **(A)** *real and* **(B)** *pantomimed grasps.*

Table 3. Confusion matrix from linear discriminant analyses for the two groups (real, pantomimed) Note that the grey diagonal highlights cross-validated grouped cases correctly classified. Actual number of observations is shown in parentheses.

CLASSIFICATION RESULTS

		Predicted group membership		
		Real	*Pantomimed*	*Total*
Original	*Real*	**92.9 % (299)**	**7.1 % (23)**	100 % (322)
	Pantomimed	**6.2 % (20)**	**93.8 % (303)**	100 % (323)

4. Discussion

The current analysis demonstrated that kinematics information of real and pantomimed grasps has enough predictive power to allow action discrimination. Indeed, classification analysis using kinematic parameters of movements as predictors outperformed chance level (93.3% of accuracy). The fact that kinematics conveys grasp type information for action discrimination, however, is not to say that it can be perceptually appreciated by human observers (Ansuini et al. 2014). For this reason, Experiment 2 was conducted to explore observers' ability in action understanding. The same movements video-recordered in Experiment 1 were used as stimuli and participants were explicitly required to infer *whether* they were facing a real or a pantomimed grasp by only looking at hand movement. The presence/absence of the object was spatially occluded so that observers could only rely on movement information to provide an answer. By using a temporal occlusion technique, we investigated *when* (i.e., at which temporal interval of movement) explicit identification of grasp type occurred (for a graphical representation of the different levels of temporal occlusion, see Figure 9) (for a similar paradigm, see Ansuini et al. 2016; Podda et al. 2017).

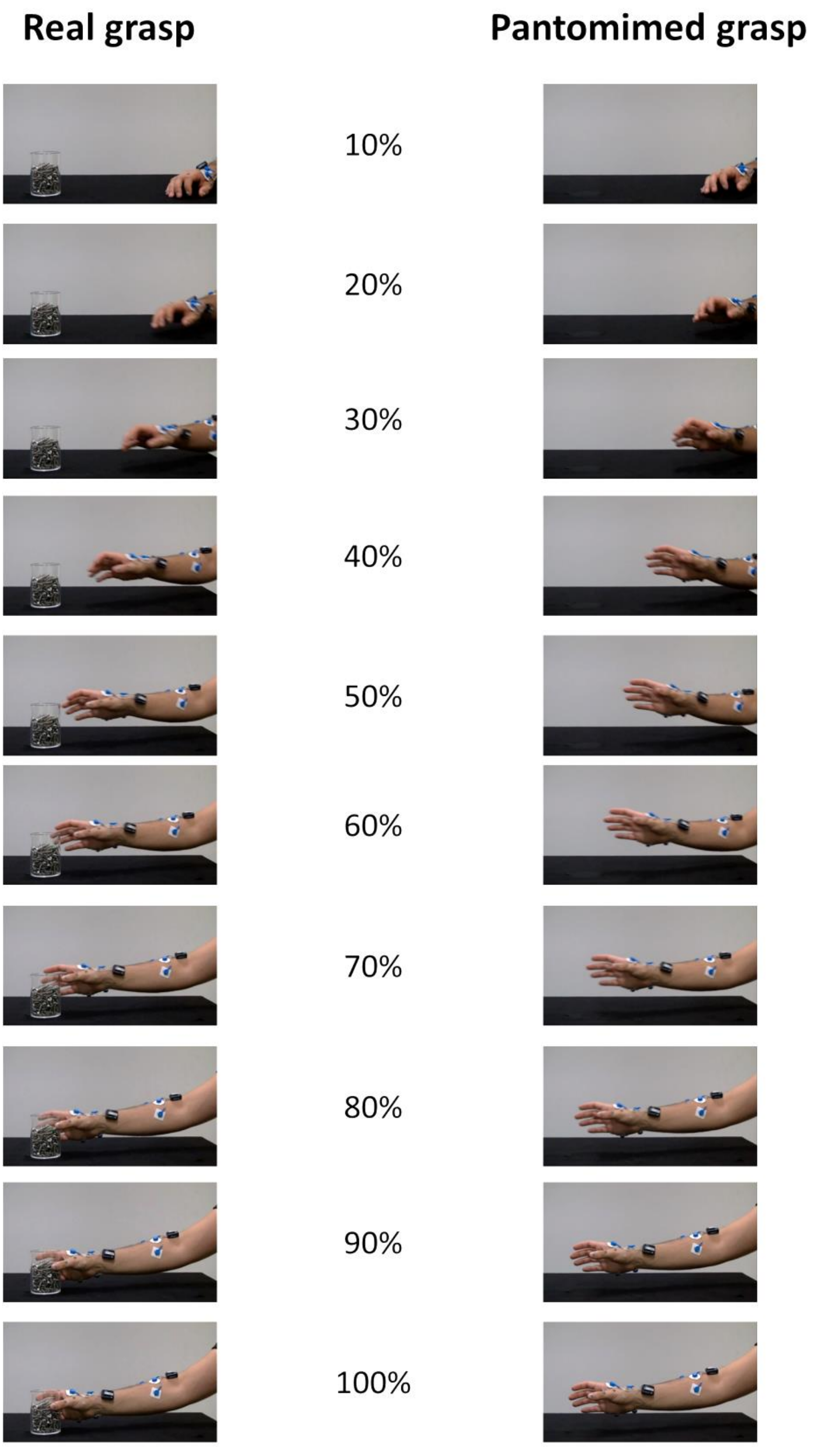


Figure 9. *Frames from two video clip examples (real, pantomimed) displaying different levels of temporal occlusion (from 10% up to 100% of normalized reaching duration, in steps of 10%).*

Experiment 2: When do we recognize fake actions?

Investigation of action discrimination abilities over time.

1. Introduction

The behavior of others supplies a rich source of information about the world around us. The ability to process this information is crucial to infer about the properties of objects acted upon, as well as to read others' intentions and expectations (Ansuini et al. 2014; Becchio et al. 2017). In real life, our actions and those of others are often partly obscured from view. Yet, even when the final part of the action is hidden, observers are able to predict the goal (i.e., object) of a grasp only by looking at hand movement (Ambrosini et al., 2011; Ansuini et al., 2016). Imagine being in front of a person picking up something off the ground. Fast discrimination of the action goal would be extremely useful for understanding others' action and reacting consequently (Ansuini et al., 2016). This reaction will have different results if you quickly understand that the person is merely pretending (i.e., pantomiming) to grasp something that is not there or if he is actually grasping something.

There is evidence that the kinematics of real and pantomimed grasps diverge during the reaching phase of the action (see Chapter 1 - Additional Analysis; Goodale et al., 1994; Cavina-Pratesi et al. 2011). This raises the possibility that, even before the final phase of a reach-to-grasp movement, observers can take advantage of kinematic information to understand if they are facing a real or a pantomimed grasp. In this study, we examined whether advance information obtained from the observation of different phases of a reach-to-grasp movement can be exploited to discriminate real and pantomimed actions. Participants viewed reach-to-grasp movements toward an occluded object position. The object behind the mask was physically present during real grasp and absent during pantomimed grasp. Participants were asked to make predictive grasp type judgments from the observation of reach-to-grasp movements. To determine the timing of advance information pickup (i.e., how rapidly observers were able to predict the grasp type) we manipulated information availability by presenting reach-to-grasp movements under different levels of temporal occlusion (for a similar method, see Abernethy et al., 2008; Ansuini et al., 2016)

Separate analyses for each level were conducted to determine the participants' ability to predict the grasp type. Therefore, we were able to investigate *whether* and *when* observers were able to discriminate between real and pantomimed grasps.

2. Methods

2.1. Participants

Twenty right-handed participants (10 women, mean ± SD = 25.05 ± 3.3 years old; age range = 19-29 years old) took part in Experiment 2. We based our sample size on previously published studies testing action perception (Stapel et al., 2012; Cavallo et al., 2016; Podda et al., 2017). All participants were right-handed, had normal or corrected-to-normal vision and no history of either psychiatric or neurological disorders. They were naïve to the purpose of the experiment, gave their written informed consent and received financial compensation in return of participation. The experimental procedures were approved by local ethical committee (ASL 3 Genovese) and were carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Association, 2013).

2.2. Stimuli selection

The observed stimuli were video clips of reach-to-grasp movements collected in Experiment 1 (see Chapter 1 – Additional Analysis). Within the space defined via the LDA, the 20 movements that minimized the Mahalanobis distance for each grasp type were selected. This way, we identified a final set of 40 representative movements (50% real).

2.3. Video editing

All the 80 video clips corresponding to the selected movements were edited using Adobe Premiere Pro CS6 (.avi format, disabled audio, 25 frames/s) and modified using Adobe After Effect CC 2016 (Adobe Systems Software Ltd, Dublin, Ireland). Each video clip was edited so as to begin at reach onset and to end immediately after reach offset. To prevent participants from viewing whether the object was present or not, a grey rectangular mask (height = 1080, width = 744 pixels) was superimposed onto the object position. The size and the position of this mask were kept constant across trials and participants.

2.4. Procedure

The experiment was run in a quiet, dimly illuminated, and well-ventilated room. Participants seated on a comfortable chair in front of a computer (1920x1080 pixels, refresh rate = 50 Hz). Participants observed the video clips containing the selected movements that could end at different levels of temporal occlusion (from 10% up to 80% of the normalized reaching duration). To prevent anticipation and to ensure that participants could temporally attend to movement sequences, +4 (160 ms), +8 (320 ms), or +12 (480 ms) static frames were randomly added at the beginning of all the video clips. Participants were asked to judge as accurately and as quickly as possible whether the observed movement was real or pantomimed, and indicate their response by pressing with the right index or the middle finger one of two keys (left or right arrow) on a keyboard. Responses and keys were counterbalanced between participants. Participants were instructed to respond after the video, within a maximum of 3000 ms. After indicating a response, they were requested to rate the confidence of their decision on a 4-point scale by pressing a key (from 1 = least confident, to 4 = most confident; see Figure 10). Participants were encouraged to use the entire confidence scale.

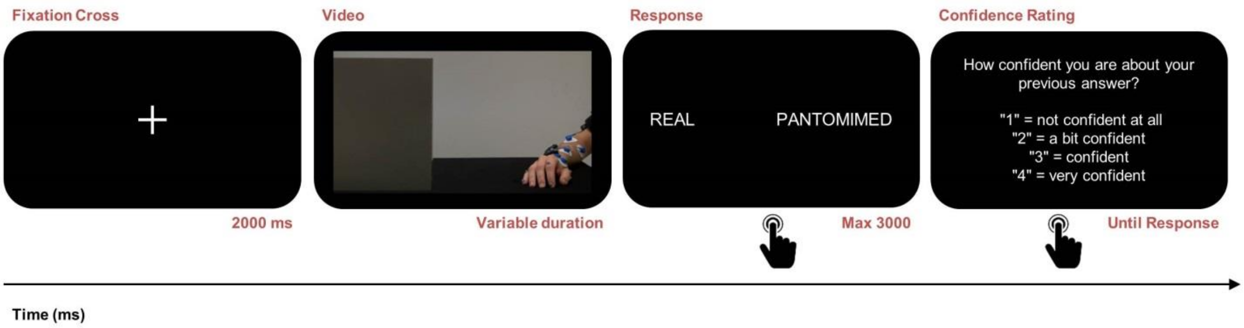


Figure 10. *Trial procedure.* Each trial started with a white Fixation Cross lasting 2000 ms. The end of the video clip was followed by a Response Slide, on which participants had to respond. Then, the Confidence Rating appeared, and lasted until the response.

Participants completed 8 blocks of 80 trials (50% real movements), for a total of 640 trials. There was a 5-minutes break between each block. Video clips were pseudo-randomized over the blocks so that within each block any movement occurred only once at one level of temporal occlusion. At the beginning of an experimental session, participants were presented with eight movement samples (i.e., two for each movement type repeated twice) without spatial occlusion, so that they could see the entire phase during which the agent grasped - or pantomimed to grasp - the glass. Participants also completed a practice session of 16 trials (50% real, all levels of temporal occlusion were showed once for grasp type) to familiarize themselves with the task. Stimuli presentation, timing, and randomization procedures were controlled using E-prime version 2.0.10.242 (Psychology Software Tools, Inc., Sharpsburg, PA, USA). Each experimental session lasted about 120 minutes.

2.5. Dependent measures and analyses

Participants' correct responses whose Response Times (RTs) deviated by more than ± 2.5 SD were treated as outliers. Outliers and no-response trials (less than 2.5% of all the trials) were removed from further analyses. Signal Detection Theory (SDT) was used to analyze action judgments' parameters. For each level of temporal occlusion (from 10% up to 80%), real grasps were arbitrarily designated as 'signal' and pantomimed grasps were designated as 'noise'. The proportion of hits and false alarms was calculated for each participant, and combined with confidence ratings to determine points on an empirical receiver operating characteristic (ROC) curve. The ROC curve plots the hit rate as a function of the false alarm rate at different degrees of confidence. Because each response (real, pantomimed) had four ratings associated with it, there were eight possible responses for each trial (graded from the most confident real action to the most confident pantomimed action), resulting in seven points on the ROC curve. The area under the curve (AUC) equals the proportion of times participants would correctly identify the target, if the target and non-target were presented simultaneously. The AUC can be any value between 0 and 1. A diagonal curve, which coincides with an AUC of 0.50, corresponds to a situation where the number of hits and false alarms are equal, showing a chance level classification score. On the contrary, an AUC of 1.00, which corresponds to a ROC curve on the left upper bound of the diagonal, indicates a perfect positive prediction with no false positives. Importantly, unlike average accuracy, AUC is a measure of sensitivity unaffected by response bias, robust to imbalanced problems and independent of the statistical distribution of the classes (for a similar approach, see Azzopardi & Cowey 1997; Tamietto et al. 2014; Stock et al. 2014). The AUCs were estimated for each participant. To investigate action discrimination abilities, above chance significance across participants was computed, separately for each level of temporal occlusion, by means of one-sample t-tests. Alpha level of significance was set to 0.05 and False Discovery Rate was used for multiple comparisons correction (Benjamini & Hochberg, 1995). All analyses were performed using SPSS statistical software (version 21.0).

3. Results

Table 4 summarizes the separate single t-tests results of AUC mean values computed at each level of temporal occlusion. Results showed that participants' performance was above chance level consistently in time from the 20% up to 80% of normalized reaching duration (FDR corrected).

Table 4. *Single t-test results on AUC means for each level of temporal occlusions (DoF = 19).*

test value = 0.5				
Levels of temporal occlusion	*AUC mean*	*t value*	*p value*	*95% Confidence interval from the mean*
10%	.507	.311	.759	.007
20%	**.598**	**3.655**	**.002***	**.098**
30%	**.644**	**4.034**	**.001***	**.144**
40%	**.633**	**3.281**	**.004***	**.133**
50%	**.718**	**7.603**	**.0000001***	**.218**
60%	**.662**	**3.319**	**.004***	**.162**
70%	**.677**	**3.846**	**.001***	**.177**
80%	**.674**	**4.488**	**.0002***	**.174**

4. Discussion

In the present study, we investigated *whether* and *when* observers can take advantage of information gleaned from the observation of reach-to-grasp movements to discriminate between real and pantomimed grasps.

It has been shown that real and pantomimed grasp are different on different kinematic variables (Goodale et al., 1994; Cavina-Pratesi et al. 2011). Of interest, it has been demonstrated that this difference varies over time (see Chapter 1 - Additional Analysis). In addition, real and pantomimed kinematics retain enough information to allow action discrimination (see Chapter 2 – Action and Perception). In the present experiment we found clear evidence of advance information pickup early on in the movement which was not assessed in previous studies: participants were able to correctly identify real and pantomimed grasps from 20% up to 80% of normalized reaching duration. Since there were no contextual cues in the observed movements, our speculation is that observers had capitalized on movement kinematics to correctly identify the nature of the action.

For instance, the velocity profile of the wrist and the displacement of the thumb on the dorsal/palmar plane are the two kinematic parameters that differs between real and pantomimed grasps around 20% of the normalized reaching duration (see Chapter 1 - Additional Analysis). Early on in the movement, observers might had exploited these differences to discriminate between the two grasp type.

It is well known that observers are able to extract object size from early kinematics (Ambrosini et al., 2011; Ansuini et al. 2016). Here we suggest that observers are able to detect movement kinematics to make predictions and form expectations about the nature of the action, being real or pantomimed. Can this detection be automatic? In other terms, can movement kinematics be processed even without an explicit identification of the action nature? For instance, can this detection have an impact on object representation? The following experiment (Experiment 3) investigated these questions by using a visuo-motor prime paradigm.

Experiment 3: Perceiving objects through actions.

Real – and not pantomimed – grasps prime object presence.

1. Introduction

The perception of an object automatically primes an action representation congruent with the physical properties of that object (Craighero et al., 1998; Tucker & Ellis, 1998, 2001; Grèzes et al., 2003; Costantini et al., 2011). For example, Tucker and Ellis (2001) demonstrated that the execution of a motor response (power or precision grip) in an object categorization task (natural versus man-made) was affected by the size of the object to be categorized. A power grip response was executed with faster reaction times in response to a large object - affording a power rather than a precision grip. Conversely, a precision grip was executed with faster reaction times in response to small objects - affording a precision rather than a power grip. To note, object size information was task-irrelevant (Tucker & Ellis, 2001).

Despite the large literature on how object perception impacts actions representation, very little is known about the impact of action perception on objects representation. For instance, it has been demonstrated that observing a video clip depicting an interaction with an object can prime the recognition of a subsequently presented manipulable object that typically involves a similar action (Helbig et al., 2010; Sim et al., 2015). Converging evidence, however, showed that observers are able to extract object information even before the hand-object contact (i.e., during the reach-to-grasp phase of movements, Ambrosini et al., 2011; Ansuini et al. 2015).

Here we tested wheter the observation of real and pantomimed reach-to-grasp movements might impact objects' representation. It has been demonstrated that pantomimed and real actions have different kinematics (Goodale et al., 1994; Cavina-Pratesi et al. 2011). Real grasps are usually acted toward a present object, meanwhile pantomimed grasps are acted toward an imaginary object. The hypothesis was that real kinematics might convey information about the presence of the object, meanwhile pantomimed kinematics might convey information about the absence of the object. To test this, we asked participants to detect the presence or the absence of an object in a target stimulus (i.e., *object detection* task). Before the target stimulus, a video clip - depicting a real or a pantomimed grasp - was presented. To note, the observation of the action was irrelevant to perform the *object detection* task. We predicted faster response times on object detection task when the action prime was congruent with the target stimulus (real-grasp/present-object or pantomimed-grasp/absent-object) compared to when the action prime was incongruent with the target stimulus (real-grasp/absent-object or pantomimed-grasp/present-object).

In addition, we tested a possible modulation of the action processing nature on object detection task. In Experiment 3A and 3B. – in 20% of trials - we asked participants to do an *explicit* action discrimination task (i.e., identify if the video clip depicted a real or a pantomimed grasp). In Experiment 3C, we replaced action discrimination task with an *implicit* action observation task (i.e., report if the hand performing the action flashed green or not). Our hypothesis was that, even without an explicit recognition, movement kinematics was processed automatically, affecting object detection.

Experiment 3A

2. Methods of Experiment 3A

2.1. Participants

Twenty right-handed participants (9 women, mean ± SD = 22.75 ± 2.8 years old; age range = 19-29 years old) took part in Experiment 3A. We based our sample size on previously published studies testing action perception (Podda et al., 2017; Cavallo et al., 2016; Stapel et al., 2012). All participants were right-handed, had normal or corrected-to-normal vision and no history of either psychiatric or neurological disorders. They were naïve to the purpose of the experiment, gave their written informed consent and received financial compensation in return of participation. The experimental procedures were approved by local ethical committee (ASL 3 Genovese) and were carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Association, 2013).

2.2. Stimuli selection

The observed stimuli were video clips of reach-to-grasp movements collected in Experiment 1 (see Chapter 1 – Additional Analysis). Within the space defined via the LDA, the 40 movements that minimized the Mahalanobis distance for each grasp type were selected. This way, we identified a final set of 80 representative movements (50% real).

2.3. Action primes and target stimuli editing

The 80 unique video clips corresponding to the selected movements were used as action primes in the experiment. They were edited using Adobe Premiere Pro CS6 (Adobe Systems Software Ltd, Dublin, Ireland; .mp4 format, disabled audio, 25 frames/s, 1920x1080 pixels). All the video clips were edited using Adobe Premiere Pro CS6 (.avi format, disabled audio, 25 frames/s) and modified using Adobe After Effect CC 2016 (Adobe Systems Software Ltd, Dublin, Ireland). Each video clip was edited so as to begin at reach onset and to end immediately after reach offset. To prevent participants from viewing whether the object was present or not, a grey rectangular mask (height = 1080, width = 744 pixels) was superimposed onto the object position. The size and the position of this mask were kept constant across trials and participants.

The target stimuli images were edited using Microsoft Paint v. 6.1 (Microsoft Corporation, United States; .jpg format, 744x1080 pixels). One target stimulus, namely the present-object target stimulus, consisted of an image showing the grasped object (i.e., the glass filled with iron screws) at the object position. The other target stimulus, namely absent-object target stimulus, consisted of an image showing no-object at the object position. The two images used as target stimuli were similar in size to the mask used to create the spatial occlusion in the action primes.

2.4. Procedure

The experiment took place in a dimly lit room. Stimuli were presented on a 22-inches computer screen (1920x1080 pixels; refresh rate = 60 Hz) at a viewing distance of 60 cm. Two experimental tasks involved participants: an *object detection* and an *action discrimination* task. In the *object detection* task, we assessed the effects of action primes on response speed to target stimuli (i.e., present-object or absent-object). In the *action discrimination* task, we tested how well participants could recognize the type of action in the prime (i.e., real or pantomimed). Trials for *object detection* and *action discrimination* task were presented in random order. Stimulus sequence and timing for *object detection* and *action discrimination* task are described in Figure 11.

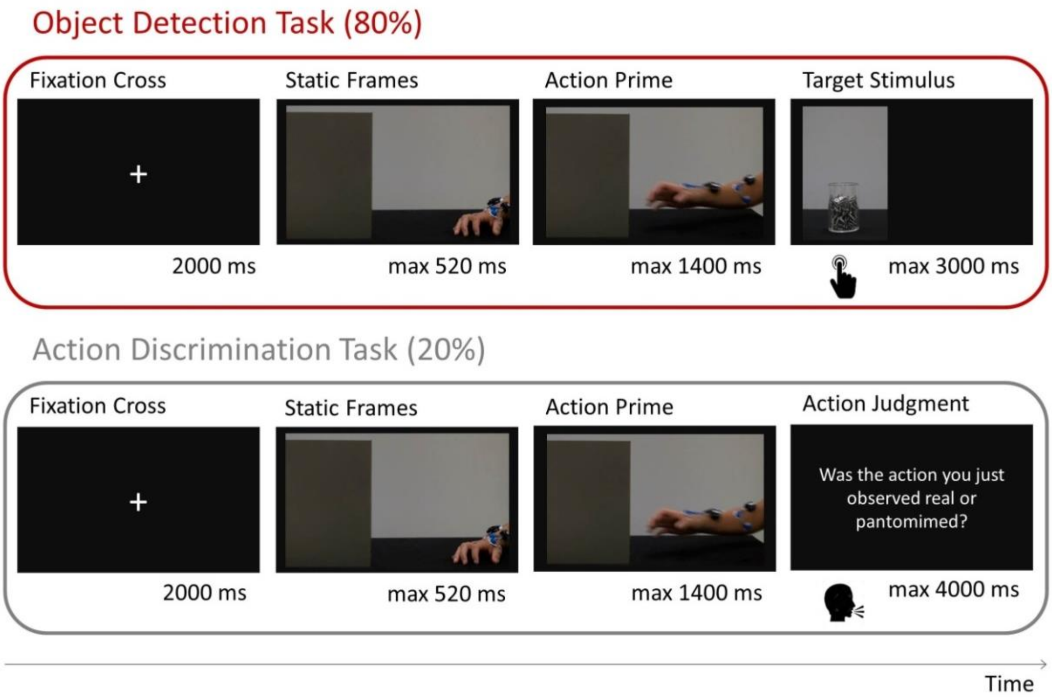


Figure 11. *Trial procedure of Experiment 3A.* Each trial started with a white fixation cross at the center of the screen, followed after 2000 ms by the action prime. At the end of the action prime a Target Stimulus image (*object detection* task on the 80% of all trials) or an Action Judgment question (*action discrimination* task on the 20% of all trials) was displayed.

The action prime could depict either a real or a pantomimed reach-to-grasp movement. To provide participants enough time to focus on movement start and prevent anticipation, +9 (360 ms), +11 (440 ms), or +13 (520 ms) static frames were randomly added at the beginning of all action prime stimuli.

In the *object detection* task (80% of experimental trials), the offset of the action prime was immediately followed by either the *present-object* or the *absent-object* target stimulus. The target stimulus was presented on the far left of the screen, in a position compatible with that occupied by the object position within the action prime (see Figure 11). Participants were asked to judge as quickly and as accurately as possible about the presence of the object in the target stimulus; i.e., present-object versus absent-object. Responses were given by pressing with the index or the middle finger of the right hand one of two keys on a wireless keyboard touchpad. The key order was counterbalanced across participants. The target stimulus disappeared upon participant's response (maximum duration 3000 ms). There were four experimental conditions obtained by crossing action primes (real-grasp vs. pantomimed-grasp) and target stimuli (present-object vs. absent-object): real-grasp/present-object; real-grasp/absent-object; pantomimed-grasp/present-object; pantomimed-grasp/absent-object. In 75% of the trials for the *object detection* task, the action prime was paired with a congruent target stimulus (real-grasp/present-object or pantomimed-grasp/absent-object). In the remaining 25% of the trials for the *object detection* task, the action prime was paired with an incongruent target stimulus (real-grasp/absent-object or pantomimed-grasp/present-object). It was not mentioned to participants that the reach-to-grasp movement within the action prime could be either congruent or incongruent with respect to the target stimulus.

In the *action discrimination* task (20% of experimental trials), right after the offset of the action prime, participants were asked to judge as quickly and as accurately as possible whether the observed action was real or pantomimed. Responses were made by saying the Italian word *reale* (real) or *mimata* (pantomimed). Participants' vocal reaction times (RTs) were collected via a voice key (sample rate: 48 kHz, 16 bit). A maximum of 4000 ms was allowed as responding interval for the *action discrimination* task. Before the beginning of next trial, an experimenter manually recorded participants' response by pressing one of two buttons on a wireless keyboard. In the *action discrimination* task, participants observed a real action in half of the trials and a pantomimed action in the other half of the trials.

A single experimental session included 200 trials. For the *object detection* task there were 160 trials: 120 congruent (60 real-grasp/present-object and 60 pantomimed-grasp/absent-object) and 40 incongruent (20 real-grasp/absent-object and 20 pantomimed-grasp/present-object) trials. The assignment of each video-clip to either congruent or incongruent trials was randomized across participants. For the *action discrimination* task, 40 trials (20 real and 20 pantomimed grasp video clips) were randomly selected within each video set for each participant. To familiarize participants with the procedure, at the beginning of the experiment, a 20 trials practice session was administered (80% vs. 20% for *object detection* and *action discrimination* task, respectively). Stimuli, timing and randomization procedure were controlled using E-Prime software (Version 2.0). The entire experiment lasted approximately 30 minutes.

Data analyses. RTs (ms) and accuracy (%) were collected for both *object detection* and *action discrimination* task. Trials with response omissions (< 1% considering both *object detection* and *action discrimination* task, respectively) and RTs deviating more than 2.5 SD from single participant's mean were counted as outliers and discarded (< 3% and < 2% for *object detection* and *action discrimination* task, respectively). Trials with errors (< 2% and < 38% for *object detection* and *action discrimination* task, respectively) were excluded from RTs analyses. The responses registered during the practice block were not included in the analysis.

Manual RTs for the *object detection* task were submitted to a 2 x 2 repeated-measures analysis of variance (ANOVA) with 'action prime' (real-grasp vs. pantomimed-grasp) and 'target stimulus' (present-object vs. absent-object) as within-subject factors. Vocal RTs for the *action discrimination* task were submitted to a paired t-test. Accuracy for both *object detection* and *action discrimination* task was submitted to one sample t-tests to compare participants' performance against chance level (.5). For all statistical tests the alpha level of significance was set to .05.

3. Results of Experiment 3A

For what concerns the *object detection task*, the 2 x 2 ANOVA on RTs revealed a main effect of 'target stimulus' (F(1, 19) = 12.13, p = .002, η_p^2 = .390). Participants were faster to respond to present-object (M = 618 ms, 95% CI = [574.73, 661.27]) than to absent-object target stimulus (M = 655.39 ms, 95% CI = [609.92, 700.85]). While the main effect of 'action prime' failed to reach significance (F(1, 19) = 1.42, p = .248, η_p^2= .070), a significant 'action prime' by 'target stimulus' interaction was found (F(1, 19) = 7.05, p = .016, η_p^2 = .271). Post-hoc contrasts revealed that when participants observed real-grasp primes their responses were faster to present-object (606.45 ms, 95% CI = [560.50, 652.40]) than to absent-object target stimulus (M = 659.27 ms, 95% CI = [610.92, 707.61], p < .001, 95% CI of the difference between target stimuli = [-71.39, -34.23]; see Figure 12). However, if they observed pantomimed-grasp primes, no similar difference was found (present-object: M = 629.55 ms, 95% CI = [586.86, 672.24]; absent-object: M = 651.51, 95% CI [607.51, 695.91], p = .154, 95% CI of the difference between target stimuli [-52.93, 9.01]). Moreover, participants were faster to respond to present-object target stimulus when it was preceded by a real-grasp prime (M = 606.45 ms, 95% CI = [560.50, 652.40]) compared to when it was preceded by a pantomimed-grasp prime (M = 629.55 ms, 95% CI = [586.86, 672.24], p = .023, 95% CI of the difference between action primes = [-42.59, -3.60]; see Figure 12). In contrast, responses to absent-object target stimulus were similar regardless of the type of action prime (real-grasp prime: M = 659.27, 95% CI [610.92, 707.61] and pantomimed-grasp prime: M = 651.51, 95% CI [607.51, 695.51], p > .250, 95% CI of the difference between action primes = [-8.91, 24.42]). One sample t-test on accuracy revealed that participants' performance at the *object detection* task was significantly above chance level (*M* = .98, 95% CI = [.97, .99]; t(19) = 130.04, $p < .001$, 95% CI of the difference from chance level = [.47, .49]).

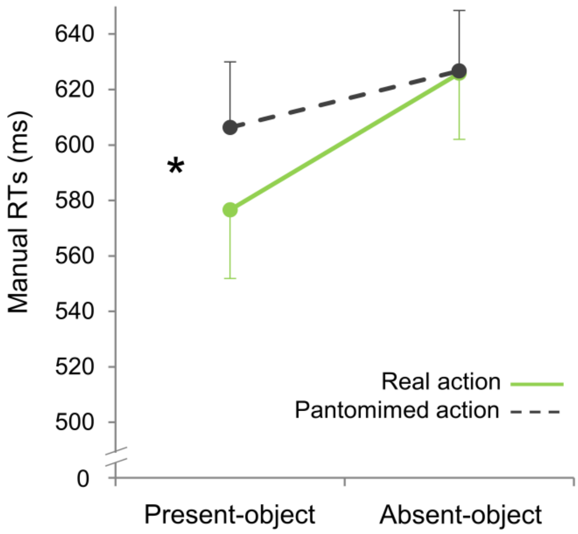


Figure 12. *Manual RTs of object detection task.* The asterisk represents the significant difference on the present-object target stimulus after observing real compared to pantomimed action primes.

For what concerns the *action discrimination task,* paired-sample t-test on RTs revealed that participants took a similar time to identify real (*M* = 1414.18 ms, 95% CI = [1238.10, 1590.26]) and pantomimed actions (*M* = 1373.97 ms, [1213.73, 1534.21], t(19) = .97, $p > .250$, 95% CI of the difference between conditions = [-46.59, 127]). Moreover, results of one sample t-test on accuracy indicated that they were able to correctly identify whether the action prime was real or pantomimed (*M* = .62, 95% CI = [.57, .66]; t(19) = 5.72, $p < .001$, 95% CI of the difference from chance level = [.07, .16]).

Experiment 3B

To rule out the possibility that priming effects reported in Experiment 3A were due to the high informativeness of action primes (75% of congruent trials versus 25% of incongruent trials), in Experiment 3B action primes were paired equally often with congruent as with incongruent target stimuli.

4. Methods of Experiment 3B

4.1. Participants

A new group of twenty participants (9 women; mean ± SD = 23.45 ± 2.81 years old; age range = 20-30 years old) with no history of neurological problems took part in Experiment 3B. All were right-handed and had normal or corrected-to-normal vision. As in Experiment 3A, participants were naïve to the purpose of the experiment and provided written informed consent. They received financial compensation in return of their participation. Participants' group in Experiment 3A and 3B were age-matched (t(38) = .787, *p* > .250, 95% CI of the difference between groups = [-1.10, 2.50]).

4.2. Stimuli, procedure and data analysis

Stimuli, experimental procedure, and data analysis were the same as in Experiment 3A, except that, in the *object detection* task, action prime and target stimulus were congruent (i.e., real-grasp/present-object and pantomimed-grasp/absent-object) in half of the trials and incongruent (i.e., real-grasp/absent-object and pantomimed-grasp/present-object) in the other half of the trials. The experimental session included 80 trials for the *object detection* task: 40 congruent (i.e., 20 real-grasp/present-object and 20 pantomimed-grasp/absent-object) and 40 incongruent trials (i.e., 20 real-grasp/absent-object and 20 pantomimed-grasp/present-object). Thus, the entire experiment consisted in 100 trials and it lasted approximately 15 minutes. Trials with response omissions and RTs deviating from their individual mean by 2.5 SD or more were counted as outliers and discarded (no omissions, and < 2% and < 1% for *object detection* and *action discrimination* task, respectively). Trials with errors (< 3% and < 42% for *object detection* and *action discrimination* task, respectively) were excluded from RTs analyses.

5. Results of Experiment 3B

For what concerns the *object detection* task, the 2 x 2 repeated-measures ANOVA on RTs yielded a main effect of 'target stimulus' (F(1, 19) = 20.26, $p < .001$, $\eta_p^2 = .516$). Participants were faster to respond to present-object (*M* = 591.47 ms, 95% CI = [541.88, 641.06]) than to absent-object target stimulus (*M* = 626.29 ms, 95% CI = [578.98, 673.60]). Moreover, results revealed a main effect of 'action prime' (F(1, 19) = 5.98, $p = .024$, $\eta_p^2 = .240$). Participants' responses were faster when the action prime was real (*M* = 601.25 ms, 95% CI = [551.47, 651.02]) compared to when it was pantomimed (*M* = 616.51 ms, 95% CI = [568.89, 663.14]). Main effects were further qualified by a significant 'action prime' by 'target stimulus' interaction (F(1, 19) = 6.59, $p = .019$, $\eta_p^2 = .258$). As in Experiment 1, participants were faster to respond to present-object target stimulus when it was preceded by a real-grasp prime (*M* = 576.62 ms; 95% CI = [524.78, 628.46]) than when it was preceded by a pantomimed-grasp prime (M = 606.32 ms, 95% CI = [556.77, 655.87], *p* = .009, 95% CI of the difference between action primes = [-50.88, -8.51]). No similar difference was evident when participants responded to absent-object (real-grasp prime: *M* = 625.87 ms, 95% CI = [576, 675.75] and pantomimed-grasp prime: *M* = 626.71 ms, 95% CI = [581.17, 672.24]; *p* > .250, 95% CI of the difference between action primes = [-13.84, 12.17]). One sample t-test on accuracy revealed that participants' performance at the *object detection* task was significantly above chance level (*M* = .97, 95% CI = [.96, .99]; t(19) = 80.33, *p* < .001, 95% CI of the difference from chance level = [.46, .49]).

For what concerns the *action discrimination* task, participants took a similar time to discriminate real (*M* = 1404.39 ms, 95% CI = [1218.08, 1590.70]) and pantomimed action primes (1337.66 ms, 95% CI = [1165.89, 1509.44], t(19) = 2.03, *p* = .057, 95% CI of the difference between conditions = [-2.06, 135.52]). Finally, one sample t-test on accuracy revealed that they were able to correctly judge whether the action prime was real or pantomimed (*M* = .58, 95% CI = [.52, .63], t(19) = 3.13, *p* = .005, 95% CI of the difference from chance level = [.02, .13]).

Experiment 3C

In Experiment 3A the explicit request to discriminate the action prime might have played a role on priming effects. To rule out this possibility, in Experiment 3C the *action discrimination* task was replaced with a *color detection* task where the hand could flash green and participants had to detect whether this occurred or not. We predicted that if the effect observed in Experiment 3A were due to the explicit recognition of action primes in the *action observation* task, they should disappear in Experiment 3C. Conversely, if the mere processing of the action prime (i.e. without explicit recognition) is sufficient to trigger an automatic representation of the congruent target stimulus, we expected priming effects equivalent to those reported in Experiment 3A.

6. Methods of Experiment 3C

6.1. Participants

A new group of twenty participants (12 women; mean ± SD = 24.25 ± 4.56 years OLD; age range = 18-30 years old) with no history of neurological problems took part in Experiment 3C. All were right-handed and had normal or corrected-to-normal vision. As in Experiment 3A, participants were naïve to the purpose of the experiment and provided written informed consent. They received financial compensation in return of their participation. Participants' group in Experiment 3A and 3C were age-matched (t(38) = -1.25, *p* = .218, 95% CI of the difference between groups = [-3.92, .92]).

6.2. Stimuli, procedure and data analysis

Stimuli, experimental procedure, and data analysis were the same as in Experiment 3A. In the *object detection* task (80% of experimental trials), the offset of the action prime was immediately followed by either the *present-object* or the *absent-object* target stimulus. The *action discrimination* task was replaced with a *color detection* task (20% of experimental trials).

To create the stimuli to use in the *color detection* task, 40 video clips (20 real and 20 pantomimed movements) were randomly selected from the original 80 video clips (refer to the section *Stimuli: action primes and target stimuli* for Experiment 1a). In half of these video clips (10 real and 10 pantomimed movements), digital video editing (Adobe Premiere Pro CS6; Adobe Systems Software Ltd, Dublin, Ireland) was used to create a color change in the reaching hand. This was obtained by superimposing a green mask on the hand area (see Figure 13). The color change started at a fixed time for each video clip (i.e., one time chosen in the interval from 10% up to 50% of normalized reaching duration) and lasted for three frames (i.e., 120 ms).

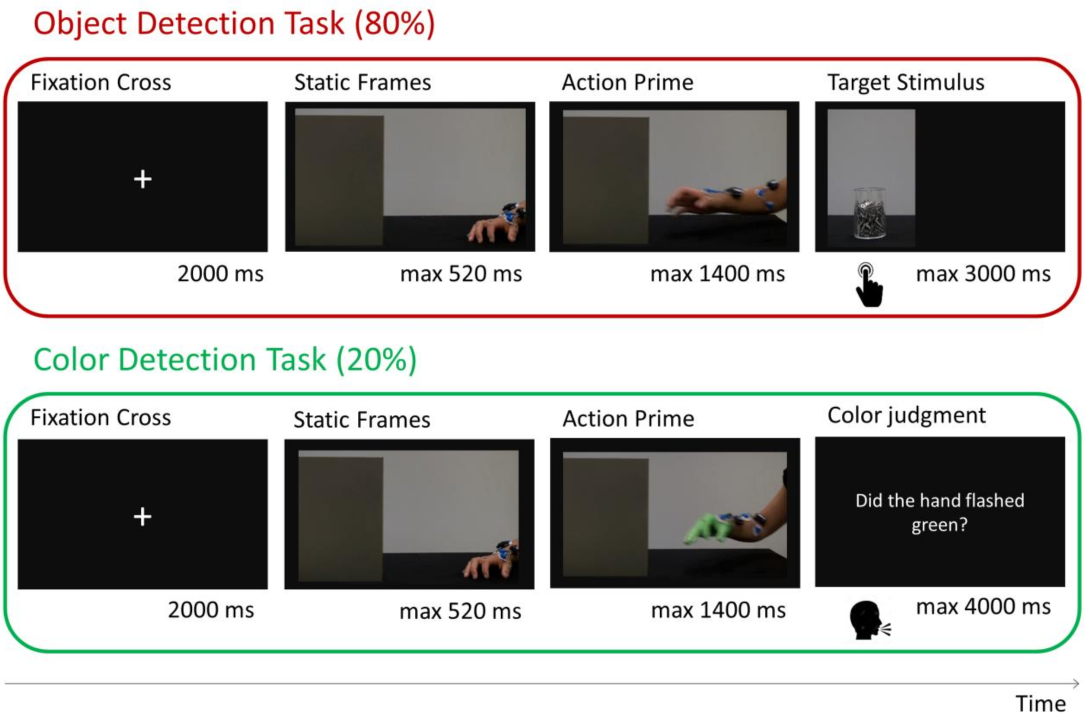


Figure 13. *Trial procedure of Experiment 3C.* Each trial started with a white fixation cross at the center of the screen, followed after 2000 ms by the action prime. At the end of the action prime a Target Stimulus image (*object detection* task on the 80% of all trials) or a Color Judgment question (*color detection* task on the 20% of all trials) was displayed.

In the *color detection* task, 20 trials with the color change present (10 real and 10 pantomimed movements) and 20 trials with the color change absent (10 real and 10 pantomimed movements) were randomly showed. Right after the offset of the observed action, participants were asked to judge as quickly and as accurately as possible whether they had detected a color change of the hand or not. Responses were made by saying the Italian word *si* (yes) or *no* (no). The entire experiment lasted approximately 30 minutes. Trials with response omissions (< 1% and no omission for *object detection* and *color detection* task, respectively) and RTs deviating from their individual mean by 2.5 SD or more were counted as outliers and discarded (< 2% and < 2% for *object detection* and *color detection* task, respectively). Trials with errors (< 2% and <1 % for *object detection* and *color detection* task, respectively) were excluded from RTs analyses.

7. Results of Experiment 3C

For what concerns the *object detection* task, the 2 x 2 repeated-measures ANOVA on RTs revealed no main effect of 'target stimulus' (F(1, 19) = 0.93, p = .199, η_p^2= .005) and no main effect of 'action prime' (F(1, 19) = 1.77, p > .250, η_p^2= .085). However, a significant 'target stimulus' by 'action prime' interaction effect was found (F(1, 19) = 5.32, p = .032, η_p^2 = .219, see Figure 14). As in Experiment 3A, post-hoc comparisons revealed that participants were faster to respond to present-object target stimulus when it was preceded by a real-grasp prime (*M* = 503.44 ms; 95% CI = [463.01, 542.88]) than when it was preceded by a pantomimed-grasp prime (M = 521.05 ms, 95% CI = [476.71, 565.4], p = .044, 95% CI of the difference between action primes = [-34.67, -.55]). No similar difference was evident when participants responded to absent-object target stimulus (real action prime: *M* = 516.24 ms, 95% CI = [465.45, 567.3] and pantomimed action prime: *M* = 513.58 ms, 95% CI = [462.41, 564.75]; p > .250, 95% CI of the difference between action primes = [-9.51, 15.1], Figure 14). One sample t-test on accuracy revealed that participants' performance was significantly above chance level (*M* = .98, 95% CI = [.97, .98]; t(19) = 153.62, p < .001, 95% CI of the difference from chance level = [.47, .48]).

For what concerns the *color detection* task, participants were faster to respond when they had to report the presence of the color change (*M* = 553.15 ms, 95% CI = [475.51, 630.79]) with respect to its absence (M = 1000.6 ms, 95% CI = [881.02, 1120.18]; t(19) = 13.57, p < .001, 95% CI of the difference between conditions = [-516,53 -378.37]). Finally, one sample t-test on accuracy revealed that participants' performance in the *color detection* task was significantly above chance level (*M* = .99, 95% CI = [.99, .98], t(19) = 160.55, p < .001, 95% CI of the difference from chance level = [.48, .50]).

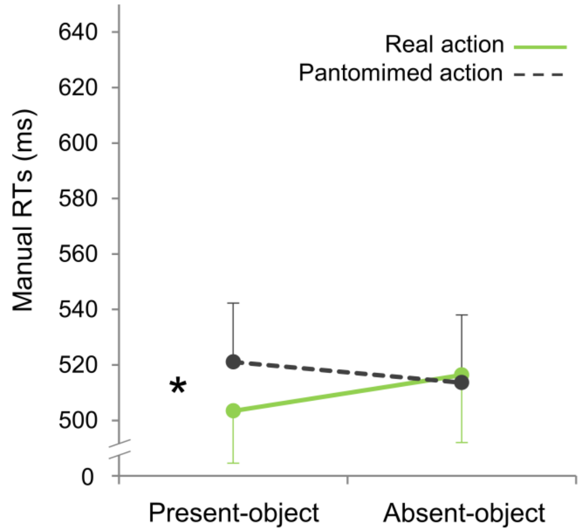


Figure 14. *Manual RTs of object detection task.* The asterisk represents the significant difference on the present-object target stimulus after observing real compared to pantomimed action primes.

8. Discussion

Here we investigated whether reach-to-grasp movement observation can prime object detection. Our findings revealed that when the target stimulus was the present-object image, having previously observed a congruent action (i.e., real-grasp, rather than a pantomimed grasp) - resulted in faster reaction times on object detection task. Experiment 3A demonstrated that real – and not pantomimed – grasps prime object presence detection (i.e., *real-grasp priming*), meanwhile pantomimed grasps fail to prime object absence detection. Experiment 3B showed that this *real-grasp priming* effect is independent from the high informativeness of action primes. Experiment 3C reveald that the *real-grasp priming* effect is independent from the nature of action processing (i.e., *explicit* vs. *implicit*).

Previous studies demonstrated that observers can take advantage of kinematic information to learn about the properties of objects acted upon, as well as to read others' intentions and expectations (Ambrosini et al., 2011; Ansuini et al. 2014; Ansuini et al. 2016; Becchio et al. 2017). It has been showed that real and pantomimed grasps differed in terms of movement kinematics (see Chapter 1 – Additional Analysis). Since observers were not provided of any contextual cues during action prime observation, our speculation is that the processing of real movement kinemtics had an impact on object detection performance.

In Experiment 3A and 3B, kinematics processing might had been modulated by the explicit recognition of the grasp type. In Experiment 3C, the action discrimination task was replaced by a color detection task. Surprisingly, even without an explicit recognition of action primes, we replicated *real-grasp priming* effect. This evidence support the idea that movement kinematics can be automatically processed.

How could this effect be functionally mediated? It is well known that humans use internal predictive models to provide sensory expectations to monitor and control own goal-directed actions (Wolpert and Ghahramani 2000). Analogously, it has been claimed that the same internal modeling mechanisms are reused when we observe another's action in terms of our own motor repertoire (Gallese et al. 1996; Rizzolatti & Craighero 2004; Fazio et al. 2009). In the present case, the automatic processing of real kinematics might have provided the sensory expectation that the observed hand was directed toward a physically present object.

Ecological approach to perception suggested that people not only perceive the physical properties of an object or a tool, but also what they can do with it (i.e., the possibilities for action, or *object affordances*) (Tucker & Ellis, 2001). Our evidence suggest that the mere exposure to an action might automatically elicit the representation of the object toward which the action is directed. Further studies need to be done on this direction to investigate whether the other side of affordance - the *action affordance* - exists.

Why pantomimed-grasp did not work as a prime for the absent-object detection? It might be that pantomimed grasps are more difficult to process than real grasps. In everyday life, indeed, it is unusual to perform and/or observe a pantomimed grasps. What if some individuals are familiar in doing this? Would they have an advange compared to naïve people in pantomimed grasp processing? The next experiment (Experiment 4) explored these questions by comparing action discrimination abilities of a group of expert performers against a group of naïve people.

Experiment 4: The role of expertise.

Enhanced detection of pantomimed grasps in professional magicians.

Paper under review

1. Introduction

Most of us are poor at faking actions, including everyday actions. When pantomiming to pick up an object, for example an imaginary glass on the table, we move and shape our hands differently than when we grasp a real glass (Goodale et al., 1994). For actual grasping, the hand opens wider than the diameter of the glass during the reach and closes again when approaching the glass (Goodale et al., 1994; Laimgruberg et al., 2005). When doing a pantomimed grasp, in contrast, most people open the hand approximately to the width of the glass and then move to the imaginary glass without further changing the aperture of their grip.

Professional magicians regularly using pantomimed grasps to deceive their audience do not make this mistake. Their pantomimed grasps resemble real grasps to the point that they can almost convince us they picked up an object that is not really there (Cavina-Pratesi et al., 2011). It is proposed that this remarkable skill does not simply result from an increased awareness of the kinematics involved in the action being simulated (i.e., attention to the kinematics of the real grasp), but rather reflects *action re-calibration* (Cavina-Pratesi et al., 2011). Grasping real objects engages automatic visuomotor transformations within the cortical grasping network. These transformations are normally not available when the object is taken away or displaced. With prolonged practice, however, professional magicians learn to recalibrate control of their reaching movements targeting the information from the real objects toward a spatially separate location (Cavina-Pratesi et al., 2011).

This study addresses whether this skill also influences action observation. An influential hypothesis in psychology and neuroscience is that an observer's understanding of another's actions results from mapping the observed action onto sensorimotor representations of that same action in the observer’s brain (Flanagan et al., 2006). This hypothesis predicts that the more experienced an observer is in producing an action, the more accurate will be the perception of the same action performed by another person (Schütz-Bosbach & Prinz, 2007). Based on this, we expect that professional magicians, who routinely perform pantomimed grasps, will be better able to detect observed pantomimed grasps compared to naïve. This advantage is not expected for real grasps, for which magicians and non-magicians have equal motor familiarity. We call this the *specific advantage hypothesis.* Alternatively, one might hypothesize that by studying closely how real grasps are performed, magicians are generally more aware of movement kinematics. Based on this, they will be better at detecting both real and pantomimed grasps. We call this the *general advantage hypothesis*.

In this study, we formalized and tested these hypotheses using a drift diffusion model (DDM) approach. The DDM is a sequential sampling model that regards a decision process as the accumulation of sensory information over time until a decision boundary threshold for choice is reached (Bogacz 2007; Gold & Shadlen 2007; Ratcliff & McKoon 2008; Wagenmakers 2009; Ratcliff et al. 2016). In the experiment reported here, magicians and naïve were asked to judge whether reach-to-grasp movements towards an occluded object were *real* or *pantomimed*. Fitting alternative versions of the DDM revealed a specific advantage for magicians in the processing of pantomimed but not real grasps.

2. Methods

2.1. Participants

Seventeen professional magicians (all males, mean ± SD age = 44.12 ± 8.27 years; age range: 30 – 60 years) and seventeen age-matched naïve participants (all males, mean ± SD age = 46.35 ± 9.91 years; age range: 31 – 65 years, $t(32) = -0.71$, $p = .48$) took part in the experiment. All participants were right-handed, with normal or corrected-to-normal vision, and with no history of either psychiatric or neurological disorders. Professional magicians were screened to ensure that they had practiced magic tricks for at least 10 years preceding the day of the experiment (mean experience = 23.41 years, range = 10 – 42 years). Data from one participant in the magician group were discarded due to problems with data recording. After data examination, participants with overall errors or reaction times >2.5 SD from their respective group mean were excluded from subsequent analysis; as a result, analyses included 15 participants in the magician group (mean ± SD age = 44.47 ± 7.62 years) and 16 participants in the naïve group (mean ± SD age = 46.31 ± 10.23 years, $t(29) = -0.57$, $p = .14$). All research methods were approved by the local ethics committee (ASL 3 Genovese), and carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Association General Assembly, 2008). Written informed consent was obtained from all participants.

2.2. Stimuli selection

The observed stimuli were video clips of reach-to-grasp movements collected in Experiment 1 (see Chapter 1 – Additional Analysis). Within the space defined via the LDA, the 50 movements that minimized the Mahalanobis distance for each grasp type were selected. This way we identified a final set of 100 representative movements (50% real).

2.3. Procedure

The experiment took place in a dimly lit room. Participants sat in front of a 17-inch computer screen (1280 x 800 pixels; refresh rate = 75 Hz) at a viewing distance of 50 cm and perform the experiment individually. They were presented with video clips of the reach-to-grasp phase of the selected movements. A one-interval discrimination design was employed (see Figure 15). Participants were asked to observe the video clip and judge as accurately and as quickly as possible whether the observed movement was real or pantomimed, and indicate their response by pressing with their right index or middle finger, one of two buttons on a keyboard. Participants were instructed to respond either during the video, or within a maximum of 3000 ms after the video ended. To prevent anticipation and to ensure that participants could temporally attend to movement sequences, a random number of static frames (range: 14-23 frames) were added to the beginning of all video clips presented to participants. To equalize stimulus duration within each movement condition (real vs. pantomimed observed movement), static frames were also added at the end of video clips (range: 1-18 frames) so that each video clip lasted 2000 ms.

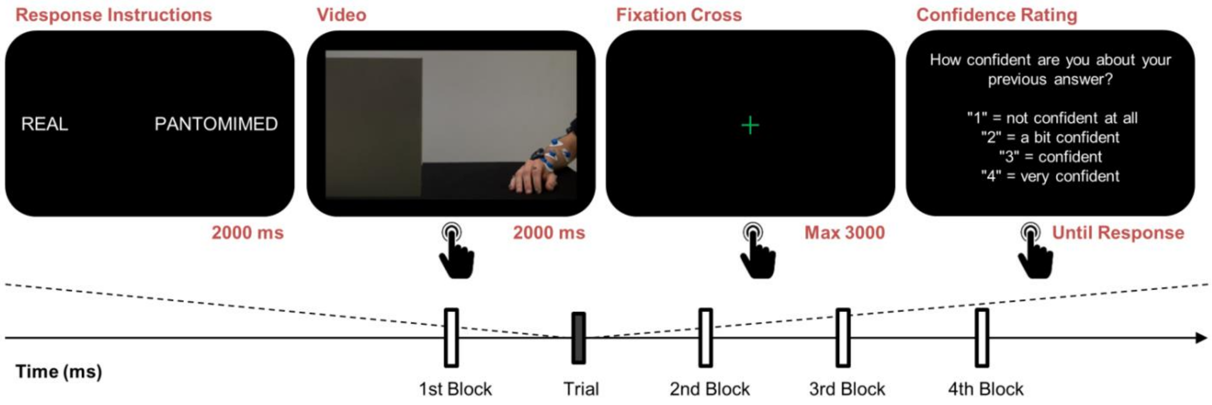


Figure 15. *Trial procedure.* In each trial participants first observed an instruction slide indicating the buttons to press for the movement type ('real' or 'pantomimed'), followed by a video-clip showing the reach-to-grasp phase of the movement. Participants could respond either during the presentation of the video or up to 3000 ms after the end of the video.

Participants completed four blocks of 100 trials (50% real grasp trials). There was a 5-minutes break between each block. Video-clips were pseudo-randomized over the blocks so that within each block any movement occurred only once. At the beginning of an experimental session, participants were presented with eight movement samples (i.e., two for each movement type repeated twice) without spatial occlusion, so that they could see the phase during which the agent grasped (or pantomimed to grasp) the glass, and lift it. Participants also completed a practice session of 10 trials (50% real) to familiarize themselves with the task. Stimuli presentation, timing, and randomization procedures were controlled using E-prime version 2.0.10.242 (Psychology Software Tools, Inc., Sharpsburg, PA, USA). Each experimental session lasted about 90 minutes.

2.4. Data analyses

Participant performance was assessed by fitting alternative drift diffusion models (DDMs) to accuracies and reaction times obtained in the discrimination task. In DDMs, evidence is stochastically accumulated in a single decision-variable (DV) from a predetermined starting-point z, located at some point between two decision boundaries, separated by a distance a. As evidence is sampled, the DV drifts towards the boundary supported by the signal at an average rate of v, called the drift-rate. Evidence accumulation is terminated once the DV reaches one of the two criterion boundaries, initiating the corresponding choice and marking the response time (Ratcliff, 2002; Ratcliff & McKoon, 2008) (Figure 16).

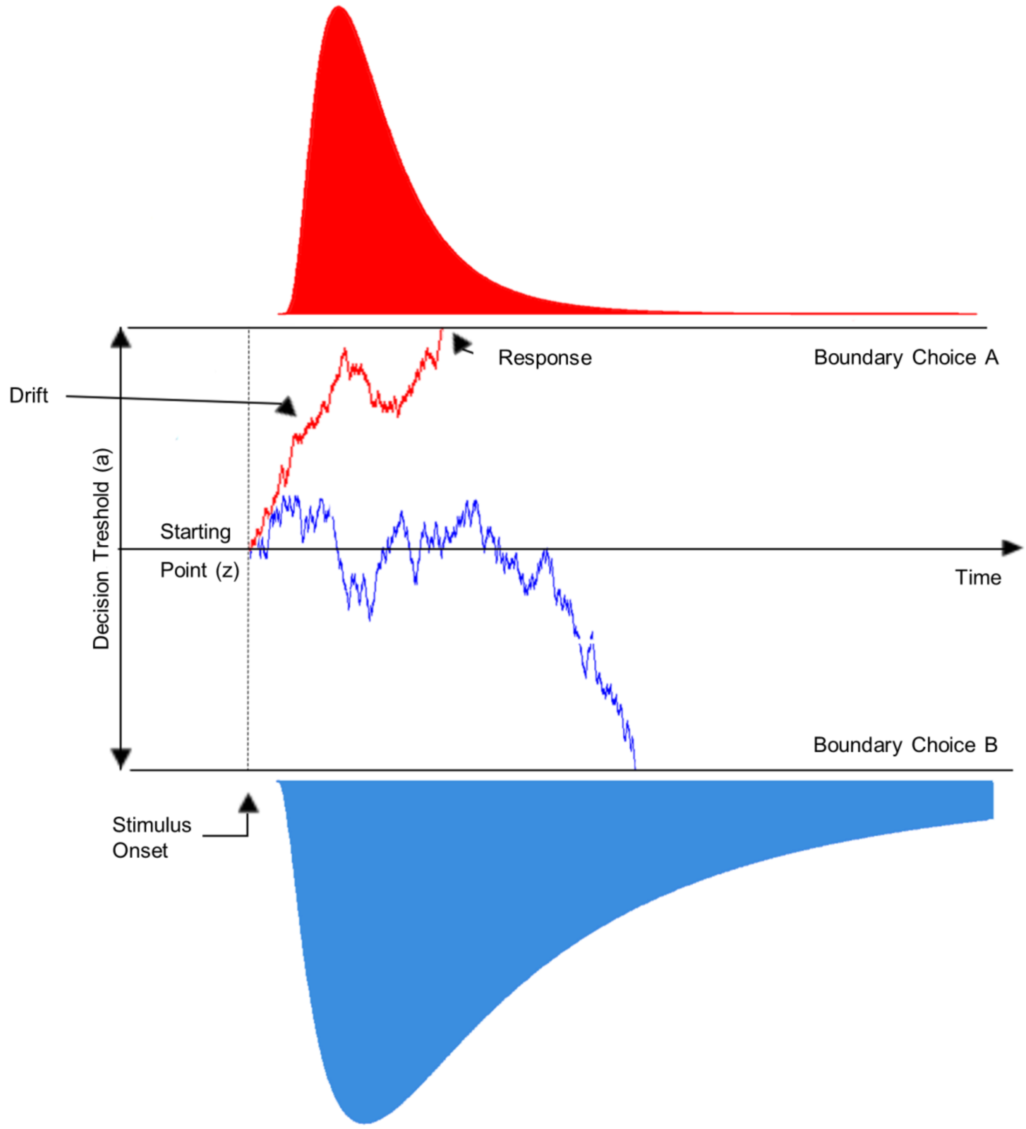


Figure 16. *Representation of a DDM.* The DDM models decision process as an accumulation of evidence over time from an initial starting-point (‘z’) towards one of two criterion boundaries separated by a distance ‘a’. The average rate of accumulation of evidence is denoted as drift rate (‘v’) and provides a measure of perceptual sensitivity for the stimulus.

We used a hierarchical Bayesian approach to estimate DDM parameters, as implemented in the toolbox Hierarchical Drift Diffusion Model (HDDM) (Wiecki et al., 2013). We compared three hypothetical diffusion models that differed in drift rate parameter: a *no advantage model* (M0), in which drift rate was constrained to be of equal magnitude for magicians and naïve for both grasp types (real vs. pantomimed); a *general advantage model* (M1), in which drift rate was allowed to vary as a function of group, but was fixed between grasp types; a *specific advantage model* (M2), in which drift rate was allowed to vary both between groups and grasp types. To evaluate HDDM model performance, we used the Deviance Information Criterion (DIC) (Spiegelhalter et al., 2002). A difference of more than 10 between model DIC scores was interpreted as evidence in favour of the better (lower) scoring model (Dunovan et al., 2014). For the best-fit model, follow-up contrasts were performed to test whether drift rate reliably changed across conditions. Since the HDDM toolbox utilizes a Bayesian framework, significance testing can be performed directly on the posterior distributions and results can be interpreted in terms of probabilities. We thus calculated the proportion of the posteriors in which the drift rate for each condition was higher than the other. A difference of less than 5% in the posterior distribution overlap (Pp|D) was considered significant (suggesting a higher probability of difference between the conditions).

We also evaluated whether the drift rates were significantly greater than zero to ascertain the likelihood of drifting towards the correct alternative. A drift rate close to 0 corresponds to a process which is equally likely to move towards either of the choices, indicating a slow rate of evidence accumulation. On the contrary, a higher positive drift rate indicates faster evidence accumulation towards the correct alternative. Since the hierarchical estimation procedure violates the independence assumption, we did not analyse subject parameter estimates in frequentist tests.

3. Results

The *specific advantage model* (DIC = 33877.30) fit significantly better than the *general advantage model* (DIC = 34164.75) or the *no advantage model* (DIC = 34164.06). The *specific advantage model* predicts that the experience of magicians in the execution of pantomimed grasps allows them to better detect a pantomimed grasp. To investigate this hypothesis more precisely, we next tested the significance of the estimated parameter for the four conditions resulting from the factorial combination of group (magician vs. naïve) and grasp type (real vs. pantomimed): magician_real, magician_pantomimed, naïve_real, naïve_pantomimed.

As predicted by the *specific advantage model*, drift rates for pantomimed grasps were significantly faster in the magician group compared to the naïve group (Pp|D [magician_pantomimed > naïve_ pantomimed] = 0.041, permutation p - value < 0.05), whereas no such between-group difference was observed for real grasps (Pp|D [magician_real > naïve_real] = 0.34; permutation p - value > 0.05). This point out that the magician's experience confers them a tangible benefit in the processing of pantomimed grasps (for a graphical representation of drift rate distributions, see Figure 17).

Interestingly, comparison of drift rates between grasp types indicated that drift rates for real grasps were significantly higher than drift rates for pantomimed grasps in the naïve group (Pp|D [naïve_real > naïve_pantomimed] < 0.001; permutation *p* - value < 0.001), but not in the magician group (Pp|D [magician_real > magician_pantomimed] = 0.81; permutation *p* - value > 0.05). This suggest that for experienced magicians the processing of observed pantomimed grasps is as effective as the processing of observed real grasps.

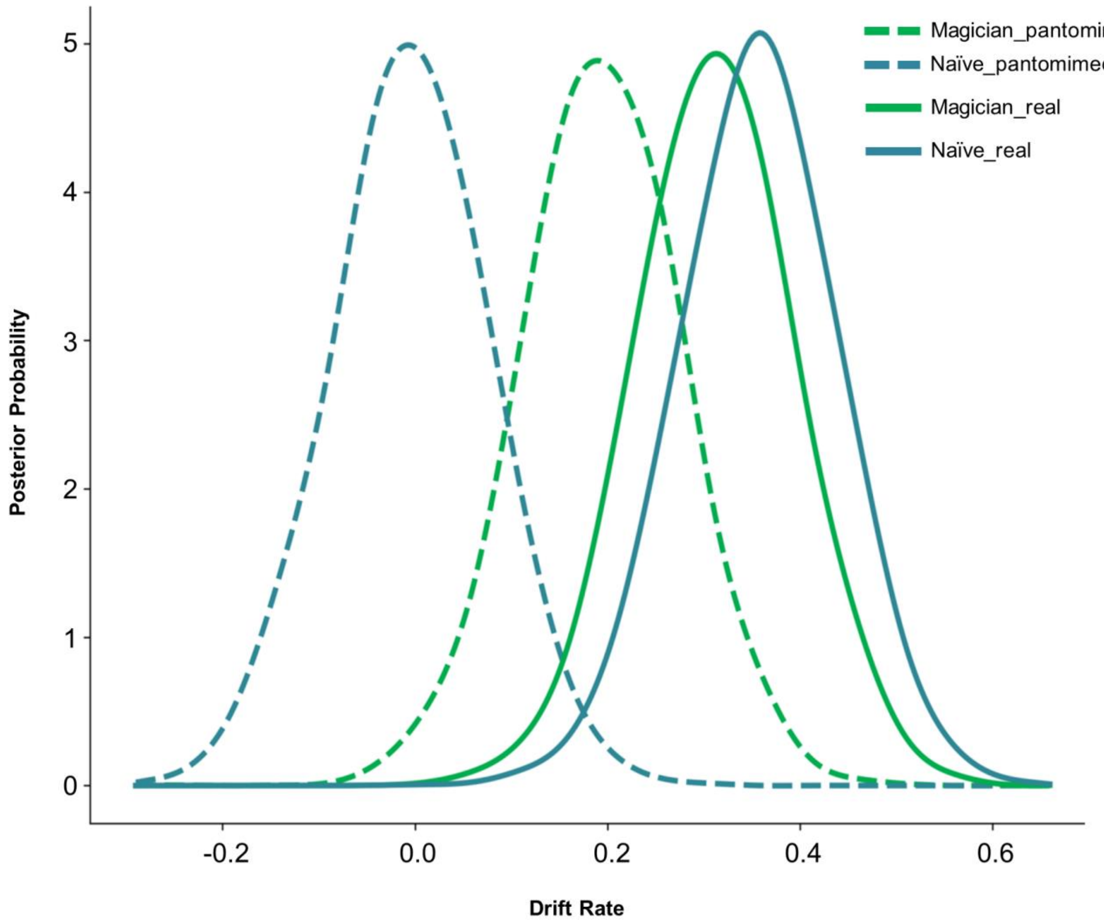


Figure 17. *Posterior distribution densities of drift rates for magicians and naïve while processing real and pantomimed grasps.* Posterior distribution densities for magician_pantomimed (dashed green), naïve_pantomimed (dashed blue), magician_real (continuous green), and naïve_real (continuous blue) drift rates. Significantly greater drift rates were obtained for pantomimed grasps for magicians compared to naïve while no difference was observed between the groups for real grasps. Differences were considered significant when the overlap between distributions was less than 5%.

Reinforcing this interpretation, drift rates were significantly higher than 0 for all conditions (Pp|D [magician_real < 0] < 0.001; Pp|D [magician_pantomimed < 0] < 0.01; Pp|D [naïve_real < 0] < 0.001), except for the processing of pantomimed grasps by naïve (Pp|D [naïve_pantomimed < 0] = 0.49).

4. Discussion

In contrast to the unrealistic efforts of most people, professional magicians can produce very convincing movements with imaginary objects. The present study is the first to show that magicians are also better than naïve at detecting pantomimed grasps, but not real grasps. While experts and naïve could detect real grasps equally well, magicians outperformed naïve in detecting pantomimed grasps. These results argue against a *general advantage* in processing grasping movements as would be expected if magicians were generally more aware of movement kinematics. Rather, they suggest that prolonged practice confers magicians a *specific advantage* in the processing of pantomimed movements.

Evidence that action perception and anticipation is precisely tuned to an individual's acquired motor repertoire comes from sports psychology. Expert performers are better than naïve at predicting the outcome of highly learned and practiced actions, such as predicting the landing position of a volleyball or tennis serve (Abernethy, 1989; Jackson et al., 2006; Müller et al., 2006; Abernethy & Zawi, 2007). Most relevant to the present research, expert performers are also better at detecting deceptive movements. For example, (Sebanz & Shiffrar, 2009) reported that expert basketball players were better than naïve at judging whether a perceived action would lead to a basketball pass or a fake. This suggests a link between motor expertise and the superior detection of nonverbal deception from bodily movement. Our findings suggest a similar link between magicians' experience and the enhanced ability to detect pantomimed grasps. Professional magicians that regularly use pantomimed actions are better than naïve at detecting pantomimed grasps from bodily movement.

In expert-naïve research studies, the influence of motor expertise on action perception is typically investigated by comparing the observation of movement patterns previously learned (and therefore within the observer's *acquired* motor repertoire) and unfamiliar patterns. An interesting aspect of the present study relates to the possibility of comparing patterns within the observer's *acquired* motor repertoire (pantomimed grasps) with fundamental patterns already present at birth (real grasps). This comparison revealed a significant expert-naïve difference. While for naïve, drift rates for pantomimed grasps were close to zero and significantly slower than drift rates for real grasps, for magicians, drift rates showed a substantial overlap between movement types, suggesting that processing of pantomimed grasps was as good as processing of real grasps.

While these findings might be interpreted as indicating that *action re-calibration* mechanisms transfer to action observation, we urge caution, not only because our measurements cannot address this issue, but also because the mechanisms implied in the control of pantomimed movements are still debated (e.g., Holmes et al. 2013; Rinsma et al., 2017). A crucial difference between pantomimed and real grasp executions lies in the way the appropriate motor schema for a given object is triggered. In the pantomimed condition, the motor schema has to be triggered internally, whereas during real object grasp, the physical properties of the object trigger the appropriate motor schema (Niessen et al., 2014). An important task for future work will be to determine to what extent observation of pantomimed grasps recruit motor representations associated with real grasps and whether expertise influences this recruitment. The hypothesis of action re-calibration makes the distinctive prediction that practice in pantomimed grasp execution leads to a shift toward the automatic visuomotor control involved in grasping real objects. To the extent that recalibration applies to observation, we would expect a similar shift in predictive and monitoring processes to occur during observation of pantomimed grasps.

In the current study, we did not record the kinematics of magicians. This limits inferences regarding the potential relationship (if any) between magicians' motor expertise and their readout of pantomimed kinematics. A second limitations, which is intrinsic to most expertise studies in the action observation field, concerns the interpretation and the design. Experts performers, being magicians, basketball players or dancers, have a motor experience of the observed movements (i.e., motor familiarity) and a visual experience of the movement they have learned (i.e., visual familiarity). Despite some evidence showed specific contributes of motor over visual familiarity of expert performers in action understanding abilities (Calvo-Merino et al., 2006; 2010), our design is not able to disentangle whether results are driven by one or both familiarities.

CHAPTER 3

NEURAL UNDERPINNINGS OF ACTION OBSERVATION

Experiment 5: Goal or kinematics?

Beta and alpha oscillations during real and pantomimed grasp observation

1. Introduction

A fundamental issue in cognitive neuroscience is how the brain encodes others' actions. The discovery of a particular class of visuo-motor neurons in the premotor cortex of the nonhuman primates was a potential step further in this field. The preliminary study reported that these neurons were active when the monkey executed a reach-to-grasp movement. Surprisingly, these neurons responded also when the monkey observed another individual performing the same action, even if the monkey was not moving (di Pellegrino et al., 1992). Several investigations have demonstrated the existence of the so-called Mirror Neurons System (MNS) in humans by using behavioral approaches, transcranial magnetic stimulation (TMS), electroencephalography (EEG), functional magnetic resonance imaging (fMRI) and human single-cell recordings (Mukamel et al., 2010; for reviews, see Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010; Rizzolatti & Fogassi, 2014). Some authors uphold that action observation exploits the same neural mechanisms that is necessary for action execution (i.e., mirror neurons), as if observers were performing (i.e., simulating) in their brain the same action they were observing. This simulation is called *action/motor simulation* and is suggested to play a key role in action understanding via action perception (Rizzolatti & Craighero, 2004).

However, an accordance is still missing around *what* mirror neurons' response actually reflects. It has been claimed that MNS activity encodes action goals, and not just the joints' displacement (i.e., movement kinematics) of the observed actions (Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2016). Relevant reports corroborated this argument by showing that MNS responds if an action is directed toward an object (i.e., a present action goal) that is hidden behind a mask such that the observer knows it is there (Umiltà et al., 2001; Villiger et al., 2011). However, these studies lacked a fine-grained kinematics quantification of hand movement, and conclusions on mirror neurons' activity might be questioned. Indeed, at least from a behavioural point of view, converging evidence revealed that humans are able to use movement kinematics to predict the outcome or the goal-object of an observed movement (Abernethy & Zawi 2007; Abernethy et al., 2008; Aglioti et al. 2008; Ambrosini et al., 2011; Stapel et al., 2012; Ansuini et al. 2015; Cavallo et al. 2016). Moreover, most of action-observation studies showed video clips in which movement kinematics was congruent with action goals, leading to possible confounding effects. Therefore, the relative contribution between these two factors has not been properly disentangled.

The main aim of the present research is to elucidate the relative contribution of action goals and movement kinematics in human MNS activity. In human literature, MNS is often investigated within a broader network, defined as Action Observation Network (AON) (Gazzola & Keysers, 2009; Avenanti et al, 2012). Our hypothesis is that AON is sensitive to the congruence/incongruence between action goals and movement kinematics. This idea come from a recent model on AON (Kilner et al., 2007). The authors stated that:

For action observation the essence of this approach is that, given a prior expectation about the goal of the person we are observing, we can predict their motor commands. Given their motor commands we can predict the kinematics on the basis of our own action system. The comparison of this predicted kinematics with the observed kinematics generates a prediction error (Kilner et al., 2007)

Our prediction, therefore, is that when action goals and movement kinematics are incongruent, the comparison between predicted and observed kinematics generates a prediction error and the AON is able to detect the incongruence.

To test this, we investigated brain response during the observation of reach-to-grasp movements. We collected video clips of real (i.e., grasps toward a physically present goal-object) and pantomimed (i.e., grasps toward an imagined, “absent” goal-object) movements (see Chapter 1 – Additional analysis and Chapter 2 - Introduction). Several studies have shown that pantomimed grasps differ distinctively from real grasps in their kinematic parameters (Goodale et al., 1994; Cavina-Pratesi et al. 2011; Holmes et al. 2013; Rinsma et al. 2017). Of interest, this difference varies over time (see Chapter 1 – Additional Analysis). Keeping in mind that in real and pantomimed grasps action goals and movement kinematics are paired congruently (i.e. present-object/real-grasp and absent-object/pantomimed-grasp), we created video clips in which the action goal was incongruent with movement kinematics (i.e., absent-object/real-grasp and present-object/pantomimed-grasp). We showed participants congruent and incongruent video clips and used the electroencephalography (EEG) technique to measure *whether* and *when* observers’ brains will pick up the mismatch between goal-object and movement kinematics.

Box 1.1. Mirror Neurons System in EEG

A corpus of evidence using the electroencephalography (EEG) technique have shown that the observation and the execution of a motor act is accompanied by an event-related desynchronization reflected in a relative decrease in power of sensory-motor alpha (8–13 Hz) and beta (13–30 Hz) frequency bands. These alpha and beta oscillations are thought to reflect neural activation related to the MNS (Babiloni et al., 2002; Muthukumaraswamy et al., 2004; Pineda, 2005; Hari, 2006; Fox et al., 2016; Bimbi et al., 2018; Angelini et al., 2018).

As a control experiment, we run a behavioural experimental session after the EEG experiment. In this session, the same participants of EEG experiment were called back and we assessed their ability to correctly recognize real and pantomimed grasp by only observing hand motion (i.e., the presence/absence of the object were prevented from participants' view). The same movements used for the EEG experiment were showed in the behavioral experiment, at different levels of temporal occlusion. This way, we were able to know whether and when participants were able to explicitly recognize real and pantomimed grasps.

Results suggested that the initial phase of the observed movement is crucial to detect the incongruence between the action goal information and movement kinematics. In particular, beta band oscillations revealed a stronger desynchronization during incongruent compared to congruent movement observation. In addition, alpha band desynchronization revealed that a stronger activation occurred during congruent compared to incongruent movement observation. Results are discussed in terms of predictive and simulative processes.

2. Methods

2.1. Participants

Sixteen participants (8 females, age mean ± SD = 24.18 ± 3.27 years old, age range: 19-31 years old) took part in the experiment. All of them were right handed (Oldfield, 1871), with normal or corrected-to-normal vision, and with no history of either psychiatric or neurological disorders. The research was approved by the local ethical committee (ASL 3 Genovese), and was carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Association General Assembly, 2008). All participants completed an EEG and a Behavioural session. The two sessions were performed one week apart. Each participant provided written informed consent and was paid in return for participation.

2.2. Stimuli

The observed stimuli were video clips of reach-to-grasp movements collected in Experiment 1 (see Chapter 1 – Additional Analysis). Within the space defined via the LDA, the 40 movements that minimized the Mahalanobis distance for each grasp type were selected. This way we identified a final set of 80 representative movements (50% real).

All video clips were cut so as to begin at reach onset and to end immediately after the hand touched (or pantomimed to touch) the glass (i.e. contact time). The duration of the videos varied according to the actual duration of the movement (duration mean ± SE = 983 ± 22 ms, duration range = 640 to 1400 ms). Video clips were further edited using Adobe Premiere Pro CS6 (.avi format, disabled audio, 25 frames/s) and modified using Adobe After Effect CC 2016 (Adobe Systems Software Ltd, Dublin, Ireland).

2.3. EEG session

Video editing. To ensure that movement sequences could be temporally attended, i.e., that participants had enough time to focus on the hand before movement start, 25 (corresponding to 1000 ms), 30 (1200 ms), or 35 (1400 ms) static frames were randomly added at the beginning of each video clip. These static frames depicted the presence/absence of the object and the initial hand posture as displayed in the first frame of the to-be-observed video clip. Before movement onset, 26 additional static frames (1040 ms) were added and an occluder (i.e., a grey rectangular mask, height = 1080, width = 744 pixels) was designed to slide onto the object position during the first 13 of these 26 frames. The remaining 13 static frames were added to separate the end of the sliding of the occluder from the actual onset of the movement. In order to prevent participants to see the presence or the absence of the object during the movement, the occluder masked the object position until the end of each video clip.

In all the video clips, the presence/absence of the object and the grasp type were paired congruently: present-object/real-grasp and absent-object/pantomimed-grasp. We also created an incongruent version of the same video clips: i) we removed the object from the object position in real grasp video clips; ii) we added the object at object position in pantomimed grasp video clips. We also edited a copy of the resulting 160 video clips (80 congruent and 80 incongruent) to include a green frame at the borders of the occluder during the reach-to-grasp movement. The green frame appeared at one time interval (20%, 40%, 60%, or 80% of the normalized reaching duration of each video clip) and lasted until the end of the video clip. These video clips were used for the EEG session as *catch trials*. The final video-set was thus composed by 320 video clips.

Design and procedure. Experimental conditions were obtained by crossing the presence/absence of the object (present-object vs. absent-object) and the grasp type (real-grasp vs. pantomimed-grasp). Therefore, we obtained 2 congruent (present-object /real-grasp; absent-object /pantomimed-grasp) and 2 incongruent (present-object /pantomimed-grasp; absent-object /real-grasp) conditions.

The experiment was run in a quiet, dimly illuminated, and well-ventilated room. Participants seated on a comfortable chair in front of a monitor (1920x1080 pixels, refresh rate = 50 Hz). Instructions were provided before the experiment. Each trial started with a white Fixation Cross (1000 ms), followed by the video clip of a reach-to-grasp movement. The end of the video clip was followed by a 2000 ms black screen that used as Inter-Trial Interval (ITI). Participants were told that they would have observed video clips of real and pantomimed movements; to note, they were not aware about the presence of incongruent conditions. Participants were asked to pay attention to the video clips and only during *catch trials* they had to perform a *time estimation task*: they had to determine the time at which the hand would have lifted the glass or pantomimed the lifting by pressing the ‘0’ key on a keyboard with the right index finger. In the remaining trials (i.e., the *EEG trials*) they had to watch the video clips without providing any response (for a graphical representation of the experimental procedure, see Figure 18).

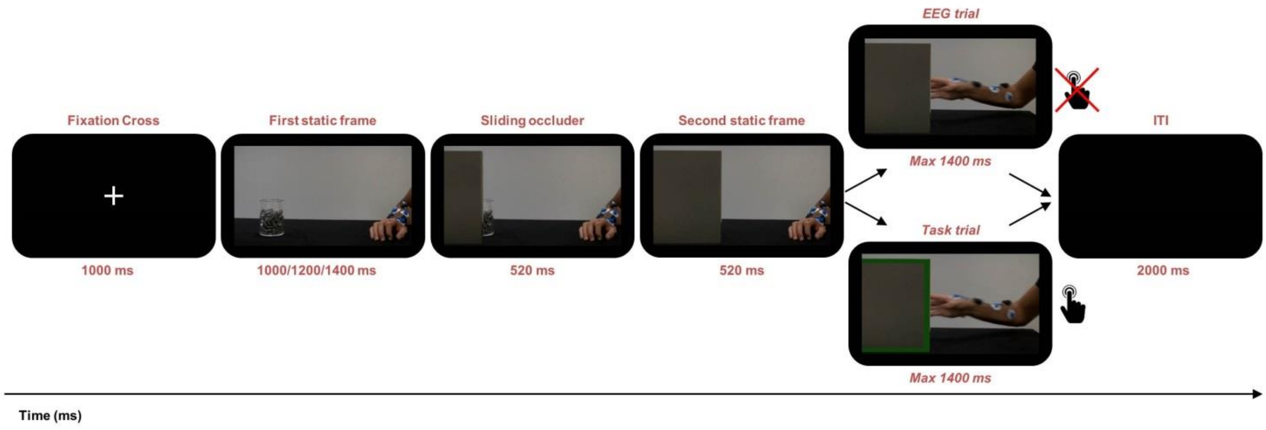


Figure 18 *Trial procedure of the EEG session.* Each trial started with a white Fixation Cross lasting 1000 ms, followed by the video clip of the reach-to-grasp movement. An example of (A) an *EEG trial* and an example of (B) a *catch trial* are illustrated. The end of the video clip was followed by an Inter-Trial Interval (ITI) showing a black screen that lasted for 2000 ms.

Participants completed 8 blocks of 50 *EEG trials* (40 congruent and 10 incongruent trials) and 10 *catch trials* (8 congruent and 2 incongruent trials) each, for a total of 400 *EEG trials* (80% congruent, 20% incongruent) and 80 *catch trials* (80% congruent, 20% incongruent). *EEG* and *catch trials* were presented randomly within each block. After each block, participants had a break of 5 minutes. Before the experimental session, they completed a practice session (30 *EEG trials* and 6 *catch trials*). Stimuli, timing and randomization procedure were controlled using E-Prime software (Version 2.0). The experiment lasted about 75 minutes.

EEG recordings. A 64-channel EEG-System (Brain Amp MR Plus and ActiCap, Brain Products, München, Germany) was used for data acquisition. EEG activity was recorded in the international 10–20 system. The montage included the following scalp positions: Fp1, Fp2, AFz, AF3, AF4, Fz, F1, F2, F3, F4, F5, F6, F7, F8, FCz, FC1, FC2, FC3, FC4, FC5, FC6, FT7, FT8, Cz, C1, C2, C3, C4, C5, C6, T7, T8, CPz, CP1, CP2, CP3, CP4, CP5, CP6, TP7, TP8, Pz, P1, P2, P3, P4, P5, P6, P7, P8, POz, PO3, PO4, PO7, PO8, Oz, O1, O2, and Right and Left Mastoids. Ground and reference electrodes were set at the place of AFz electrode and Left Mastoid (M1), respectively. Vertical and horizontal eye movements were monitored using bipolar electro-oculography (EOG) electrodes positioned above, beneath the right eye, and at the outer canthi of both eyes. EEG signal was amplified with two BrainAmp MR plus amplifiers (Brain Products), digitized at 1,000 Hz. Impedances of all electrodes were kept below 15 kOhm. EEG was submitted to an anti-alising filter and was down-sampled at 500 Hz. EEG signal was acquired in continuous mode using Brain Vision Recorder (Brain Products, München, Germany). During each trial, 11 triggers were delivered, from 0% to 100% in step of 10% of normalized reaching duration. Triggers procedure was controlled using E-Prime software.

EEG signal pre-processing. Data from one participant were discarded due to technical problems during the EEG recording. All the *catch trials* were removed from the pre-processing procedure and not analysed. Thus, *EEG trials* were pre-processed and analysed. Data pre-processing was performed using EEGlab (Delorme & Makeig, 2004). The current line artifact was removed by a notch filter (50 Hz, ± 5 Hz), then EEG signal was band-passed (0.5 to 100 Hz) and down-sampled (250Hz). In order to remove motion and physiological artifacts, such as muscular and skin potentials, we filtered the signal using an adaptive spatial filtering called Artifact Subspace Reconstruction (ASR). The ASR filter is designed to detect and remove high-amplitude data components (for instance, stemming from eye blinks, muscle, and sensor motion) relative to some artifact-free reference data, while recovering EEG background activity that lies in the subspace spanned by the artifact components (Mullen et al., 2015). Constant fixed-source noise/artifacts/signals, such as ocular movements, were removed by means of the Independent Component Analysis (ICA) toolbox in EEGlab (Delorme & Makeig, 2004). Artifacted components were identified by visual inspection and eliminated from the entire signal. Bipolar and mastoids electrodes were removed from continuous data. EEG recordings were re-referenced offline using the average of all connected electrodes. The averaged signal from − 600 to − 200 ms before the ITI offset was used as baseline.

Channels and time windows selection. We had a 2 (*object*: present vs. absent) x 2 (*grasp type*: real vs. pantomimed) x 11 (*time bin*: from 0% up to 100% of the normalized reaching duration) within subject factorial design. In order to isolate the response mostly related to each normalized reaching duration and to reduce the effect of the following overlapped normalized reaching durations, we considered relatively short epochs between 0 and + 400 ms around each *time bin* (trigger). This temporal interval is consistent with previous EEG and MEG action observation studies (Hari et al., 1998; Babiloni et al., 2002; Rossi et al., 2002; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy et al., 2004; Streltsova et al., 2010; Avanzini et al., 2012)

Then, time–frequency decompositions were performed on all the epochs. Event Related Spectral Perturbations (ERSP) were calculated for the baseline and for all single epochs. In order to obtain the ERSP signal, a Fast Fourier Transform (FFT) was computed on a window of 256 ms (Hanning-tapered) with a sliding step of 10 ms. We calculated the ERSP in the alpha (8-13 Hz) and the beta (14-30 Hz) band.

Afterwards, a separate Grand average ERSP matrix for each band was calculated by averaging factors (*object, grasp type,* and *time bin*) and participants ERSP. For each channel and frequency band, a bootstrap of 1000 resampling (with replacement) was calculated using the baseline signal points in order to obtain a baseline distribution. Thus, significant spectral power changes with respect to baseline were quantified by z-tests. Specifically, each time point of each channel of the Grand average ERSP matrix was compared against the relative channel baseline distribution by means of a z-test (alpha level of significance was set to .05). After that, *p* values were corrected for multiple comparison using Holm's method (Holm, 1979). We selected the channel/time window (i.e., *ch/tw*) within the epoch (0-400 ms) in which the ERSP was significantly different from the baseline. Analyses were performed on the selected *ch/tw* (for a graphical representation of a Grand average ERSP matrix and selected *ch/tw*, see Appendix A, Figure 22)..

Dependent measures and data analyses. ERSP minimum value (i.e., *min*), as an indicator of the strongest activation, the latency of ERSP minimum value (i.e., *t_min*), to get a temporal hierarchy in the activation in different scalp areas, and ERSP mean value (i.e., *mean*), as a robust descriptor of the activation, were calculated as Dependent Measures (DMs) (for a similar approach, see Klopp et al., 2001; Makeig, 1993; Makeig et al., 2004). Separately for each band (alpha, beta) and factor (*object*, *grasp type*, and *time bin*), DMs were extracted within the selected *ch/tw* for each participant. DMs extraction was performed using EEGlab (Delorme & Makeig, 2004).

Each DM was submitted to a 2 (*object*: present vs. absent) x 2 (*grasp type*: real vs. pantomimed) x 11 (*time bin*: from 0% up to 100% of the normalized reaching duration) repeated-measures analysis of variance (ANOVA). After that, for each DM, we selected those *ch/tw* that: a) showed a significant 3-ways interaction b) showed at least one significant post-hoc within the 3-ways interaction (for a resume table of all the significant interactions and main effects, see Appendix B). We used post-hoc exploration to identify *time bins* at which there was a significant difference between conditions (present-object/real-grasp, absent-object/pantomimed-grasp, absent-object/real-grasp, present-object/pantomimed-grasp). Then, to test our experimental hypotheses, planned comparisons between congruent (present-object/real-grasp, absent-object/pantomimed-grasp) and incongruent (absent-object/real-grasp, present-object/pantomimed-grasp) conditions were performed on the selected *ch/tw* at each identified *time bin*. Furthermore, to test whether alpha and beta oscillations for single conditions were significantly desynchronized with respect to the baseline, one sample t-tests against the value of 0 were performed (2-tailed, Bonferroni corrected for multiple comparisons). All data analyses were computed using R (R Core Team; Vienna, Austria).

2.3. Behavioural session

Video editing. All the video clips corresponding to the selected 80 movements (see *Stimuli Selection* section) were edited using Adobe Premiere Pro CS6 (.avi format, disabled audio, 25 frames/s) and modified using Adobe After Effect CC 2016 (Adobe Systems Software Ltd, Dublin, Ireland). Each video clip was edited so as to begin at reach onset and to end at contact time. Before each movement onset, 13 (520 ms) static frames were added and a grey rectangular mask (height = 1080, width = 744 pixels) was designed to occlude the object position from participants' view during the entire video clip duration. The size and the position of this mask were kept constant across video clips.

Stimuli, Design and Procedure. Each selected movement was presented at eight levels of temporal occlusion (i.e., the movie could stop from 10% to 80% of normalized reaching duration, in steps of 10%). Participants were asked to judge as accurately and as quickly as possible whether the observed movement was real or pantomimed, by pressing with the right index or the middle finger one of two keys (left or right arrow) on a keyboard. Responses and keys were counterbalanced between participants. Participants were instructed to respond after the end of the video. After indicating a response, they were requested to rate the confidence of their decision on a 4-point scale by pressing a key (from 1 = least confident, to 4 = most confident; see Figure 19). Participants were encouraged to use the entire confidence scale.

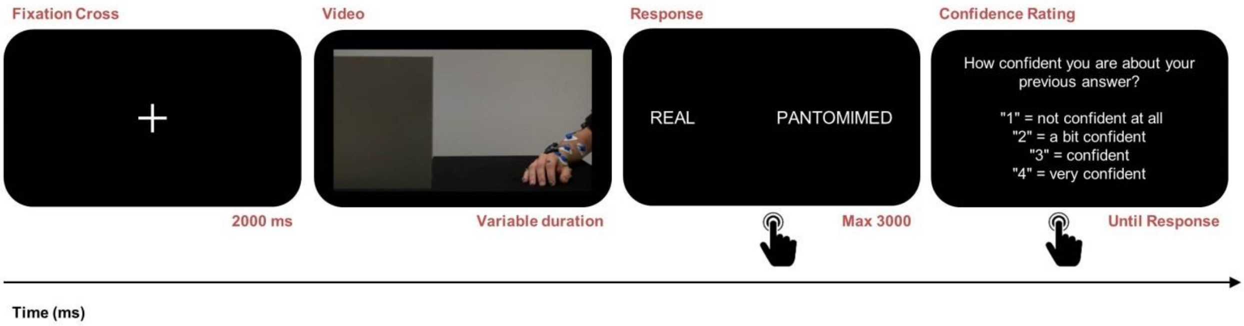


Figure 19 *Trial procedure of the Behavioural session.* Each trial started with a white Fixation Cross lasting 2000 ms. Next, to prevent anticipation and to ensure that participants could temporally attend to movement sequences, the first static frame of each video clip could last for a randomly chosen duration of 4 (corresponding to 160 ms), 8 (320 ms), or 12 (480 ms) frames. The end of the video clip was followed by a Response Slide, on which participants had to respond. Then, the Confidence Rating appeared, and lasted until the response.

Participants completed 8 blocks of 80 trials (50% real grasps), for a total of 640 trials. There was a 5-minutes break between each block. Video clips were pseudo-randomized over the blocks so that within each block any movement occurred only once at one normalized reaching duration. At the beginning of the experimental session, participants were presented with eight video examples (i.e., two for each grasp type, repeated twice) without the temporal and the spatial occlusion, so that they could see the phase during which the agent grasped - or pantomimed to grasp - the glass. Participants also completed a practice session of 16 trials (50% real, each time interval was showed once for grasp type) to familiarize themselves with the task. Stimuli presentation, timing, and randomization procedures were controlled using E-prime version 2.0.10.242 (Psychology Software Tools, Inc., Sharpsburg, PA, USA). The behavioural session lasted about 120 minutes.

Dependent measures and analyses. Participants' correct responses whose Response Times (RTs) deviated by more than ± 2.5 SD were treated as outlier. Outliers and no-response trials (less than 2.5% of all the trials) were removed from further analyses. Signal Detection Theory (SDT) was used to analyse movement judgments parameters (Stanislaw & Todorov, 1999). For each time interval (from 10% up to 80%), pantomimed grasps were arbitrarily designated as 'signal' and real grasps were designated as 'noise'. The proportion of hits and false alarms was calculated for each participant, and combined with confidence ratings to determine points on an empirical receiver operating characteristic (ROC) curve. The ROC curve plots the hit rate as a function of the false alarm rate at different degrees of confidence. Because each response (real, pantomimed) had four ratings associated with it, there were eight possible responses for each trial (graded from the most confident real action to the most confident pantomimed action), resulting in seven points on the ROC curve. The area under the curve (AUC) equals the proportion of times participants would correctly identify the target, if the target and non-target were presented simultaneously. The AUC value can range between 0 and 1. A diagonal curve, which coincides with an AUC of 0.50, corresponds to a situation where the number of hits and false alarms are equal, showing a chance level classification score. On the contrary, an AUC of 1.00, which corresponds to a ROC curve on the left upper bound of the diagonal, indicates a perfect positive prediction with no false positives The AUCs were estimated for each participant at each time interval. To verify participants' ability to infer the *grasp type*, AUC values were tested against the chance level of 0.5 by means a one-sample t-test for each time interval. Alpha level of significance was set to 0.05 and corrected for multiple comparisons using False Discovery Rate correction (Benjamini & Hochberg, 1995).

3. Results

3.2. EEG session

3.2.1. Beta band at 20% of normalized reaching duration

ANOVAs results revealed an '*object*' by '*grasp type*' by '*time bin*' significant interaction in the *mean* measure on FC1 within the 0-400 time window ($F_{(10,140)}$ = 2.663, p = .0005). Post hoc comparisons showed that, at the 20% of normalized reaching duration, when the object was present, beta band for pantomimed grasp was more desynchronized compared to real grasp (mean ± SE: for present-object/pantomimed-grasp = - 2.01 ± 0.34 dB, for present-object/real-grasp = - 1.13 ± .30 dB; $t_{(14)}$ = -4.327, p = .0006). No other *time bins* showed significant differences. Planned comparison between congruent (present-object/real-grasp and absent-object/pantomimed-grasp) and incongruent (absent-object/real-grasp and present-object/pantomimed-grasp) conditions reveald that beta band was significantly more desynchronized during incongruent compared to congruent conditions at 20% of normalized reaching duration ($F_{(1,14)}$ = 11.620, p = .004, see Figure 20, *left panel*).

Paired t-test revealed that, compared to the baseline, beta band was significantly desynchronized in all conditions (i.e., lower than 0; mean ± SE: for present-object/real-grasp = - 1.13 ± .30 dB, for present-object/pantomimed-grasp = - 2.01 ± .34 dB, for absent-object/real-grasp = - 1.98 ± .35 dB, for absent-object/pantomimed-grasp = - 1.42 ± .40 dB; $t_{(14)}$ range = from - 3.478 up to - 5.918, p range = from .002 up to .004, Bonferroni corrected).

3.2.2. Alpha band at 30% of the normalized reaching duration

ANOVAs results revealed an '*object*' by '*grasp type*' by '*time bin*' significant interaction in the *min* measure on FC3 within the 0-400 time window ($F_{(10,140)}$ = 2.028, *p* = .034). Post hoc comparisons using Bonferroni's correction showed that, at the 30% of normalized reaching duration , when the object was absent, alpha band for pantomimed grasp was more desynchronized compared to real grasp (mean ± SE: for absent-object/pantomimed-grasp = - 3.77 ± .69 dB, for absent-object/real-grasp = - 2.15 ± .71 dB; $t_{(14)}$ = - 4.142, *p* = .0009). No other *time bins* showed significant differences. Planned comparison between congruent (present-object/real-grasp and absent-object/pantomimed-grasp) and incongruent (absent-object/real-grasp and present-object/pantomimed-grasp) conditions reveald that alpha band was more desynchronized during congruent compared to incongruent conditions at 30% of normalized reaching duration, ($F_{(1,14)}$ = 14.983, *p* = .002, see Figure 20, *right panel*).

Paired t-test revealed that, compared to the baseline, alpha band was significantly desynchronized in all conditions (i.e., lower than 0 value; mean ± SE: for present-object/real-grasp = - 3.59 ± .53 dB, for present-object/pantomimed-grasp = - 3.15 ± .72 dB, for absent-object/real-grasp = - 2.15 ± .71 dB, for absent-object/pantomimed-grasp = - 3.77 ± .69 dB; $t_{(14)}$ range = from- 3.002 up to- 6.719, *p* range from .0001 up to .01, Bonferroni corrected).

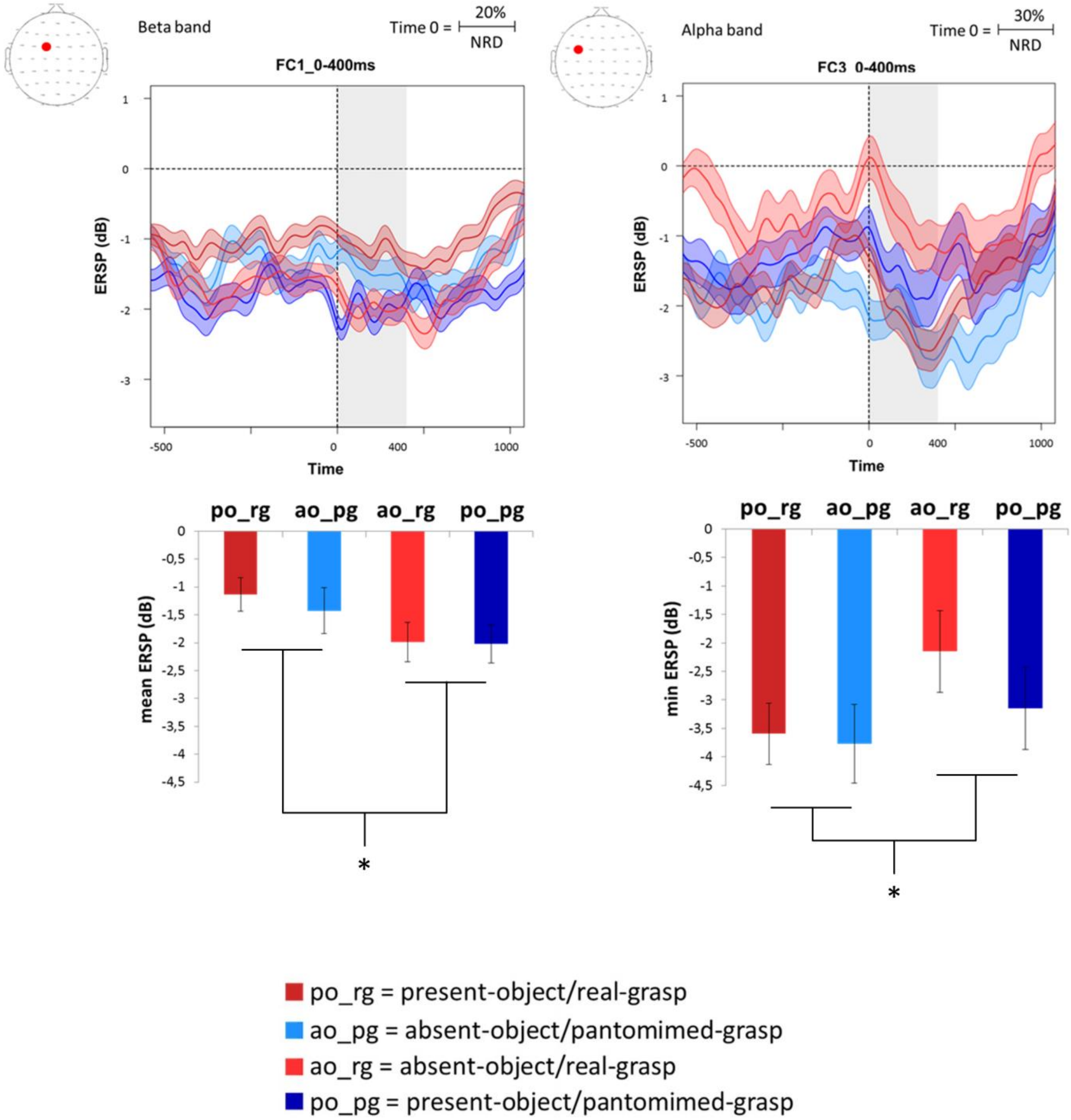


Figure 20 *Alpha and beta modulations***.** Beta modulation anchored at 20% of normalized reaching duration (NRD in the figure) on FC1 from 0 to 400 ms (*left panel*), curve (shaded regions represent ± ½ standard error) and *mean* measure plot (error bars represent ± standard error); alpha modulation anchored at 30% of normalized reaching duration (NRD in the figure) on FC3 from 0 to 400 ms (*right panel*), curve (shaded regions represent ± ½ standard error) and *min* measure plot (error bars represent ± standard error). The asterisk (*) represents the significant planned comparisons.

3.3. Behavioural session

Table 1 summarizes the results of t-tests performed on AUC values for each level of temporal occlusion. Participants' performance was above chance level consistently in time from 40% up to 80% of normalized reaching duration (FDR corrected).

Table 5. *Single t-tests results on AUC means for each levels of temporal occlusions (DoF = 14).*

test value = 0.5				
Levels of temporal occlusion	*AUC mean*	*t value*	*p value*	*95% Confidence interval from the mean*
10%	,5515	2,031	.062	.05147
20%	**,5966**	**3,805**	**.002****	**.09660**
30%	,5591	1,945	.072	.05913
40%	**,6123**	**2,703**	**.017****	**.09667**
50%	**,6169**	**2,980**	**.010****	**.11227**
60%	**,6169**	**3,279**	**.005****	**.11687**
70%	**,5994**	**2,417**	**.030****	**.09940**
80%	**,5909**	**2,636**	**.020****	**.09087**

4. Discussion

The main aim of the present research was to elucidate the relative contribution of action goals and movement kinematics to action understanding in human Mirror Neurons System (MNS), or, more broadly, human Action Observation Network (AON). In particular, we wanted to investigate *whether* and *when* observers' brain can detect the incongruence between goal information and movement kinematics. To do so, we investigated the temporal profile of brain activity during action observation by mean of the electroencephalography (EEG) technique. We manipulated the presence and the absence of a goal-object and the corresponding movement kinematics (i.e., real and pantomimed grasp, respectively) in order to obtain congruent (object-present/real-grasp, object-absent/pantomimed-grasp) and incongruent (object-absent/real-grasp, object-present/pantomimed-grasp) conditions. We investigated how AON activity evolved during the time course of the observed action in a 2 (*object*: present vs. absent) x 2 (*grasp type*: real vs. pantomimed) x 11 (*time bin*: from 0% up to 100% of normalized reaching duration, in steps of 10%) factorial design.

4.1. Brain activity and time anchoring

We found two modulations of AON: a beta desynchronization anchored at 20% of normalized reaching duration, and an alpha desynchronization anchored at 30% of normalized reaching duration.

We have two arguments supporting the idea that these modulations (alpha and beta desynchronizations) are anchored to the specific onset of the corresponding percentage of normalized reaching duration (i.e., *time bin)*. First, these effects are absent on previous and following *time bins*. If a modulation were independent from the time course of the observed movement, we would have found the same effect on more than one *time bin*. However, this is not the case. Second, there was no modulation before the onset of the *time bin* where the effect have been found. The same analysis procedure was run on new epochs segmented from –400 up to 0 ms before each *time bin*. By looking at the same dependent measure and band of the previous analysis, none of the *tw/ch* showed significant 3-ways interactions. This means that, since there were not effects before the *time bins,* alpha and beta modulations are anchored at the onset of the corresponding *time bins*.

Beta oscillations were more desynchronized for incongruent – rather than congruent – conditions. Contrariwise, alpha oscillations were more desynchronized for congruent – rather than incongruent – conditions. The difference in band, time of occurrence, and modulations of AON activity is probably depending on different underlying mechanism involved in action observation.

4.2. Beta band activity and predictive processes

On beta band, a significant 3-ways interaction has been found on FC1 electrode between 0 and 400 ms. Post-hoc analysis showed that a significant difference between conditions was anchored at the *time bin* of 20%. Results of planned comparisons revealed that beta oscillations specifically anchored at the 20% of normalized reaching duration were more desynchronized while observing incongruent (object-absent/real-grasp, object-present/pantomimed-grasp) compared to congruent (object-present/real-grasp, object-absent/pantomimed-grasp) conditions.

This result is consistent with the hypothesis that human brain can detect the incongruence between movement kinematics and goal information, and that this detection is anchored to a specific and early time interval of the observed movement. This finding is coherent with previous studies showing that beta band is modulated by the observed action correctness, being more desynchronized when the action is incorrect (Koelewijn et al., 2008; Meyer et al., 2016).

How can this detection be achieved by observers' brain? Previous research on action execution revealed that beta band is strictly connected to motor behaviour, in particular beta oscillatory activity have an influence on the velocity of voluntary movement (Pogosyan et al,, 2009; Yuan et al., 2010). Of interest, it has been found that beta band responds to the velocity profile of the observed movements (Avanzini et al., 2012; Press et al., 2012; Meirovitch et al., 2015). In the present case, hand velocity of the observed movements was higher for real compared to pantomimed grasps from 10% to 50% of normalized reaching duration (see Chapter 1 – Additional analysis). Since beta modulation was found to be anchored at 20% of normalized reaching duration, our hypothesis is that human brain exploited the difference in hand velocity (from 10% to 20% of normalized reaching duration) to assess the congruence/incongruence between goal information and movement kinematics.

How can this process be functionally mediated? One possibility is that the functional role of Action Observation Network (AON) is essentially predictive (Kilner, Friston, & Frith, 2007; Press et al., 2011; Avenanti et al., 2012; Pezzulo & Cisek, 2016). When participants observed the object presence, a predictive motor command was formed. After that, when a pantomimed grasp was shown, the motor command did not match with the observed kinematics, leading to an increased prediction error. Contrariwise, when participants observed real grasp, the motor command matched with the observed kinematics, and the prediction error remained small. The same process occurred when the object was absent. Beta oscillations might thus reflect the large and the small prediction errors generated by the observation of incongruent (object-absent/real-grasp, object-present/pantomimed-grasp) and congruent (object-present/real-grasp, object-absent/pantomimed-grasp) conditions, respectively.

4.3. Alpha band activity and action simulation

On alpha band, a significant 3-ways interaction has been found on FC3 electrode between 0 and 400 ms. Post-hoc analysis showed that a significant difference between conditions was anchored at the *time bin* of 30%. Results of planned comparisons revealed that alpha oscillations specifically anchored at 30% of normalized reaching duration were more desynchronized while observing congruent (object-present/real-grasp, object-absent/pantomimed-grasp) compared to incongruent (object-absent/real-grasp, object-present/pantomimed-grasp) movements.

This result is coherent with previous action observation studies on mirror neurons activity. Indeed, Kraskov and colleagues (Kraskov et al., 2009) showed that grasping an object, and pantomiming the same action activate mirror neurons in pre-motor brain regions of non-human primates. This evidence was confirmed in humans by using the fMRI technique (Turella et al., 2012).

It has been proposed that alpha band would reflect a predominant sensorimotor function that translates perception into action through action/motor simulation (Sebastiani et al., 2014). Some authors have claimed that *observing others' actions triggers the sensorimotor resources of the observer via an action simulation mechanism that drives the inverse model in order to translate other's action into a motor command, thus allowing the representation of the observed kinematics into a motor format* (Gazzola & Keysers, 2009; Wolpert & Ghahramani, 2000). In the present case, we propose that movement kinematics, translated into motor format, was compared with goal information and, when the two information were congruent - rather than incongruent - a stronger action simulation (i.e., alpha desynchronization) occurred in pre-motor brain regions (i.e. mirror response).

4.4. Limits and future perspectives

Our findings reported new insights on the type of processing occurring within the human AON during action observation. The central advance was the demonstration that the knowledge of the presence (or the absence) of an action goal and the corresponding movement kinematics modulate the activity over the fronto-central regions of AON (FC1 and FC3 are two electrodes that are proposed to overlie pre-motor and motor cortex, Babiloni et al., 2002; Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy et al., 2004; Avanzini et al., 2012; Bimbi et al., 2018; Angelini et al., 2018).

These results support the idea that pre-motor regions of AON play a role in both predictive and simulative processes. The dissociation found in time dimension suggests that, when goal information is provided, predictive processes are first called into play to solve computational challenges posed by action perception, that is, to fill-in ambiguous information between goal information and movement kinematics. Then, action simulation processes are modulated to be more active for those movements congruent with the observed goal (being present or absent). Therefore, action simulation may rather be a consequence of action prediction that occurred once the congruence/incongruence between movement kinematics and action goals has been detected. However, despite the difference in band desynchronization between congruent and incongruent movements anchored at 30% of normalized reaching duration, alpha oscillations were significantly desynchronized for both congruent and incongruent movements. An alternative interpretation is that an *aspecific* action simulation occurred since movement onset, but it was *specified* by the predictive process.

This modulation support the idea that predictive and simulative processes are linked with an inverse relationship: the less an observed action generates a prediction error, the more it is subsequently internally simulated. This last speculation can be a new challenge for future studies. Since EEG has a high temporal resolution but low spatial resolution, fMRI technique can be used to explore precise neural localizations underlying the generation of a prediction error and action simulation. It is plausible that other neural regions coupling action perception and execution (e.g., parietal regions) may contributes to these processes.

It would be intriguing to test the hypothesis on prediction errors using two different objects having the same physical features but different common use. Previous studies showed that movement kinematics convey action intention information that observers can pick up for action understanding (Becchio et al., 2017; Cavallo et al., 2016; Sartori et al., 2011). Might human brain detect a grasp performed with the intention to use an object in an uncommon way? If AON activity is sensitive to familiar/common actions performed on objects, the answer would be positive. This prediction would provide further knowledge on AON learning mechanisms.

4.5. Conclusions

The dissociation between alpha and beta bands is not surprising: the relationship between the two bands is still under debate. In fact,

these rhythms do not seem to reflect a unitary phenomenon, but rather a combination of different processes, potentially involved in the transformation of "seeing into doing" (Pineda, 2005).

The present research revealed that both predictive and simulative mechanisms might be involved in this transformation. Our results suggest that beta and alpha band oscillations may express a generation of a prediction error and an action simulation process, respectively, within the pre-motor regions of human AON. To our knowledge, for the first time, we demonstrated that these mechanisms are anchored to specific time intervals of the observed movements, adding further evidence to the idea that the time course of specific kinematic parameters is crucial for action understanding.

CONCLUSIONS AND FUTURE PERSPECTIVES

In the present thesis, I adopted a multi modal approach and integrated techniques of motion capture, psychophysics, and neurophysiology complimented by advanced multivariate analyses to investigate how pantomimed grasps are executed and which information individuals can obtain by observing real and pantomimed grasps.

All in all, this research showed that:

a. Pantomimed grasps can demonstrate the features of imaginary objects toward which they are executed; in other terms, pantomimed kinematics retains object (weight) information;
b. The way pantomimed grasps are performed differs from real grasps in terms of kinematic profile over time;
c. Real and pantomimed kinematics have enough predictive power to allow action discrimination; in other terms, real and pantomimed grasp can be classified by their kinematics;
d. Early on in the movement, real and pantomimed grasps can be correctly recognized by human observers;
e. Real – and not pantomimed – grasp perception primes object presence;
f. Having a motor expertise on pantomimed grasp execution gives a specific advantage on pantomimed grasp processing;
g. Action Observation Network is sensitive to the congruence/incongruence between goal information and movement kinematics.

The methodological approach followed within this research provided a defined structure to investigate action/perception coupling. The combination of different techniques, paradigms and analytical approaches allowed to establish a relationship between action execution (Experiment 1), action recognition (Experiment 2) and action perception (Experiment 3, 4 and 5) processes. In particular, the technique of temporal occlusion, combined with MANOVA and LDA, led to link the time course of movement kinematics (Experiment 1) with explicit action understanding abilities (Experiment 2) and neural activities during action perception (Experiment 5). Conclusions have been driven indirectly by the speculation that kinematics differences found at a specific percentage of movement have affected discrimination performance and neural activity reported at that specific percentage of movement. Future studies need to directly test this link by investigating the shape and the direction of this relationship. For instance, which kinematic features are more relevant for action understanding? Is there a difference between expert performer and naïve people on the extraction of kinematic features from movement observation? Are there neural oscillations sensitive to specific kinematic features during action execution? Which neural patterns related to movement kinematics are similar between action execution and perception? Which common neural mechanisms underlined action execution, action perception and action recognition?

Whether action recognition relies on action simulation taking place within the motor system (i.e., motor theories) or on the access of conceptual knowledge outside motor areas (i.e., inference theories) is still debated (Hickok, 2009; Kilner & Lemon, 2013; Rizzolatti & Sinigaglia, 2010; Tucciarelli et al., 2015). For instance, an alternative theoretical account posit that action simulation (i.e., mirror response) can be a consequence – rather than a cause – of action recognition, and that it is driven by inferencial processes (Csibra & Gergely, 2007). Even if Experiment 5 results suggested that both simulative and predictive processes occur within the pre-motor area of the brain during action perception, further studies are needed to directly takle this issue. First of all, future research should disentangle action recognition from action perception neural markers during an EEG (or magnetoencephalography, MEG) study. Then, Beamforming technique can be applied to localize signal sources within brain cortical regions. This way, it is possible to shed new lights on the temporal recruitement of motor and non-motor brain regions during both action recognition and action perception processes. Combined techniques (TMS and EEG) can be used to further explore brain connectivity between the recruited brain areas. Time course of brain activity and functional as well as structural connectivity between different brain areas could contribute to better understand how actions of others can be percieved and recognized.

In the current work, the communicative aspect of pantomimed action, as a link between action execution and action recognition, has not been fully investigated. In Experiment 1, it has been demonstrated that pantomimed grasp can convey information about imaginary objects' weight by the way they are executed (Ansuini et al., 2016). Of interest, these differences can be perceptually appreciated by observers to correctly recognize imaginary object weight (Podda et al., 2017). Since neuropsychological and neuroimaging investigation of pantomimed grasp execution, in both clinical and non-clinical populations, has been crucial in order to build brain models of human motor control (Goodale et al., 1994; Milner & Goodale, 1998; Milner & Goodale, 2008; Goodale & Milner, 2018), the exploration of the communicative aspect of pantomimed actions may have a key role for building brain models on the human ability to communicate through actions..

In conclusion, the present exploration of pantomimed grasp improved the current knowledge on the way our brain controls hands' movements and provided new insights on the mechanisms involved in action observation as well as action perception and recognition (for a resume of the achieved results, see Figure 21); however, a lot of work has still to be done. Research on how this specific gesture is executed and perceived is decisive for building more complete models of brain functions. In cognitive neuropsychology, this knowledge can be used to build new and more efficient assessment devices as well as rehabilitation therapies. In basic and applied research, this knowledge can shed new lights on how actions can be exploited for more successful human interactions.

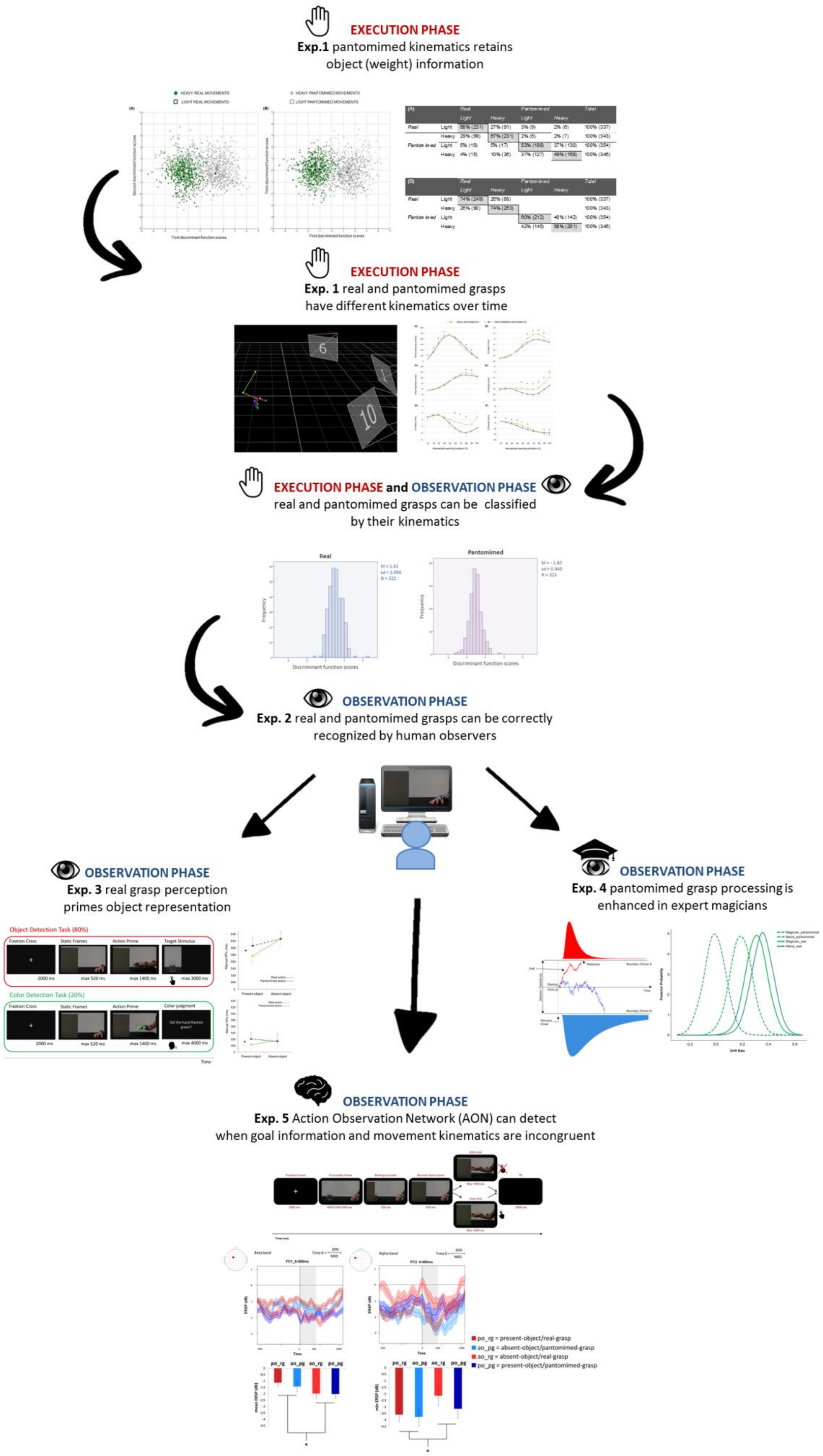


Figure 21 *Graphical pathway of the present research.*

Appendix A

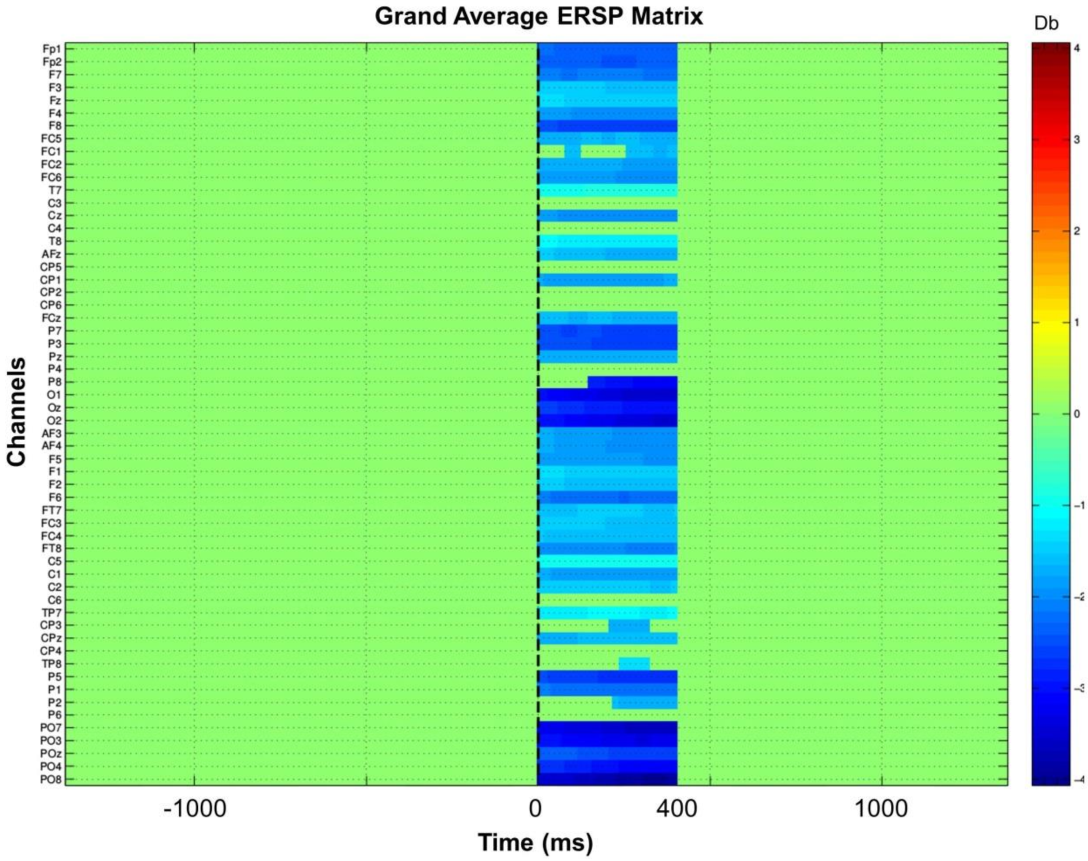


Figure 22 *Grand Average matrix of alpha ERSP*. The figure shows (in shades of blue) alpha modulations (Db) from 0 to 400 ms, averaged across factors (*object*, *grasp type*, and *time bin*) and participants, that were significantly different from baseline.

Appendix B

Table 6. *Resume table of all main effects and significant interactions of ANOVAs results in Experiment 5.* In bold, all the *ch/tw* that showed a 3-way significant interactions; highlighted in yellow, all the *ch/tw* that showed a 3-way significant interactions and in which the exploration of post-hocs revealed a significant difference between conditions at some *time bin*.

Band	Measure	ch/tw	Effect	DFn	DFd	F	p	ges
Alpha	Min	AF4_0_400	timeS	10	140	2.714924	4.46E-03	0.047576115
		C1_0_400	timeS	10	140	3.018177	1.74E-03	0.05545021
		C5_0_400	timeS	10	140	2.3802	1.23E-02	0.041529263
		CP1_0_400	timeS	10	140	3.034021	1.66E-03	0.044288456
		CP3_200_320	timeS	10	140	4.45829	1.86E-05	0.068193721
		CPz_0_400	timeS	10	140	2.956708	2.11E-03	0.043325219
		Cz_0_400	timeS	10	140	2.491337	8.83E-03	0.041484549
		F3_0_400	**action:object:timeS**	**10**	**140**	**1.935972**	**4.51E-02**	**0.018182118**
		F4_0_400	timeS	10	140	2.525799	7.95E-03	0.046611053
		F5_0_400	timeS	10	140	1.939989	4.45E-02	0.038399926
		F6_0_400	timeS	10	140	3.251442	8.40E-04	0.050234056
		F7_0_400	timeS	10	140	3.082073	1.43E-03	0.059446269
		F8_0_400	timeS	10	140	3.943506	9.44E-05	0.05507369
		FC1_252_400	**action:object:timeS**	**10**	**140**	**2.111709**	**2.72E-02**	**0.019376556**
		FC1_72_120	action:object	1	14	6.910729	1.98E-02	0.020803372
		FC1_72_120	action:timeS	10	140	2.010449	3.65E-02	0.015927193
		FC2_0_400	timeS	10	140	2.01875	3.56E-02	0.049025285
		FC2_0_400	object:timeS	10	140	1.97656	4.02E-02	0.020043168
		FC3_0_400	action:timeS	10	140	1.935195	4.52E-02	0.018739894
		FC3_0_400	**action:object:timeS**	**10**	**140**	**2.028384**	**3.46E-02**	**0.021484386**
		FC4_0_400	timeS	10	140	2.692143	4.79E-03	0.04799022
		FC4_0_400	object:timeS	10	140	2.170522	2.29E-02	0.02483767
		FC5_0_400	timeS	10	140	3.020706	1.73E-03	0.057414063
		FC5_0_400	object:timeS	10	140	2.105389	2.77E-02	0.024510939
		FC6_0_400	timeS	10	140	2.895577	2.55E-03	0.043681018
		Fp1_0_400	timeS	10	140	2.417453	1.10E-02	0.047705968
		Fp2_0_400	timeS	10	140	2.277265	1.68E-02	0.04008629
		O1_0_400	timeS	10	140	4.378278	2.39E-05	0.136720083
		O2_0_400	object	1	14	6.246857	2.55E-02	0.024332159
		O2_0_400	timeS	10	140	2.901428	2.51E-03	0.077047191
		Oz_0_400	timeS	10	140	3.41799	4.97E-04	0.098110187
		Oz_0_400	action:object	1	14	6.45636	2.35E-02	0.013977464
		P1_0_400	timeS	10	140	2.226981	1.94E-02	0.043358565
		P2_212_400	timeS	10	140	2.468796	9.45E-03	0.04699084
		P3_0_400	timeS	10	140	2.502877	8.52E-03	0.047271194
		P5_0_400	timeS	10	140	3.24476	8.58E-04	0.065180101
		P5_0_400	object:timeS	10	140	2.093977	2.87E-02	0.020922118
		P7_0_400	object	1	14	6.538328	2.28E-02	0.040468934
		P7_0_400	timeS	10	140	2.895817	2.55E-03	0.058435392

		P7_0_400	object:timeS	10	140	1.917081	4.75E-02	0.018783098
		P8_140_400	timeS	10	140	2.861053	2.84E-03	0.066945376
		PO3_0_400	timeS	10	140	4.92493	4.28E-06	0.111444938
		PO4_0_400	timeS	10	140	3.032292	1.67E-03	0.075180961
		PO7_0_400	timeS	10	140	4.048948	6.76E-05	0.109630325
		PO8_0_400	timeS	10	140	3.289983	7.44E-04	0.084860212
		POz_0_400	timeS	10	140	4.576259	1.28E-05	0.097199942
		Pz_0_400	timeS	10	140	2.3088	1.53E-02	0.040342031
		T7_0_400	timeS	10	140	2.61989	5.97E-03	0.042763343
		TP7_0_400	object:timeS	10	140	2.708291	4.55E-03	0.03178795
Alpha	T_min	AF4_0_400	object	1	14	5.005791	4.20E-02	0.006212545
		AF4_0_400	timeS	10	140	3.356849	6.03E-04	0.066227121
		C1_0_400	timeS	10	140	3.808504	1.45E-04	0.06857292
		C2_0_400	timeS	10	140	4.433167	2.01E-05	0.070144747
		C5_0_400	timeS	10	140	3.09366	1.38E-03	0.059413668
		CP1_0_400	timeS	10	140	6.194331	8.47E-08	0.1018498
		CP3_200_320	timeS	10	140	3.944223	9.42E-05	0.05559117
		CPz_0_400	timeS	10	140	5.14506	2.15E-06	0.10318785
		Cz_0_400	timeS	10	140	3.19515	1.00E-03	0.054007092
		Cz_0_400	action:timeS	10	140	2.866469	2.79E-03	0.043459857
		F4_0_400	action:timeS	10	140	2.351138	1.35E-02	0.027407738
		F5_0_400	object	1	14	4.733023	4.72E-02	0.009662391
		F5_0_400	timeS	10	140	2.90092	2.51E-03	0.055348036
		F6_0_400	timeS	10	140	2.397357	1.17E-02	0.052475567
		F7_0_400	timeS	10	140	7.873645	5.82E-10	0.1199516
		F8_0_400	timeS	10	140	3.218788	9.31E-04	0.070703511
		FC1_72_120	action:object	1	14	4.660097	4.87E-02	0.002026259
		FC2_0_400	timeS	10	140	2.428791	1.07E-02	0.04832025
		FC3_0_400	timeS	10	140	3.755439	1.71E-04	0.068610563
		FC4_0_400	action	1	14	4.988356	4.24E-02	0.006075605
		FC4_0_400	object:timeS	10	140	2.448401	1.00E-02	0.033078268
		FC5_0_400	timeS	10	140	5.878838	2.22E-07	0.102550045
		FC5_0_400	action:object	1	14	7.59794	1.54E-02	0.014368073
		FC6_0_400	timeS	10	140	2.891503	2.59E-03	0.06182774
		Fp1_0_400	timeS	10	140	4.205312	4.12E-05	0.077300858
		Fp2_0_400	object	1	14	9.089058	9.28E-03	0.01002448
		Fp2_0_400	timeS	10	140	3.015769	1.76E-03	0.06641432
		FT7_0_400	timeS	10	140	4.503929	1.61E-05	0.078908591
		FT8_0_400	action	1	14	6.230422	2.57E-02	0.003379738
		FT8_0_400	timeS	10	140	4.42927	2.03E-05	0.07108501
		O1_0_400	timeS	10	140	4.945054	4.02E-06	0.09520032
		O2_0_400	timeS	10	140	2.561349	7.14E-03	0.050862435
		Oz_0_400	timeS	10	140	2.863184	2.82E-03	0.044938617
		P1_0_400	action	1	14	5.30319	3.71E-02	0.005842197
		P1_0_400	timeS	10	140	3.591738	2.87E-04	0.075596347
		P3_0_400	action	1	14	7.878011	1.40E-02	0.006255522
		P3_0_400	timeS	10	140	4.243911	3.65E-05	0.06906725
		P5_0_400	timeS	10	140	4.86829	5.11E-06	0.086417776

		P7_0_400	timeS	10	140	2.882561	2.66E-03	0.04931429
		P8_140_400	timeS	10	140	6.152119	9.63E-08	0.09285949
		PO3_0_400	timeS	10	140	4.494758	1.65E-05	0.08110683
		PO7_0_400	timeS	10	140	4.285658	3.20E-05	0.08113529
		POz_0_400	timeS	10	140	2.682604	4.93E-03	0.05347664
		Pz_0_400	timeS	10	140	3.004237	1.82E-03	0.06435995
		T7_0_400	timeS	10	140	2.351258	1.34E-02	0.0382923
Alpha	Mean	AF3_0_400	timeS	10	140	2.082172	2.97E-02	0.05403517
		AF4_0_400	timeS	10	140	2.952406	2.14E-03	0.060434754
		AFz_0_400	timeS	10	140	1.900398	4.98E-02	0.049387359
		C1_0_400	timeS	10	140	3.057295	1.54E-03	0.068238829
		C2_0_400	timeS	10	140	2.041663	3.33E-02	0.036790724
		C2_0_400	object:timeS	10	140	2.168431	2.31E-02	0.023890288
		C5_0_400	timeS	10	140	2.718468	4.41E-03	0.04805481
		C5_0_400	object:timeS	10	140	2.172781	2.28E-02	0.02162892
		CP1_0_400	timeS	10	140	4.112452	5.53E-05	0.06013501
		CP3_200_320	object	1	14	4.633092	4.93E-02	0.015163161
		CP3_200_320	timeS	10	140	4.732537	7.82E-06	0.074671559
		CPz_0_400	timeS	10	140	3.023881	1.71E-03	0.047122304
		Cz_0_400	timeS	10	140	2.390575	1.20E-02	0.05097522
		Cz_0_400	action:timeS	10	140	2.537505	7.67E-03	0.02471048
		F1_0_400	action:object	1	14	5.442195	3.51E-02	0.02281295
		F3_0_400	action:timeS	10	140	2.335295	1.41E-02	0.021254709
		F4_0_400	timeS	10	140	2.450604	9.98E-03	0.051412504
		F6_0_400	timeS	10	140	2.426618	1.07E-02	0.04759657
		F7_0_400	timeS	10	140	2.975814	1.99E-03	0.07067292
		F8_0_400	timeS	10	140	3.244683	8.58E-04	0.05561443
		FC1_252_400	**action:object:timeS**	**10**	**140**	**2.048839**	**3.27E-02**	**0.01863319**
		FC1_72_120	action:object	1	14	7.422846	1.64E-02	0.02229711
		FC1_72_120	action:timeS	10	140	2.195631	2.13E-02	0.01694361
		FC2_0_400	timeS	10	140	2.01747	3.57E-02	0.051511965
		FC2_0_400	object:timeS	10	140	2.395157	1.18E-02	0.022462764
		FC3_0_400	action:timeS	10	140	1.957863	4.24E-02	0.015054176
		FC4_0_400	timeS	10	140	2.733122	4.22E-03	0.048551457
		FC4_0_400	object:timeS	10	140	2.117163	2.68E-02	0.023696221
		FC5_0_400	timeS	10	140	1.975404	4.03E-02	0.048236355
		FC5_0_400	object:timeS	10	140	2.268573	1.72E-02	0.024831664
		FC6_0_400	timeS	10	140	3.855694	1.25E-04	0.059616654
		FCz_0_400	action:object	1	14	4.785494	4.62E-02	0.01769257
		Fp1_0_400	timeS	10	140	3.447175	4.54E-04	0.084367536
		Fp2_0_400	timeS	10	140	2.846422	2.97E-03	0.064684812
		FT8_0_400	timeS	10	140	2.303135	1.55E-02	0.034195758
		O1_0_400	timeS	10	140	4.278601	3.27E-05	0.143804435
		O1_0_400	action:timeS	10	140	1.933878	4.53E-02	0.012704704
		O2_0_400	object	1	14	5.428519	3.53E-02	0.018500852
		O2_0_400	timeS	10	140	3.094014	1.38E-03	0.087338243
		Oz_0_400	timeS	10	140	3.411651	5.07E-04	0.106877651
		Oz_0_400	action:object	1	14	6.639935	2.19E-02	0.014473145

		P1_0_400	timeS	10	140	2.194656	2.14E-02	0.050848977
		P2_212_400	timeS	10	140	2.521916	8.04E-03	0.054993863
		P3_0_400	timeS	10	140	3.459945	4.36E-04	0.07677501
		P5_0_400	timeS	10	140	3.55726	3.20E-04	0.079334115
		P5_0_400	object:timeS	10	140	1.933526	4.54E-02	0.016819225
		P7_0_400	timeS	10	140	2.743771	4.08E-03	0.064897993
		P8_140_400	timeS	10	140	3.041005	1.62E-03	0.081064894
		PO3_0_400	timeS	10	140	4.977461	3.63E-06	0.127521598
		PO4_0_400	timeS	10	140	2.928178	2.31E-03	0.084294398
		PO7_0_400	timeS	10	140	4.187118	4.37E-05	0.126139484
		PO7_0_400	action:timeS	10	140	2.687095	4.86E-03	0.019326861
		PO7_0_400	object:timeS	10	140	2.029922	3.45E-02	0.014875318
		PO8_0_400	timeS	10	140	3.641175	2.46E-04	0.09819364
		POz_0_400	timeS	10	140	3.947081	9.34E-05	0.107571637
		T7_0_400	timeS	10	140	2.075186	3.03E-02	0.037954236
		T8_0_400	timeS	10	140	2.092918	2.88E-02	0.027738493
Beta	Min	AF3_0_400	timeS	10	140	3.106919	1.32E-03	0.040926637
		AF4_0_400	timeS	10	140	2.340147	1.39E-02	0.02724774
		C1_0_400	timeS	10	140	3.486503	4.01E-04	0.05699202
		C2_0_400	timeS	10	140	2.997565	1.86E-03	0.040984168
		C3_0_400	timeS	10	140	3.510512	3.71E-04	0.06123886
		CP1_0_400	timeS	10	140	4.668154	9.58E-06	0.052888086
		CP2_0_400	action	1	14	4.694847	4.80E-02	0.017249862
		CP2_0_400	timeS	10	140	3.527093	3.52E-04	0.053207508
		CP3_0_400	timeS	10	140	4.137675	5.11E-05	0.060212383
		CP4_0_400	timeS	10	140	2.943462	2.20E-03	0.033990787
		CP6_0_400	timeS	10	140	2.164637	2.33E-02	0.029424771
		CP6_0_400	**action:object:timeS**	**10**	**140**	**3.179174**	**1.05E-03**	**0.033979233**
		CPz_0_400	timeS	10	140	3.671755	2.23E-04	0.052923576
		CPz_0_400	action:timeS	10	140	1.923785	4.66E-02	0.024413998
		Cz_0_400	timeS	10	140	3.950019	9.25E-05	0.05222019
		F1_0_400	object	1	14	5.186177	3.90E-02	0.0429647
		F1_0_400	timeS	10	140	2.83216	3.11E-03	0.035509372
		F2_0_400	timeS	10	140	1.972199	4.07E-02	0.026749525
		F3_0_400	object	1	14	5.928601	2.89E-02	0.040326374
		F3_0_400	timeS	10	140	1.955826	4.26E-02	0.030315565
		F4_0_400	timeS	10	140	3.014994	1.76E-03	0.033744561
		F5_0_400	action:timeS	10	140	2.189442	2.17E-02	0.023978115
		F5_0_400	object:timeS	10	140	2.506661	8.43E-03	0.029515606
		F6_0_400	timeS	10	140	2.123954	2.63E-02	0.02475935
		F6_0_400	action:timeS	10	140	1.970337	4.09E-02	0.02400599
		F7_0_400	timeS	10	140	3.296501	7.29E-04	0.054190757
		F8_0_400	action:timeS	10	140	1.91365	4.80E-02	0.027641949
		FC1_0_400	timeS	10	140	4.626555	1.09E-05	0.06462508
		FC2_0_400	timeS	10	140	4.530733	1.48E-05	0.050989597
		FC3_0_400	timeS	10	140	2.859529	2.86E-03	0.032163178
		FC4_0_400	timeS	10	140	3.049545	1.58E-03	0.030013387
		FC5_0_400	timeS	10	140	2.791447	3.52E-03	0.037320226

		FCz_0_400	timeS	10	140	3.25549	8.29E-04	0.044310888
		Fp1_0_400	timeS	10	140	2.432433	1.05E-02	0.032027896
		Fp1_0_400	action:timeS	10	140	2.13649	2.53E-02	0.023499022
		Fp2_0_400	timeS	10	140	2.160178	2.37E-02	0.026946293
		Fz_0_400	timeS	10	140	2.275386	1.69E-02	0.03299278
		O1_0_400	timeS	10	140	3.706047	2.00E-04	0.074139233
		O2_0_400	timeS	10	140	2.95864	2.10E-03	0.047312286
		Oz_0_400	timeS	10	140	2.875328	2.72E-03	0.052026052
		Oz_0_400	action:object	1	14	5.187811	3.90E-02	0.019980465
		P1_0_400	timeS	10	140	2.717951	4.42E-03	0.043658125
		P2_0_400	action	1	14	4.997642	4.22E-02	0.022415267
		P2_0_400	timeS	10	140	5.620327	4.92E-07	0.076475235
		P3_0_400	timeS	10	140	5.068577	2.73E-06	0.059194301
		P4_0_400	timeS	10	140	4.528726	1.49E-05	0.06080399
		P5_0_400	timeS	10	140	5.128222	2.26E-06	0.061322033
		P6_0_400	timeS	10	140	4.831984	5.72E-06	0.06560853
		P7_0_400	timeS	10	140	3.406587	5.15E-04	0.042607588
		P8_0_400	timeS	10	140	3.710316	1.98E-04	0.050279204
		PO3_0_400	timeS	10	140	4.137523	5.11E-05	0.068857552
		PO4_0_400	timeS	10	140	6.265589	6.82E-08	0.088984549
		PO7_0_400	timeS	10	140	3.548881	3.29E-04	0.058563407
		PO8_0_400	timeS	10	140	4.020683	7.40E-05	0.055344521
		POz_0_400	timeS	10	140	3.511495	3.70E-04	0.058238166
		Pz_0_400	timeS	10	140	2.920951	2.36E-03	0.042234837
Beta	T_min	AF3_0_400	timeS	10	140	3.782325	1.57E-04	0.07012391
		AFz_0_400	timeS	10	140	2.204154	2.08E-02	0.04488428
		C1_0_400	timeS	10	140	14.455896	2.21E-17	0.2128739
		C2_0_400	timeS	10	140	10.811179	1.79E-13	0.155011641
		C3_0_400	timeS	10	140	12.77205	1.24E-15	0.185687519
		C4_0_348	timeS	10	140	4.496529	1.64E-05	0.09174841
		C5_0_400	timeS	10	140	4.544327	1.41E-05	0.08333463
		C6_0_400	timeS	10	140	6.775011	1.47E-08	0.1215632
		C6_0_400	**action:object:timeS**	**10**	**140**	**2.010039**	**3.65E-02**	**0.03114627**
		CP1_0_400	timeS	10	140	14.396888	2.54E-17	0.175298608
		CP1_0_400	**action:object:timeS**	**10**	**140**	**1.911491**	**4.83E-02**	**0.027872193**
		CP2_0_400	timeS	10	140	9.906721	1.99E-12	0.155881733
		CP3_0_400	timeS	10	140	17.76659	1.45E-20	0.242731967
		CP4_0_400	timeS	10	140	8.078456	3.23E-10	0.1494839
		CP5_0_400	timeS	10	140	4.877861	4.96E-06	0.09692971
		CP5_0_400	object:timeS	10	140	1.936315	4.50E-02	0.02485316
		CP6_0_400	timeS	10	140	6.191254	8.55E-08	0.1128182
		CPz_0_400	timeS	10	140	8.941211	2.81E-11	0.144121579
		Cz_0_400	object	1	14	6.623946	2.21E-02	0.011282253
		Cz_0_400	timeS	10	140	8.745843	4.86E-11	0.130529209
		Cz_0_400	action:timeS	10	140	3.249472	8.45E-04	0.054673225
		Cz_0_400	**action:object:timeS**	**10**	**140**	**2.536664**	**7.69E-03**	**0.039239259**
		F1_0_400	timeS	10	140	3.631681	2.53E-04	0.067982065
		F2_0_400	action	1	14	8.260525	1.23E-02	0.011445871

F2_0_400	timeS	10	140	2.651921	5.41E-03	0.049867243
F2_0_400	**action:object:timeS**	**10**	**140**	**2.065329**	**3.12E-02**	**0.024293056**
F3_0_400	timeS	10	140	1.941564	4.43E-02	0.04214432
F4_0_400	timeS	10	140	2.042827	3.32E-02	0.03551017
F5_0_400	timeS	10	140	2.234111	1.90E-02	0.04070331
F5_0_400	action:timeS	10	140	1.986668	3.90E-02	0.03277558
F6_0_400	timeS	10	140	3.127986	1.24E-03	0.05378425
F7_0_400	object	1	14	8.996748	9.56E-03	0.01070282
F7_0_400	timeS	10	140	2.984183	1.94E-03	0.05523576
F8_0_400	timeS	10	140	4.723729	8.04E-06	0.063670983
FC1_0_400	object	1	14	6.77676	2.08E-02	0.00716036
FC1_0_400	timeS	10	140	6.994822	7.64E-09	0.121920454
FC1_0_400	action:timeS	10	140	2.537883	7.66E-03	0.042350394
FC2_0_400	timeS	10	140	7.809282	7.01E-10	0.1349929
FC3_0_400	timeS	10	140	8.908031	3.08E-11	0.135661912
FC3_0_400	action:object	1	14	6.45782	2.35E-02	0.005458668
FC4_0_400	timeS	10	140	3.29763	7.26E-04	0.06318841
FC5_0_400	timeS	10	140	5.480239	7.58E-07	0.092953276
FC6_0_400	timeS	10	140	2.768851	3.78E-03	0.05078247
FCz_0_400	timeS	10	140	7.84899	6.25E-10	0.117257329
FCz_0_400	action:object	1	14	6.03093	2.77E-02	0.0063435
FCz_0_400	**action:object:timeS**	**10**	**140**	**2.034386**	**3.40E-02**	**0.032380666**
Fp1_0_400	timeS	10	140	2.146068	2.46E-02	0.04387481
Fp2_0_400	timeS	10	140	2.305614	1.54E-02	0.04654285
FT7_0_400	timeS	10	140	4.382307	2.36E-05	0.066496462
FT8_0_400	timeS	10	140	2.318044	1.48E-02	0.040263723
FT8_0_400	action:timeS	10	140	2.331785	1.43E-02	0.031592985
Fz_0_400	action	1	14	5.851138	2.98E-02	0.008468978
Fz_0_400	timeS	10	140	4.25311	3.55E-05	0.08123269
O1_0_400	timeS	10	140	6.874942	1.09E-08	0.13550088
O1_0_400	action:timeS	10	140	2.464119	9.58E-03	0.03491592
O2_0_400	timeS	10	140	8.093049	3.10E-10	0.133129115
Oz_0_400	timeS	10	140	9.021011	2.25E-11	0.158746952
Oz_0_400	action:timeS	10	140	2.146841	2.46E-02	0.031465609
P1_0_400	timeS	10	140	10.672008	2.58E-13	0.1564186
P2_0_400	timeS	10	140	12.374123	3.32E-15	0.1975639
P3_0_400	timeS	10	140	17.472187	2.71E-20	0.212029108
P4_0_400	timeS	10	140	7.570845	1.40E-09	0.1506423
P4_0_400	action:timeS	10	140	2.087587	2.92E-02	0.02599744
P5_0_400	timeS	10	140	9.864138	2.23E-12	0.1620644
P5_0_400	action:timeS	10	140	2.686873	4.86E-03	0.04331378
P6_0_400	timeS	10	140	12.227409	4.78E-15	0.1857051
P7_0_400	object	1	14	7.131708	1.83E-02	0.005682641
P7_0_400	timeS	10	140	5.64661	4.53E-07	0.103863077
P7_0_400	action:object	1	14	7.251619	1.75E-02	0.016487206
P8_0_400	timeS	10	140	11.853947	1.22E-14	0.1986645
PO3_0_400	timeS	10	140	8.64628	6.43E-11	0.138658763
PO3_0_400	action:timeS	10	140	2.108681	2.75E-02	0.03313605

		PO4_0_400	timeS	10	140	13.709385	1.29E-16	0.2015104
		PO7_0_400	action	1	14	8.739725	1.04E-02	0.008724583
		PO7_0_400	timeS	10	140	7.514976	1.65E-09	0.128448238
		PO7_0_400	action:timeS	10	140	2.474771	9.28E-03	0.034558683
		PO7_0_400	**action:object:timeS**	**10**	**140**	**2.608904**	**6.17E-03**	**0.038585309**
		PO8_0_400	timeS	10	140	9.091681	1.85E-11	0.1328098
		POz_0_400	object	1	14	11.622278	4.24E-03	0.009411916
		POz_0_400	timeS	10	140	9.756077	2.99E-12	0.164795379
		Pz_0_400	timeS	10	140	11.267519	5.48E-14	0.1696646
		Pz_0_400	**action:object:timeS**	**10**	**140**	**2.188922**	**2.17E-02**	**0.030803**
		T8_0_400	timeS	10	140	2.977025	1.98E-03	0.050124836
		TP7_0_400	timeS	10	140	1.96931	4.10E-02	0.037241379
		TP8_0_400	timeS	10	140	5.18251	1.91E-06	0.08782352
Beta	Mean	AF3_0_400	timeS	10	140	2.654555	5.37E-03	0.037777352
		AF4_0_400	timeS	10	140	1.919815	4.72E-02	0.026806211
		C1_0_400	timeS	10	140	7.25224	3.57E-09	0.108789287
		C2_0_400	timeS	10	140	5.956399	1.75E-07	0.081322178
		C3_0_400	timeS	10	140	5.66045	4.34E-07	0.09664103
		C5_0_400	timeS	10	140	2.488959	8.89E-03	0.03495037
		C6_0_400	timeS	10	140	2.271805	1.70E-02	0.0338158
		CP1_0_400	timeS	10	140	8.866405	3.46E-11	0.105582608
		CP2_0_400	action	1	14	8.619871	1.08E-02	0.031118068
		CP2_0_400	timeS	10	140	5.098571	2.48E-06	0.072936014
		CP3_0_400	timeS	10	140	6.237485	7.43E-08	0.1021679
		CP4_0_400	timeS	10	140	3.867784	1.20E-04	0.0507297
		CP5_0_400	timeS	10	140	3.493484	3.92E-04	0.053708087
		CP6_0_400	timeS	10	140	2.868878	2.77E-03	0.045057807
		CP6_0_400	**action:object:timeS**	**10**	**140**	**2.75292**	**3.97E-03**	**0.030120606**
		CPz_0_400	timeS	10	140	5.605585	5.14E-07	0.077390739
		Cz_0_400	timeS	10	140	7.925181	5.02E-10	0.09338593
		F1_0_400	timeS	10	140	3.312423	6.93E-04	0.043707255
		F2_0_400	timeS	10	140	2.160232	2.37E-02	0.03237914
		F3_0_400	object	1	14	4.628376	4.94E-02	0.035337248
		F3_0_400	timeS	10	140	2.584772	6.65E-03	0.040419036
		F4_0_400	timeS	10	140	3.145902	1.17E-03	0.039855706
		F6_0_400	timeS	10	140	2.026566	3.48E-02	0.0260647
		F6_0_400	action:timeS	10	140	1.922389	4.68E-02	0.02105895
		F7_0_400	timeS	10	140	3.400906	5.25E-04	0.06205318
		FC1_0_400	timeS	10	140	6.167646	9.19E-08	0.091379914
		FC1_0_400	**action:object:timeS**	**10**	**140**	**2.663012**	**5.23E-03**	**0.034488676**
		FC2_0_400	timeS	10	140	5.936908	1.86E-07	0.076617618
		FC3_0_400	timeS	10	140	4.63991	1.05E-05	0.051951195
		FC4_0_400	timeS	10	140	5.69165	3.95E-07	0.064283982
		FC4_0_400	action:timeS	10	140	2.177509	2.25E-02	0.024381435
		FC5_0_400	timeS	10	140	3.297372	7.27E-04	0.046408985
		FC6_0_400	timeS	10	140	3.624531	2.59E-04	0.052608678
		FCz_0_400	timeS	10	140	4.887041	4.82E-06	0.070249725
		Fp1_0_400	timeS	10	140	2.586217	6.62E-03	0.039519761

	Fp1_0_400	action:timeS	10	140	2.732918	4.22E-03	0.027465834
	Fp2_0_400	timeS	10	140	2.153774	2.41E-02	0.02820886
	Fz_0_400	timeS	10	140	2.282807	1.65E-02	0.03643913
	O1_0_400	timeS	10	140	4.938247	4.10E-06	0.110033094
	O2_0_400	timeS	10	140	3.376004	5.68E-04	0.064233869
	Oz_0_400	timeS	10	140	3.228506	9.03E-04	0.06952414
	Oz_0_400	action:object	1	14	5.072147	4.09E-02	0.024711932
	P1_0_400	timeS	10	140	5.416075	9.25E-07	0.090270403
	P2_0_400	timeS	10	140	5.53241	6.45E-07	0.088427794
	P3_0_400	timeS	10	140	6.944752	8.86E-09	0.100476025
	P4_0_400	timeS	10	140	5.390731	1.00E-06	0.077419003
	P5_0_400	timeS	10	140	6.130012	1.03E-07	0.098224589
	P6_0_400	timeS	10	140	5.867292	2.30E-07	0.082244934
	P7_0_400	timeS	10	140	4.952987	3.92E-06	0.0569835
	P8_0_400	timeS	10	140	3.76734	1.65E-04	0.060935803
	PO3_0_400	timeS	10	140	5.041728	2.97E-06	0.106497581
	PO4_0_400	timeS	10	140	6.323573	5.72E-08	0.104515527
	PO7_0_400	timeS	10	140	5.036289	3.02E-06	0.100052941
	PO8_0_400	timeS	10	140	4.491676	1.67E-05	0.074728873
	POz_0_400	timeS	10	140	4.667488	9.60E-06	0.090628261
	Pz_0_400	action	1	14	5.965974	2.84E-02	0.051977044
	Pz_0_400	timeS	10	140	3.992561	8.09E-05	0.066853812
	T8_0_400	action:object	1	14	6.693617	2.15E-02	0.033206442
	TP8_0_400	timeS	10	140	2.228074	1.94E-02	0.034061408

REFERENCES

Abernethy, B. (1989). Expert--novice differences in perception: how expert does the expert have to be? *Canadian Journal of Sport Sciences = Journal Canadien Des Sciences Du Sport*, *14*(1), 27–30.

Abernethy, B., & Zawi, K. (2007). Pickup of essential kinematics underpins expert perception of movement patterns. *Journal of Motor Behavior*, *39*(5), 353–367. https://doi.org/10.3200/JMBR.39.5.353-368

Abernethy, B., Zawi, K., & Jackson, R. C. (2008). Expertise and attunement to kinematic constraints. *Perception*, *37*(6), 931–948. https://doi.org/10.1068/p5340

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, *11*(9), 1109–1116. https://doi.org/10.1038/nn.2182

Alaerts, K., Senot, P., Swinnen, S. P., Craighero, L., Wenderoth, N., & Fadiga, L. (2010). Force requirements of observed object lifting are encoded by the observer's motor system: A TMS study. *European Journal of Neuroscience*, *31*(6), 1144–1153. https://doi.org/10.1111/j.1460-9568.2010.07124.x

Alaerts, K., Swinnen, S. P., & Wenderoth, N. (2010). Observing how others lift light or heavy objects: Which visual cues mediate the encoding of muscular force in the primary motor cortex? *Neuropsychologia*, *48*(7), 2082–2090. https://doi.org/10.1016/j.neuropsychologia.2010.03.029

Ambrosini, E., Costantini, M., & Sinigaglia, C. (2011). Grasping with the eyes. *Journal of Neurophysiology*, *106*(3), 1437–1442. https://doi.org/10.1152/jn.00118.2011

Angelini, M., Fabbri-destro, M., Lopomo, N. F., Gobbo, M., Rizzolatti, G., & Avanzini, P. (2018). Perspective-dependent reactivity of sensorimotor mu rhythm in alpha and beta ranges during action observation : an EEG study. *Scientific Reports*, (May), 1–11. https://doi.org/10.1038/s41598-018-30912-w

Ansuini, C., Cavallo, A., Bertone, C., & Becchio, C. (2014). The visible face of intention: why kinematics matters. *Frontiers in Psychology*, *5*(July), 1–6. https://doi.org/10.3389/fpsyg.2014.00815

Ansuini, C., Cavallo, A., Campus, C., Quarona, D., Koul, A., & Becchio, C. (2016). Are We Real When We Fake? Attunement to Object Weight in Natural and Pantomimed Grasping Movements. *Frontiers in Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00471

Ansuini, C., Cavallo, A., Koul, A., D'Ausilio, A., Taverna, L., & Becchio, C. (2016). Grasping others' movements: Rapid discrimination of object size from observed hand movements. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(7), 918–929. https://doi.org/10.1037/xhp0000169

Ansuini, C., Cavallo, A., Koul, A., Jacono, M., Yang, Y., & Becchio, C. (2015). Predicting Object Size from Hand Kinematics: A Temporal Perspective. *Plos One*, *10*(3), e0120432.

https://doi.org/10.1371/journal.pone.0120432

Avanzini, P., Fabbri-Destro, M., Dalla Volta, R., Daprati, E., Rizzolatti, G., & Cantalupo, G. (2012). The dynamics of sensorimotor cortical oscillations during the observation of hand movements: An EEG study. *PLoS ONE*, *7*(5), 1–10. https://doi.org/10.1371/journal.pone.0037534

Avenanti, A., Annella, L., Candidi, M., Urgesi, C., & Aglioti, S. M. (2012). Compensatory plasticity in the action observation network: Virtual lesions of STS enhance anticipatory simulation of seen actions. *Cerebral Cortex*, *23*(3), 570–580. https://doi.org/10.1093/cercor/bhs040

Azzopardi, P., & Cowey, A. (1997). Is blindsight like normal , near-threshold vision ? *Proc. Natl. Acad. Sci*, *94*(December), 14190–14194.

Babiloni, C., Babiloni, F., Carducci, F., Cincotti, F., Cocozza, G., Del Percio, C., Rossini, P. M. (2002). Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: A high-resolution EEG study. *NeuroImage*, *17*(2), 559–572. https://doi.org/10.1016/S1053-8119(02)91192-4

Bartolo, A., Cubelli, R., Sala, S. Della, & Drei, S. (2003). Pantomimes are special gestures which rely on working memory. *Brain and Cognition*, *53*(3), 483–494. https://doi.org/10.1016/S0278-2626(03)00209-4

Becchio, C., Koul, A., Ansuini, C., Bertone, C., & Cavallo, A. (2017). Seeing mental states : An experimental strategy for measuring the observability of other minds. *Physics of Life Reviews*, *1*(October), 1–14. https://doi.org/10.1016/j.plrev.2017.10.002

Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate : A Practical and Powerful Approach to Multiple Testing. *Royal Statistical Society*, *57*(1), 289–300.

Bimbi, M., Festante, F., Coud, G., Vanderwert, R. E., Fox, N. A., & Ferrari, P. F. (2018). Simultaneous scalp recorded EEG and local field potentials from monkey ventral premotor cortex during action observation and execution reveals the contribution of mirror and motor neurons to the mu-rhythm, *175*(January), 22–31. https://doi.org/10.1016/j.neuroimage.2018.03.037

Bingham, G. P., Runeson, S., Mace, B., Shaw, B., & Turvey, M. (1987). Kinematic Form and Scaling : Further Investigations on the Visual Perception of Lifted Weight, *13*(2).

Bogacz, R. (2007). Optimal decision-making theories: linking neurobiology with behaviour. *Trends in Cognitive Sciences*, *11*(3), 118–125. https://doi.org/10.1016/j.tics.2006.12.006

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*(1–2), 3–22. https://doi.org/10.1016/S0001-6918(00)00024-X

Brouwer, A. M., Georgiou, I., Glover, S., & Castiello, U. (2006). Adjusting reach to lift movements to sudden visible changes in target's weight. *Experimental Brain Research*, *173*(4), 629–636.

https://doi.org/10.1007/s00221-006-0406-x

Calder, A. J., Burton, A. M., Miller, P., & Young, A. W. (2001). A principal component analysis of facial expressions. *Vision Research*, *41*, 1179–1208.

Calvo-Merino, B., Ehrenberg, S., Leung, D., & Haggard, P. (2010). Experts see it all: Configural effects in action observation. *Psychological Research*, *74*(4), 400–406. https://doi.org/10.1007/s00426-009-0262-y

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*(8), 1243–1249. https://doi.org/10.1093/cercor/bhi007

Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or Doing? Influence of Visual and Motor Familiarity in Action Observation. *Current Biology*, *16*(19), 1905–1910. https://doi.org/10.1016/j.cub.2006.07.065

Carpinella, I., Jonsdottir, J., & Ferrarin, M. (2011). Multi-finger coordination in healthy subjects and stroke patients: A mathematical modelling approach. *Journal of NeuroEngineering and Rehabilitation*, *8*(1). https://doi.org/10.1186/1743-0003-8-19

Carpinella, I., Mazzoleni, P., Rabuffetti, M., Thorsen, R., & Ferrarin, M. (2006). Experimental protocol for the kinematic analysis of the hand: Definition and repeatability. *Gait and Posture*, *23*(4), 445–454. https://doi.org/10.1016/j.gaitpost.2005.05.001

Cavallo, A., Koul, A., Ansuini, C., Capozzi, F., & Becchio, C. (2016). Decoding intentions from movement kinematics. *Scientific Reports*, *6*(November), 37036. https://doi.org/10.1038/srep37036

Cavina-Pratesi, C., Kuhn, G., Ietswaart, M., & da Milner, A. D. (2011). The magic grasp: Motor expertise in deception. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0016568

Costantini, M., Ambrosini, E., Scorolli, C., & Borghi, A. M. (2011). When objects are close to me: Affordances in the peripersonal space. *Psychonomic Bulletin and Review*, *18*(2), 302–308. https://doi.org/10.3758/s13423-011-0054-4

Craighero, L., Fadiga, L., Rizzolatti, G., & Umilta, C. (1998). Visuomotor Priming. *Visual Cognition*, *5*(1–2), 109–125. https://doi.org/10.1080/713756780

Csibra, G., & Gergely, G. (2007). “ Obsessed with goals ”: Functions and mechanisms of teleological interpretation of actions in humans. *Acta Psychologica*, *124*, 60–78. https://doi.org/10.1016/j.actpsy.2006.09.007

De Renzi, E. (1985). Methods of limb apraxia examination and their bearing on the interpretation of the disorder. *Neuropsychological Studies of Apraxia and Related Disoders*, 45–64.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open sorce toolbox for analysis of single-trail EEG dynamics including independent component anlaysis. *Journal of Neuroscience Methods*, *134*, 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research*, *91*(1), 176–180. https://doi.org/10.1007/BF00230027

Dowell, L. R., Mahone, E. M., & Mostofsky, S. H. (2009). Associations of Postural Knowledge and Basic Motor Skill With Dyspraxia in Autism: Implication for Abnormalities in Distributed Connectivity and Motor Learning. *Neuropsychology*, *23*(5), 563–570. https://doi.org/10.1037/a0015640

Dunovan, K. E., Tremel, J. J., & Wheeler, M. E. (2014). Prior probability and feature predictability interactively bias perceptual decisions. *Neuropsychologia*, *61*, 210–221. https://doi.org/10.1016/j.neuropsychologia.2014.06.024

Eastough, D., & Edwards, M. G. (2007). Movement kinematics in prehension are a V ected by grasping objects of di V erent mass, 193–198. https://doi.org/10.1007/s00221-006-0749-3

Efron, B. (1982). *The Jackknife, the Bootstrap and Other Resampling Plans*. Society for Industrial and Applied Mathematics. https://doi.org/10.1137/1.9781611970319

Ewen, J. B., Lakshmanan, B. M., Pillai, A. S., McAuliffe, D., Nettles, C., Hallett, M., Mostofsky, S. H. (2016). Decreased Modulation of EEG Oscillations in High-Functioning Autism during a Motor Control Task. *Frontiers in Human Neuroscience*, *10*(May), 1–11. https://doi.org/10.3389/fnhum.2016.00198

Fazio, P., Cantagallo, A., Craighero, L., D’ausilio, A., Roy, A. C., Pozzo, T., Fadiga, L. (2009). Encoding of human action in Broca’s area. *Brain*, *132*(7), 1980–1988. https://doi.org/10.1093/brain/awp118

Finkel, L., Hogrefe, K., Frey, S. H., Goldenberg, G., & Randerath, J. (2018). It takes two to pantomime: Communication meets motor cognition. *Ynicl*. https://doi.org/10.1016/j.nicl.2018.06.019

Flanagan, J. R., Bowman, M. C., & Johansson, R. S. (2006). Control strategies in object manipulation tasks, 650–659. https://doi.org/10.1016/j.conb.2006.10.005

Fox, N. A., Yoo, K. H., Bowman, L. C., Cannon, E. N., Ferrari, P. F., Bakermans-Kranenburg, M. J., Van IJzendoorn, M. H. (2016). Assessing human mirror activity With EEG mu rhythm: A meta-analysis. *Psychological Bulletin*, *142*(3), 291–313. https://doi.org/10.1037/bul0000031

Friedemann, P., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, *11*, 351–360. https://doi.org/10.1002/poc.735

Fukui, T., & Inui, T. (2013). How Vision Affects Kinematic Properties of Pantomimed Prehension Movements. *Frontiers in Psychology*, *4*(February), 1–8. https://doi.org/10.3389/fpsyg.2013.00044

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex.pdf.

Brain. https://doi.org/10.1093/brain/119.2.593

Gallivan, J. P., Cant, J. S., Goodale, M. A., & Flanagan, J. R. (2014). Representation of Object Weight in Human Ventral Visual Cortex. *Current Biology*, *24*, 1866–1873. https://doi.org/10.1016/j.cub.2014.06.046

Gazzola, V., & Keysers, C. (2009a). The Observation and Execution of Actions Share Motor and Somatosensory Voxels in all Tested Subjects : Single-Subject Analyses of Unsmoothed fMRI Data, (June). https://doi.org/10.1093/cercor/bhn181

Gazzola, V., & Keysers, C. (2009b). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: Single-subject analyses of unsmoothed fMRI data. *Cerebral Cortex*, *19*(6), 1239–1255. https://doi.org/10.1093/cercor/bhn181

Gold, J. I., & Shadlen, M. N. (2007). The Neural Basis of Decision Making. *Annual Review of Neuroscience*, *30*(1), 535–574. https://doi.org/10.1146/annurev.neuro.29.051605.113038

Goldenberg, G. (2013). Apraxia. *Wiley Interdisciplinary Reviews: Cognitive Science*, *4*(5), 453–462. https://doi.org/10.1002/wcs.1241

Goldenberg, G. (2016). Apraxia. *Oxford Textbook of Cognitive Neurology and Dementia*, (April), 173–182. https://doi.org/10.1093/med/9780199655946.003.0016

Goldenberg, G. (2017). Facets of Pantomime. *Journal of the International Neuropsychological Society*, *23*(2), 121–127. https://doi.org/10.1017/S1355617716000989

Goldenberg, G., Hartmann, K., & Schlott, I. (2003). Defective pantomime of object use in left brain damage: Apraxia or asymbolia? *Neuropsychologia*, *41*(12), 1565–1573. https://doi.org/10.1016/S0028-3932(03)00120-9

Goldenberg, G., Hentze, S., & Hermsdörfer, J. (2004). The effect of tactile feedback on pantomime of tool use in apraxia. *Neurology*, *63*(10), 1863–1867. https://doi.org/10.1212/01.WNL.0000144283.38174.07

Goldenberg, G., Hermsdörfer, J., Glindemann, R., Rorden, C., & Karnath, H. O. (2007). Pantomime of tool use depends on integrity of left inferior frontal cortex. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhm004

Good, P. (2005). *Permutation, Parametric and Bootstrap Tests of Hypotheses*. New York: Springer-Verlag. https://doi.org/10.1007/b138696

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*. https://doi.org/10.1016/0028-3932(94)90100-7

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*(10), 1159–1178. https://doi.org/10.1016/0028-3932(94)90100-7

Goodale, M. A., & Milner, A. D. (2018). Two visual pathways – Where have they taken us and where will they lead in future? *Cortex*, *98*(December), 283–292. https://doi.org/10.1016/j.cortex.2017.12.002

Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: An fMRI study of implicit processing. *European Journal of Neuroscience*. https://doi.org/10.1046/j.1460-9568.2003.02695.x

Hamilton, A., Wolpert, D., & Frith, U. (2004). Your Own Action Influences How You Perceive Another Person ' s Action, *14*, 493–498. https://doi.org/10.1016/j

Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Progress in Brain Research*, *159*(6), 253–260. https://doi.org/10.1016/S0079-6123(06)59017-X

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings National Academy of Science, USA*, *95*(December), 15061–15065.

Heilman, K. M., & Watson, R. T. (2008). The disconnection apraxias. *Cortex*. https://doi.org/10.1016/j.cortex.2007.10.010

Helbig, H. B., Steinwender, J., Graf, M., & Kiefer, M. (2010). Action observation can prime visual object recognition. *Experimental Brain Research*, *200*(3–4), 251–258. https://doi.org/10.1007/s00221-009-1953-8

Helm-Estabrooks, N., Fitzpatrick, P. M., & Barresi, B. (1982). Visual Action Therapy for Global Aphasia. *Journal of Speech and Hearing Disorders*, *47*(November 1982), 385–389. https://doi.org/10.1044/jshd.4704.385

Hickok, G. (2009). Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans. *J Cogn Neurosci*, *21*(7), 1229–1243. https://doi.org/10.1162/jocn.2009.21189

Hoeren, M., Kümmerer, D., Bormann, T., Beume, L., Ludwig, V. M., Vry, M. S., Weiller, C. (2014). Neural bases of imitation and pantomime in acute stroke patients: Distinct streams for praxis. *Brain*. https://doi.org/10.1093/brain/awu203

Holmes, S. A., Lohmus, J., Mckinnon, S., Mulla, A., & Heath, M. (2013). Distinct visual cues mediate aperture shaping for grasping and pantomime-grasping tasks. *Journal of Motor Behavior*, *45*(5), 431–439. https://doi.org/10.1080/00222895.2013.818930

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*(5), 849–878. https://doi.org/10.1017/S0140525X01000103

Iacoboni, M. (2009). Imitation, Empathy, and Mirror Neurons. *Annual Review of Psychology*, *60*(1), 653–670. https://doi.org/10.1146/annurev.psych.60.110707.163604

Jackson, R. C., Warren, S., & Abernethy, B. (2006). Anticipation skill and susceptibility to deceptive movement. *Acta Psychologica*, *123*(3), 355–371. https://doi.org/10.1016/j.actpsy.2006.02.002

Jazi, S. D., & Heath, M. (2016). Pantomime-Grasping: Advance Knowledge of Haptic Feedback Availability Supports an Absolute Visuo-Haptic Calibration. *Frontiers in Human Neuroscience*, *10*(May), 1–11. https://doi.org/10.3389/fnhum.2016.00197

Jazi, S. D., & Heath, M. (2017). The spatial relations between stimulus and response determine an absolute visuo-haptic calibration in pantomime-grasping. *Brain and Cognition*, *114*, 29–39. https://doi.org/10.1016/j.bandc.2017.03.002

Jazi, S. D., Yau, M., Westwood, D. a., & Heath, M. (2015). Pantomime-grasping: the "return" of haptic feedback supports the absolute specification of object size. *Experimental Brain Research*. https://doi.org/10.1007/s00221-015-4274-0

Kaiser, H. F. (1958). The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, *23*, 187–200.

Kaiser, H. F. (1960). the application of electronic computers to factor analysis. *Educational and Psychological Measurement*, *XX*(1), 141–151.

Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, *8*(3), 159–166. https://doi.org/10.1007/s10339-007-0170-2

Kilner, J. M., & Lemon, R. N. (2013). What we know currently about mirror neurons. *Current Biology*, *23*(23), R1057–R1062. https://doi.org/10.1016/j.cub.2013.10.051

Klopp, J., Marinkovic, K., Clarke, J., Chauvel, P., Nenov, V., & Halgren, E. (2001). Timing and localization of movement-related spectral changes in the human peri-rolandic cortex: Intracranial recordings. *NeuroImage*, *14*(2), 391–405. https://doi.org/10.1006/nimg.2001.0828

Koelewijn, T., van Schie, H. T., Bekkering, H., Oostenveld, R., & Jensen, O. (2008). Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage*, *40*(2), 767–775. https://doi.org/10.1016/j.neuroimage.2007.12.018

Koul, A., Cavallo, A., Ansuini, C., & Becchio, C. (2016). Doing it your way: How individual movement styles affect action prediction. *PLoS ONE*, *11*(10), 1–14. https://doi.org/10.1371/journal.pone.0165297

Kraskov, A., Dancause, N., Quallo, M. M., Shepherd, S., & Lemon, R. N. (2009). Corticospinal Neurons in Macaque Ventral Premotor Cortex with Mirror Properties: A Potential Mechanism for Action Suppression? *Neuron*, *64*, 922–930. https://doi.org/10.1016/j.neuron.2009.12.010

Króliczak, G., Cavina-Pratesi, C., Goodman, D. a, & Culham, J. C. (2007). What does the brain do when you fake it? An FMRI study of pantomimed and real grasping. *Journal of Neurophysiology*, *97*(3), 2410–2422. https://doi.org/10.1167/6.6.940

Laimgruber, K., Goldenberg, G., & Hermsd, J. (2005). Manual and hemispheric asymmetries in the execution of actual and pantomimed prehension, *43*, 682–692. https://doi.org/10.1016/j.neuropsychologia.2004.09.004

Makeig, S. (1993). Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalography and Clinical Neurophysiology*, *86*(4), 283–293. https://doi.org/10.1016/0013-4694(93)90110-H

Makeig, S., Delorme, A., Westerfield, M., Jung, T. P., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2004). Electroencephalographic brain dynamics following manually responded visual targets. *PLoS Biology*, *2*(6). https://doi.org/10.1371/journal.pbio.0020176

Meirovitch, Y., Harris, H., Dayan, E., Arieli, A., & Flash, T. (2015). Alpha and Beta Band Event-Related Desynchronization Reflects Kinematic Regularities. *Journal of Neuroscience*, *35*(4), 1627–1637. https://doi.org/10.1523/JNEUROSCI.5371-13.2015

Meyer, M., Braukmann, R., Stapel, J. C., Bekkering, H., & Hunnius, S. (2016). Monitoring others' errors: The role of the motor system in early childhood and adulthood. *British Journal of Developmental Psychology*, *34*(1), 66–85. https://doi.org/10.1111/bjdp.12101

Michael, J. (2011). Four models of the functional contribution of mirror systems. *Philosophical Explorations*, *14*(2), 185–194. https://doi.org/10.1080/13869795.2011.569747

Milner, A. D., & Goodale, M. A. (1998). The Visual Brain in Action, (27).

Milner, a. D., & Goodale, M. a. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774–785. https://doi.org/10.1016/j.neuropsychologia.2007.10.005

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-Neuron Responses in Humans during Execution and Observation of Actions. *Current Biology*, *20*(8), 750–756. https://doi.org/10.1016/j.cub.2010.02.045

Mullen, T. R., Kothe, C. A. E., Chi, Y. M., Ojeda, A., Kerth, T., Makeig, S., Cauwenberghs, G. (2015). Real-time neuroimaging and cognitive monitoring using wearable dry EEG. *IEEE Transactions on Biomedical Engineering*, *62*(11), 2553–2567. https://doi.org/10.1109/TBME.2015.2481482

Müller, S., Abernethy, B., & Farrow, D. (2006). How do world-class cricket batsmen anticipate a bowler's intention? *Quarterly Journal of Experimental Psychology (2006)*, *59*(12), 2162–86. https://doi.org/10.1080/02643290600576595

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip, *41*, 152–156. https://doi.org/10.1046/j.1469-8986.2003.00129.x

Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology*, *115*(8), 1760–1766. https://doi.org/10.1016/j.clinph.2004.03.004

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195–201. https://doi.org/10.1016/j.cogbrainres.2003.12.001

Næs, T., & Mevik, B. (2001). Understanding the collinearity problem in regression and discriminant analysis, (October 2000), 413–426. https://doi.org/10.1002/cem.676

Nenadic, Z. (2007). Information discriminant analysis: Feature extraction with an information-theoretic objective. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *29*(8), 1394–1407. https://doi.org/10.1109/TPAMI.2007.1156

Niessen, E., Fink, G. R., & Weiss, P. H. (2014). Apraxia, pantomime and the parietal cortex. *NeuroImage: Clinical*. https://doi.org/10.1016/j.nicl.2014.05.017 Review

Ocampo, B., & Kritikos, A. (2011). Interpreting actions: The goal behind mirror neuron function. *Brain Research Reviews*. https://doi.org/10.1016/j.brainresrev.2011.03.001

Osiurak, F., & Gall, D. Le. (2012). Apraxia : Clinical Types, Theoretical Models, and Evaluation. *Neuroscience*, *1980*(Ea 3082), 66–92. https://doi.org/10.5772/47986

Osiurak, F., Jarry, C., Baltenneck, N., Boudin, B., & Le Gall, D. (2012). Make a gesture and I will tell you what you are miming. Pantomime recognition in healthy subjects. *Cortex*. https://doi.org/10.1016/j.cortex.2011.01.007

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing.” *Brain Research Reviews*, *50*(1), 57–68. https://doi.org/10.1016/j.brainresrev.2005.04.005

Podda, J., Ansuini, C., Vastano, R., Cavallo, A., & Becchio, C. (2017). The heaviness of invisible objects: Predictive weight judgments from observed real and pantomimed grasps. *Cognition*, *168*, 140–145. https://doi.org/10.1016/j.cognition.2017.06.023

Pogosyan, A., Gaynor, L. D., Eusebio, A., & Brown, P. (2009). Boosting Cortical Activity at Beta-Band Frequencies Slows Movement in Humans. *Current Biology*, *19*(19), 1637–1641. https://doi.org/10.1016/j.cub.2009.07.074

Press, C., Cook, J., Blakemore, S.-J., & Kilner, J. (2012). Dynamic Modulation of Human Motor Activity When Observing. *J Neurosci*, *31*(8), 2792–2800. https://doi.org/10.1523/JNEUROSCI.1595-10.2011.Dynamic

Ratcliff, R. (2002). A diffusion model account of response time and accuracy in a brightness discrimination task: Fitting real data and failing to fit fake but plausible data. *Psychonomic Bulletin & Review*, *9*(2), 278–291. https://doi.org/10.3758/BF03196283

Ratcliff, R., & McKoon, G. (2008). The diffusion decision model: theory and data for two-choice decision tasks. *Neural Computation*, *20*(4), 873–922. https://doi.org/10.1162/neco.2008.12-06-420

Ratcliff, R., Smith, P. L., Brown, S. D., & McKoon, G. (2016). Diffusion Decision Model: Current Issues and History. *Trends in Cognitive Sciences*, *20*(4), 260–281. https://doi.org/10.1016/j.tics.2016.01.007

Raymer, A. M., Singletary, F., Rodriguez, A., Ciampitti, M., Heilman, K. M., & Rothi, L. J. G. (2006). Effects of gesture+verbal treatment for noun and verb retrieval in aphasia. *Journal of the International Neuropsychological Society*, *12*(6), 867–882. https://doi.org/10.1017/S1355617706061042

Rinsma, T., van der Kamp, J., Dicks, M., & Cañal-Bruland, R. (2017). Nothing magical: pantomimed grasping is controlled by the ventral system. *Experimental Brain Research*. https://doi.org/10.1007/s00221-016-4868-1

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *TINS*, *21*(1988), 1667–1669. https://doi.org/https://doi.org/10.1016/S0166-2236(98)01260-0

Rizzolatti, G., & Craighero, L. (2004). The Mirror-Neuron System. *Annual Review of Neuroscience*, *27*(1), 169–192. https://doi.org/10.1146/annurev.neuro.27.070203.144230

Rizzolatti, G., & Fogassi, L. (2014). The mirror mechanism: recent findings and perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rstb.2013.0420

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Neuroscience*, *2*(September), 1–10. https://doi.org/10.1038/35090060

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews. Neuroscience*, *11*(4), 264–74. https://doi.org/10.1038/nrn2805

Rizzolatti, G., & Sinigaglia, C. (2016). The mirror mechanism: A basic principle of brain function. *Nature Reviews Neuroscience*, *17*(12), 757–765. https://doi.org/10.1038/nrn.2016.135

Rogers, S. J., Bennetto, L., Mcevoy, R., Pennington, B. F., Development, C., & Oct, N. (1996). Imitation and Pantomime in High-Functioning Adolescents with Autism Spectrum Disorders Imitation and Pantomime in High-Functioning Adolescents with Autism Spectrum Disorders Loisa Bennetto, *67*(5), 2060–2073.

Rose, M. L., Mok, Z., & Sekine, K. (2016). Communicative effectiveness of pantomime gesture in people with aphasia. *International Journal of Language and Communication Disorders*, *52*(2), 227–237. https://doi.org/10.1111/1460-6984.12268

Rossi, S., Tecchio, F., Pasqualetti, P., Ulivelli, M., Pizzella, V., & Romani, G. L. (2002). Somatosensory processing during movement observation in humans, *113*, 16–24.

Roth, L. J. G., & Heilman, K. M. (1984). Acquisition and retention of gesture in apraxic patients. *Brain Lang*, *3*, 426–432.

Rothi, L. J. G., Mack, L., & Heilman, K. M. (1986). Pantomime agnosia. *Journal of Neurology, Neurosurgery, and Psychiatry*, 451–454.

Runeson, S., & Frykholm, G. (1983). Kinematic specification of dynamics as an informational basis for person-and-action perception: Expectation, gender recognition, and deceptive intention. *Journal of Experimental Psychology: General*. https://doi.org/10.1037/0096-3445.112.4.585

Sartori, L., Becchio, C., & Castiello, U. (2011). Cues to intention: The role of movement information. *Cognition*, *119*(2), 242–252. https://doi.org/10.1016/j.cognition.2011.01.014

Schenk, T. (2012). No Dissociation between Perception and Action in Patient DF When Haptic Feedback is Withdrawn. *The Journal of Neuroscience*, *32*(6), 2013–2017. https://doi.org/10.1523/JNEUROSCI.3413-11.2012

Schütz-Bosbach, S., & Prinz, W. (2007). Perceptual resonance: action-induced modulation of perception. *Trends in Cognitive Sciences*, *11*(8), 349–55. https://doi.org/10.1016/j.tics.2007.06.005

Sebanz, N., & Shiffrar, M. (2009). Detecting deception in a bluffing body: the role of expertise. *Psychonomic Bulletin & Review*, *16*(1), 170–175. https://doi.org/10.3758/PBR.16.1.170

Sebastiani, V., de Pasquale, F., Costantini, M., Mantini, D., Pizzella, V., Romani, G. L., & Della Penna, S. (2014). Being an agent or an observer: Different spectral dynamics revealed by MEG. *NeuroImage*, *102*(P2), 717–728. https://doi.org/10.1016/j.neuroimage.2014.08.031

Sim, E. J., Helbig, H. B., Graf, M., & Kiefer, M. (2015). When action observation facilitates visual perception: Activation in visuo-motor areas contributes to object recognition. *Cerebral Cortex*, *25*(9), 2907–2918. https://doi.org/10.1093/cercor/bhu087

Smeets, J. B. J., & Brenner, E. (1999). A New View on Grasping. *Motor Control*, *3*(3), 237–271. https://doi.org/10.1123/mcj.3.3.237

Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & van der Linde, A. (2002). Bayesian Measures of Model Complexity and Fit. *Journal of the Royal Statistical Society Series B (Statistical Methodology)*, *64*(4), 583–639. https://doi.org/10.1111/1467-9868.00353

Stanislaw, H., & Todorov, N. (1999). Calculating of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*(1), 137–149. https://doi.org/10.3758/BF03207704

Stapel, J. C., Hunnius, S., & Bekkering, H. (2012). Online prediction of others' actions: The contribution of the target object, action context and movement kinematics. *Psychological Research*, *76*(4), 434–445. https://doi.org/10.1007/s00426-012-0423-2

Stegmayer, K., Bohlhalter, S., Vanbellingen, T., Federspiel, A., Moor, J., Wiest, R., Walther, S. (2016). Structural brain correlates of defective gesture performance in schizophrenia. *Cortex*. https://doi.org/10.1016/j.cortex.2016.02.014

Stieglitz Ham, H., Bartolo, A., Corley, M., Rajendran, G., Szabo, A., & Swanson, S. (2011). Exploring the relationship between gestural recognition and imitation: Evidence of dyspraxia in autism spectrum disorders. *Journal of Autism and Developmental Disorders*. https://doi.org/10.1007/s10803-010-1011-1

Stock, J. Van Den, Tamietto, M., Zhan, M., Heinecke, A., & Hervais-adelman, A. (2014). Neural correlates of body and face perception following bilateral destruction of the primary visual cortices, *8*(February), 1–10. https://doi.org/10.3389/fnbeh.2014.00030

Streltsova, A., Berchio, C., Gallese, V., & Umilta', M. A. (2010). Time course and specificity of sensory-motor alpha modulation during the observation of hand motor acts and gestures: A high density EEG study. *Experimental Brain Research*, *205*(3), 363–373. https://doi.org/10.1007/s00221-010-2371-7

Tamietto, M., Cauda, F., Celeghin, A., Diano, M., Costa, T., Cossa, F. M., Gelder, B. De. (2014). ScienceDirect Once you feel it , you see it : Insula and sensory-motor contribution to visual awareness for fearful bodies in parietal neglect, *2*.

Tritchler, D. (1984). On Inverting Permutation Tests. *Journal of the American Statistical Association*, *79*(385), 200. https://doi.org/10.2307/2288357

Tucciarelli, R., Turella, L., Oosterhof, N. N., Weisz, N., & Lingnau, A. (2015). MEG Multivariate Analysis Reveals Early Abstract Action Representations in the Lateral Occipitotemporal Cortex. *Journal of Neuroscience*, *35*(49), 16034–16045. https://doi.org/10.1523/JNEUROSCI.1422-15.2015

Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(3), 830–846. https://doi.org/10.1037/0096-1523.24.3.830

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

Turella, L., Tubaldi, F., Erb, M., Grodd, W., & Castiello, U. (2012). Object presence modulates activity within the somatosensory component of the action observation network. *Cerebral Cortex*, *22*(3), 668–679. https://doi.org/10.1093/cercor/bhr140

Umiltà, M. a., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I Know What You Are DoingA Neurophysiological Study. *Neuron*, *31*(1), 155–165. https://doi.org/10.1016/S0896-6273(01)00337-3

Utz, K. S., Hesse, C., Aschenneller, N., & Schenk, T. (2015). Biomechanical factors may explain why grasping violates weber's law. *Vision Research*, *111*(Part A), 22–30. https://doi.org/10.1016/j.visres.2015.03.021

Valyear, K. F., Fitzpatrick, A. M., & McManus, E. F. (2017). The Neuroscience of Human Tool Use. *Evolution of Nervous Systems*, (October), 341–353. https://doi.org/10.1016/B978-0-12-804042-3.00112-3 van Nispen, K., Mieke, W. M. E., van de Sandt-Koenderman, E., & Krahmer, E. (2018). The comprehensibility of pantomimes produced by people with aphasia. *International Journal of Language and Communication Disorders*, *53*(1), 85–100. https://doi.org/10.1111/1460-6984.12328

Varney, N. R., & Benton, A. L. (1982). Qualitative aspects of pantomime recognition defect in aphasia. *Brain and Cognition*, *1*, 132–139.

Viher, P. V., Stegmayer, K., Kubicki, M., Karmacharya, S., Lyall, A. E., Federspiel, A., Walther, S. (2018). The cortical signature of impaired gesturing: Findings from schizophrenia. *NeuroImage: Clinical*, *17*(October 2017), 213–221. https://doi.org/10.1016/j.nicl.2017.10.017

Villiger, M., Chandrasekharan, S., & Welsh, T. N. (2011). Activity of human motor system during action observation is modulated by object presence, 85–93. https://doi.org/10.1007/s00221-010-2522-x

Wagenmakers, E.-J. (2009). Methodological and empirical developments for the Ratcliff diffusion model of response times and accuracy. *European Journal of Cognitive Psychology*, *21*(5), 641–671. https://doi.org/10.1080/09541440802205067

Weir, P. L., Mackenzie, C. L., Marteniuk, R. G., Sherri, L., Frazer, M. B., Weir, P. L., Frazer, M. B. (1991). The Effects of Object Weight on the Kinematics of Prehension. *Journal of Motor Behavior*, *23:3*, 192–204. https://doi.org/10.1080/00222895.1991.10118362

Westwood, D. A., Chapman, C. D., & Roy, E. A. (2000). Pantomimed actions may be controlled by the ventral visual stream, 545–548.

Wheaton, L. A., & Hallett, M. (2007). Ideomotor apraxia: A review. *Progress in Brain Research*, *164*, 61–83. https://doi.org/10.1016/S0079-6123(07)64004-7

Whitwell, R. L., Ganel, T., Byrne, C. M., & Goodale, M. A. (2015). Real-time vision, tactile cues, and visual form agnosia: removing haptic feedback from a "natural" grasping task induces pantomime-like grasps. *Frontiers in Human Neuroscience*, *9*(May), 1–18. https://doi.org/10.3389/fnhum.2015.00216

Whitwell, R. L., Milner, a. D., & Goodale, M. a. (2014). The Two Visual Systems Hypothesis: New Challenges and Insights from Visual form Agnosic Patient DF. *Frontiers in Neurology*, *5*(December), 1–8. https://doi.org/10.3389/fneur.2014.00255

Wiecki, T. V., Sofer, I., & Frank, M. J. (2013). HDDM: Hierarchical Bayesian estimation of the Drift-Diffusion Model in Python. *Frontiers in Neuroinformatics*, *7*(August), 14. https://doi.org/10.3389/fninf.2013.00014

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*(11s), 1212–1217. https://doi.org/10.1038/81497

Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, *11*(7–8), 1317–1329. https://doi.org/10.1016/S0893-6080(98)00066-5

World Medical Association. (2013). World Medical Association Declaration of Helsinki: ethical principles for medical research involving human subjects. *JAMA*, *310*(20), 2191–4. https://doi.org/10.1001/jama.2013.281053

Worthington, A. (2016). Treatments and technologies in the rehabilitation of apraxia and action disorganisation syndrome: A review. *NeuroRehabilitation*, *39*(1), 163–174. https://doi.org/10.3233/NRE-161348

Yuan, H., Christopher, P., & He, B. (2010). Relationship between Speed and EEG Activity during Imagined and Executed Hand Movements. *J Neural Eng*, *7*(2), 26001. https://doi.org/10.1088/1741-2560/7/2/026001

Żywiczyński, P., Wacewicz, S., & Sibierska, M. (2016). Defining Pantomime for Language Evolution Research. *Topoi*, 1–12. https://doi.org/10.1007/s11245-016-9425-9