

Representing tools as hand movements: Early and somatotopic visuomotor transformations



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ABSTRACT

The term affordance defines a property of objects, which relates to the possible interactions that an agent can carry out on that object. In monkeys, canonical neurons encode both the visual and the motor properties of objects with high specificity. However, it is not clear if in humans exists a similarly fine-grained description of these visuomotor transformations. In particular, it has not yet been proven that the processing of visual features related to specific affordances induces both specific and early visuomotor transformations, given that complete specificity has been reported to emerge quite late (300–450 ms). In this study, we applied an adaptation-stimulation paradigm to investigate early cortico-spinal facilitation and hand movements' synergies evoked by the observation of tools. We adapted, through passive observation of finger movements, neuronal populations coding either for precision or power grip actions. We then presented the picture of one tool affording one of the two grasps types and applied single-pulse Transcranial Magnetic Stimulation (TMS) to the hand primary motor cortex, 150 ms after image onset. Cortico-spinal excitability of the Abductor Digiti Minimi and Abductor Pollicis Brevis showed a detailed pattern of modulations, matching tools' affordances. Similarly, TMS-induced hand movements showed a pattern of grip-specific whole hand synergies. These results offer a direct proof of the emergence of an early visuomotor transformation when tools are observed, that maintains the same amount of synergistic motor details as the actions we can perform on them.

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1. Introduction

One striking example of how action and perception are interdependent is the merging of information arising from visual properties of objects with motor information deriving from the possible interaction that an agent can carry out with that object. Combining these types of information gives rise to a property usually referred as affordance (Gibson, 1977; Greeno, 1994). Different shapes offer different affordances, given the different visual-motor associations they allow. According to this view, the perception of an object or tool consists in the translation from visual to motor coordinates and thus can be reflected in the activation of premotor and motor populations of neurons coding for a specific hand configuration.

Studies carried out with single-cell recordings in monkeys supported the affordance concept. Single-unit recordings in the monkey ventral premotor cortex (F5) have shown that most neurons code for object-directed actions and are tuned for a specific grip type (Rizzolatti et al., 1988; Rochat et al., 2010). Among these neurons a subset of

visuomotor neurons (canonical neurons) in F5 discharged selectively for the execution of a hand-object interaction and, crucially, also for the visual presentation of a three-dimensional object alone (Murata et al., 1997). Activity of this population was independent from a subsequent execution of a grasp action and appeared very early after object presentation (100 ms). Canonical neurons have also been identified in the anterior intraparietal cortex (AIP) and in inferior parietal lobule (IPL) (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Bonini et al., 2010). The functional link between AIP, IPL and F5 (Matelli & Luppino, 2001) serves the matching of visual characteristics of the object with the grip that fits best with its geometrical features and its utilization. F5 modulates cortico-spinal outputs from primary motor cortex (Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009; Kraskov, Prabhu, Quallo, Lemon, & Brochier, 2011), giving rise to the effective execution of the action in a muscle- and grasp-specific manner (Prabhu et al., 2009). The canonical neuron network subsends the ability to plan the most efficient motor sequence to interact properly with the object.

Research on humans partially confirmed data on monkeys by using indirect methodologies. For instance, behavioral literature in humans suggested that visually presented objects automatically recruit the motor components that are relevant for the interaction with it (Craigero, Fadiga, Rizzolatti, & Umiltà, 1999). These associations can

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emerge even in the absence of a subsequent movement execution directed to the object (Ellis & Tucker, 2000). Furthermore, objects become associated to certain actions through experience and this form of motor knowledge can be partially evoked by the presentation of the objects, even if the object-action association is irrelevant to the task being performed (Grèzes, Armony, Rowe, & Passingham, 2003a; Tucker & Ellis, 2004). Moreover, it has been shown that stronger affordance effects can be found in response to the perception of objects implying an ongoing movement or action upon the object (for example, door handles rotated as if they were being opened) with respect to the same object in a static position (Tipper, Paul, & Hayes, 2006).

Neuroimaging research provides additional support to the recruitment of frontal and parietal areas during visual processing of manipulable objects (Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Chao & Martin, 2000; Grèzes & Decety, 2002; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003b). This motor recruitment can be shaped through experience, given that the perception of unknown objects, with no clear affordances, can activate the left inferior and middle frontal gyrus and left posterior parietal lobule after an active training on the functional properties of the objects (Bellebaum et al., 2013). Electroencephalography studies show specific and early event related potentials after visual presentation of manipulable tools in motor (Petit, Pegna, Harris, & Michel, 2006) and premotor cortex (Proverbio, Adorni, & D'Aniello, 2011), as well as mu-rhythm desynchronization (Kumar, Riddoch, & Humphreys, 2013), thus reflecting the early activation of action plans.

Regardless of the important confirmations coming from multiple techniques, a large theoretical gap still exists between human and monkey data. In fact, although EEG studies have partially confirmed the early modulation of motor activities in response to affordance-related information, neuroimaging methods could not confirm the affordance specificity part. These techniques lack the necessary combination of high spatial and temporal resolution required for this purpose. Transcranial magnetic stimulation (TMS) on primary motor cortex has partially bridged the gap between neuroimaging and behavioral evidence in humans on one hand and single-unit recordings studies in monkeys on the other hand. Patterns of cortico-spinal facilitation, resembling the object-specific pattern of muscle activity required for a correct grasping have been reported prior to the execution of an overt grasping movement (Cattaneo et al., 2005; Prabhu, Lemon, & Haggard, 2007a; Prabhu et al., 2007b). Noteworthy, no facilitation was detected during object presentation alone (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). These results suggested that information for shaping the hand in order to interact with an object reaches the primary motor cortex – or can be evidenced by TMS – only if the action is being planned. However, more recent studies report cortico-spinal facilitation also during passive observation of objects, with no movement execution requirements. One study reported an increase of motor evoked potentials (MEPs) amplitude in hand muscles during the visual presentation of objects offering an whole hand affordance (i.e. a handle) with respect to the same objects presenting a violation of that affordance (i.e. broken handle) (Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009). Other studies showed the increase of MEPs recorded from *first dorsal interosseus* (FDI) during the observation of objects offering a precision grip affordance (Makris, Hadar, & Yarrow, 2011; Franca et al., 2012), whereas a specific increase in *abductor digiti minimi* (ADM) muscle in response to power grip affordance was not found (Makris et al., 2011). One very recent study was able to detect a specific and differential motor recruitment during the vision of three-dimensional objects offering either precision or power grasp affordances and to characterize the time-course of the effect, which was reflecting muscle specificity after 450 ms from visual onset of the object (Makris, Grant, Hadar, & Yarrow, 2013).

Thus, at present, there is little evidence that the motor recruitment elicited by vision of a tool or manipulable objects is automatically

reflected in a specific motor plan (Makris et al., 2013), matching the action which would be executed to interact with the object. Moreover, no evidence is present to support both a specific and early visuomotor transformation. To understand if parietal-frontal circuits are truly translating visual-geometrical information into specific motor patterns, early differential motor activities must be detected during vision of different tools offering different affordances. An early and specific sensorimotor matching would indicate that this mechanism is not simply prompting a generic motor facilitation effect, but rather is involved in translating visual cues into a motor hand-object interaction frame of reference.

Here we designed a TMS study to test the existence of an early differential pattern of activity induced by precision and power grip affordances. We addressed this question by using the adaptation-stimulation approach, which has been used to induce changes in cortical responsiveness through visual adaptation and to test functional properties of overlapping neural populations (Silvanto, Muggleton, & Walsh, 2008; Silvanto & Muggleton, 2008a, 2008b). Indeed, during adaptation, populations of neurons coding for the adapted stimulus reduce their response and this down-regulation of activity renders them more susceptible to the effects of a TMS pulse (Silvanto & Pascual-Leone, 2008; Cattaneo & Silvanto, 2008; Cattaneo, 2010; Cattaneo et al., 2011). Thus, these protocols allow the selective adaptation of a specific neural population among spatially overlapping populations with different functional properties.

In this study we applied this paradigm of adaptation-stimulation in order to segregate cortical patterns of activations responding to the visual presentation of two different grasp actions – precision or power grip with no object. Then we presented static objects alone offering either precision or power grip affordances. Taking advantage of this approach and the TMS stimulation during passive object viewing, we expected to detect a reliable differential pattern of motor evoked potentials and movement synergies induced by the combination of adapting stimuli with different object's affordances. Single-pulse TMS was delivered over hand primary motor cortex and we measured motor evoked potentials from *abductor pollicis brevis* (APB) and ADM muscles as well as individual finger movements, through a motion capture system. We expected to find an increase in cortico-spinal excitability related to thumb-index opposition, measured through MEPs on APB and with motion capture of the first two fingers, related to the observation of precision grip hand movement followed by precision grip object. Complementary, we expected an increase in the amplitude of MEPs recorded from ADM and an increase of mobilization of the middle, ring and little fingers during the observation of power grip followed by power grip object. Furthermore, the congruency between the intransitive action adaptation and static object presentation enabled testing for the interaction between the systems of neurons coding for objects and those coding for actions' properties, namely canonical and mirror neuron systems. We indeed expected mismatching condition to flatten the specificity of the results. In fact, the adapted action stimulus affected the encoding of the observed grip type, whereas the mismatching object resembled a different grip type, thus causing an increase in the variability of the response, and thus less discriminative power of our dependent variables.

2. Materials and methods

2.1. Sample

13 healthy participants (8 females, mean age 25.5 ± 4.5 years) took part in the study. All participants were right handed according to the Edinburgh Inventory (Italian version, Salmasso & Longoni, 1985) and were screened for exclusion criteria relative to the TMS protocol. The experiments were undertaken with the understanding and written consent of each subject, with the approval of the appropriate local ethics committee, and in compliance with national legislation and the Code of Ethical

Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki). None of the participants reported immediate or delayed undesired effects concerning the stimulation protocol.

2.2. TMS stimulation protocol

TMS was delivered through a figure-eight coil (70 mm) and a Magstim Rapid stimulator (Magstim Co., Whitland, UK). For each subject, the left primary motor cortex was first functionally localized by means of visual inspection of motor evoked potentials (MEPs) recorded through electromyography (Zerowire EMG, Aurion, Italy; CED Power1401, Cambridge Electronics, UK and Signal software version 4 were used for signal data acquisition, with 5 kHz sampling rate) of the right hand *abductor pollicis brevis muscle* (APB) and on the *abductor digiti minimi muscle* (ADM). The hotspot and the resting motor excitability threshold of stimulation were established by individuating the scalp position with the lowest stimulation intensity capable of evoking at least 50 μ V MEPs (Rossini, 1994) on both muscles. During the experiment, single pulse TMS was applied to the identified hotspot, with an intensity of 130% of the resting motor threshold. TMS was triggered through the parallel port controlled by custom-made software in Matlab®.

2.3. Motion-capture recordings

Movements of the fingers were measured via passive motion capture system (VICON system) with 9 near infrared cameras with acquisition frequency set at 100 Hz. 19 reflective markers were placed on classical repere points on the right hand to allow a reconstruction of whole-hand movements evoked by TMS. For each marker were positioned on the nail, on the distal end of the first phalanx, on the head of the metacarpal bone. In addition, one marker was placed on the basis of the metacarpal

bone for the first finger, one on the radial and one on the ulnar styloid process and another one at the center of the metacarpus. This allowed us to apply a model of the hand based on these repere points which simplified the identification and labeling of each marker. The right forearm, from the elbow to the wrist, was placed on an armrest arranged individually to a comfortable height. The hand was dangling, in order to not constrain evoked movement (see Fig. 1, panel B). The three dimensional positions of each marker were recorded from the Vicon system (VICON, MX13 cameras). An external trigger, controlled by custom-made software in Matlab®, was used to synchronize TMS events with 3d data recording and EMG. Data were exported in Matlab® for post processing.

2.4. Stimuli

Two types of stimuli were used in the experiment, short video-clips and pictures, which were presented on a screen in front of the participant during the adaptation and stimulation phase, respectively. The video-clips were short recordings (around 1 s) of two different finger movements: opening and closing of the thumb against the index (precision grip) and opening and closing of all the fingers (power grip). The pictures were photographs of two different objects offering a precision grip (clothes peg) and a power grip affordance (pliers). Noteworthy, the hand movement associated with the pliers required the opposition of all the fingers against the palm (see Fig. 1 panel A), which was chosen on purpose in order to involve the least the thumb in this condition.

2.5. Procedure

A trial consisted in the presentation of one video-clip (hand movement mimicking a precision grip or a power grip), looped for 40 s (adaptation phase) followed by the presentation of one picture (object offering precision grip or power grip affordance),

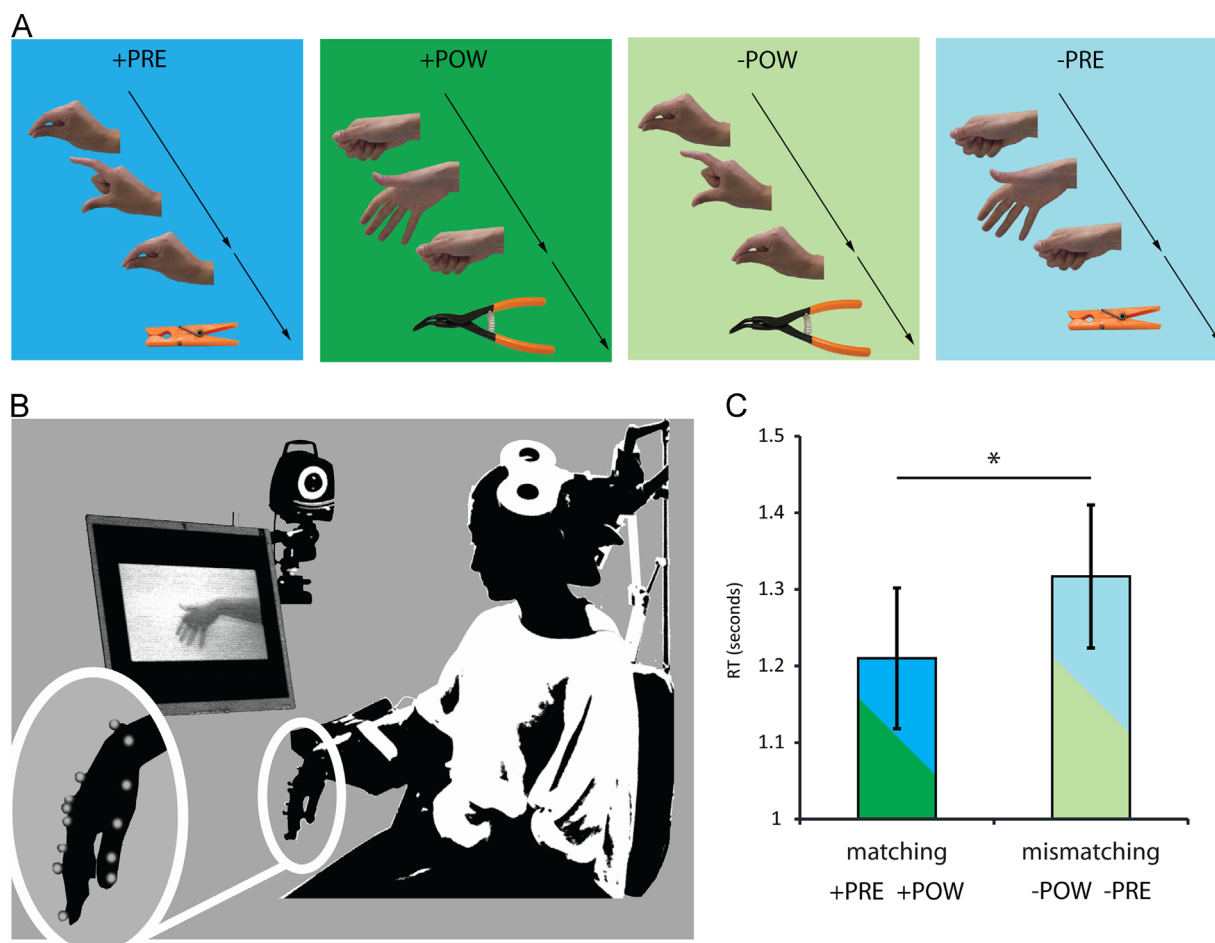


Fig. 1. Experimental setup and reaction times. Panel A. Schematic representations of one trial for each experimental condition. From left to right: +PRE: matching precision affordance; +POW: matching power affordance; -PRE: mismatching precision affordance; -POW: mismatching power affordance. Background color of each panel defines the color used to represent conditions. In each box, the first arrow represents the adaptation phase duration (40 s), the second arrow represents the stimulation phase, during which the participant received a TMS pulse (150 ms from picture onset). Panel B. Schematic representation of the setup. The participant was seated in front of a computer screen displaying the stimuli. TMS coil and one infrared camera of the motion capture system are shown, on the left is superposed a magnification of the hand position and of the markers placement. Panel C. Mean reaction times (s) for the matching (half blue half green sharp color bar) and mismatching (half blue half green faded color bar) conditions, showing shorter RTs for matching conditions with respect to mismatching ones. The asterisk represents a statistically significant difference (main effect of congruency: $p < 0.05$). The bars represent standard error of the means.

which triggered the TMS pulse after 150 milliseconds from its onset (stimulation phase). TMS timing was selected on the basis of previous studies results together with the aim to detect early muscle-specific dissociations in cortico-spinal excitability (see Discussion). The participant was required to answer if the object presented in the picture matched or not the hand movement in the video-clip by pressing the corresponding button on a response pad (behavioral testing phase) with the left hand (ipsilateral to the stimulated hemisphere). The picture disappeared and was replaced by a blank screen as soon as a button was pressed by the participant. After a variable delay of around 2 s, a new trial started. Reaction times (delay between picture onset and button press) and accuracy (correctness of response) were collected for each trial. Custom-made software using the Psychtoolbox functions running in Matlab® was used to present stimuli, trigger TMS, EMG and VICON system recordings and to detect button presses on the response pad.

The experimental design was a 2 (*affordance*: precision [PRE], power [POW]) × 2 (*congruency of adaptation*: matching [+], mismatching [−]) with respect to *affordance*) within-subject factorial design. The four resulting combinations of levels (Fig. 1, panel A) were repeated 20 times each, leading to a total of 80 trials for the completion of the experimental session, lasting around 1 h and 30 min.

2.6. Analysis

The data collected (through electromyography, motion capture and behavioral testing) was processed in Matlab and analyzed using R statistical package (R Development Core Team, 2008). All variables entered the same 2 × 2 factorial within-subject Analysis of Variance (ANOVA), using *affordance* (precision [PRE] grip *affordance* and power [POW] grip *affordance*) and *congruency* (matching [+]) and mismatching [−]) adaptation video-clip with respect to *affordance* presented) as within-subject factors. Whenever an interaction between the two factors was found, post-hoc comparisons were performed by means of multiple t-tests with Bonferroni adjustment (true alpha level for four comparisons: 0.0125) in order to identify the conditions that were responsible for the interaction. Different processing was required depending on the measures under exam in order to clean data from outliers and artifacts. In general, reaction times and motion-related measures (MEPs and motion capture data) were treated independently (i.e. a trial discarded from MEP analysis due to an excessive contraction of the muscle could be anyhow considered for reaction times analysis). This was performed given that these measures are related to different processes and the independent removal of artifacts from data may guarantee the replication of these measures separately. Proportion of correct responses was calculated for each condition in order to obtain mean accuracy measures. Incorrect responses, considered indicative of a lack of attention with respect to the stimuli, were used to discard trials from subsequent analysis on the other measures collected (RTs, MEPs, Motion capture recordings).

Reaction times exceeding 2 standard deviations from the average reaction time across all subjects (mean ± standard deviation 1.313 ± 0.567 s) were discarded as outliers (around 3% of trials).

MEPs data was processed for artifacts removal due to excessive contraction in the muscle prior to TMS pulse (3% of trials for APB muscle recordings, 5% of trials for ADM muscle recordings). Subsequently, we measured peak-to-peak amplitude of motor evoked potentials and then z-transformed it at a single-subject level.

Data recorded through the VICON system were collected on 10 subjects out of the 13 subjects of the experimental sample due to technical issues. The markers placed on the nail of the fingers were analyzed to detect the onset of the movement after TMS pulse. The distance between the position of the markers on the nails and the marker placed on the center of the metacarpus was calculated and the maximum peak of distance with respect to rest distance was extracted for each trial, as indicative of movement amplitude. Trials with no clear peak (due to excessive and repetitive movement after stimulation, resulting in multiple peaks), trials discarded from MEPs recordings due to contraction or trials showing an excessively late onset of movement (more than 40 ms after TMS pulse) were considered indicative of voluntary rather than evoked movements and therefore discarded from subsequent analysis (around 12–14% of trials). For each finger separately, the measures of maximum distance were subsequently z-transformed at a single subject level in order to allow a direct comparison with MEPs data in the same standardized units. Standardized distance measures (in z-scores) entered in the factorial design described in the analysis section as dependent variable. Raw distance measures (in centimeters) were also analyzed by means of the same factorial design (see Appendix A) to show the consistency with the analysis on standardized measures.

3. Results

3.1. Accuracy

Accuracy was in general very high (98%) and did not show modulations depending on experimental manipulation (main effect of *affordance*: $F(1,12)=3.097$, $p=0.10$; main effect of *congruency*:

$F(1,12)=0.209$, $p=0.66$; interaction *affordance***congruency*: $F(1,12)=0.098$, $p=0.76$).

3.2. Reaction times

Mean values for each combination of the experimental conditions were calculated and analyzed with the model defined in the analysis section. A significant *congruency* main effect was found ($F(1,12)=7.956$, $p=0.0154$, partial eta squared $\eta^2=0.39$), revealing shorter reaction times when the action adaptation matched the *affordance* presented (mean $1.209 \pm$ standard error of the mean 0.092 s) with respect to the mismatching condition (1.321 ± 0.093 s) (Fig. 1, panel C). The main effect of *affordance* ($F(1,12)=0.418$, $p=0.53$) and the interaction between *affordance* and *congruency* ($F(1,12)=2.653$, $p=0.13$) were both not significant.

3.3. MEPs

Z-scores from MEPs amplitudes were analyzed separately for the two muscles.

3.3.1. APB

The APB muscle showed a significant interaction between *affordance* and *congruency* ($F(1,12)=17.79$, $p=0.00119$, $\eta^2=0.59$) whereas the main effect of *affordance* ($F(1,12)=2.915$, $p=0.11$) and of *congruency* ($F(1,12)=0.174$, $p=0.68$) did not reach significance threshold (Fig. 2, panel A). Post-hoc comparisons (true alpha level=0.0125) revealed that the mean z-score for the precision grip *affordance* with matching adaptation (+PRE: mean 0.235 ± 0.040) was significantly higher than mean z-score for power grip *affordance* with matching

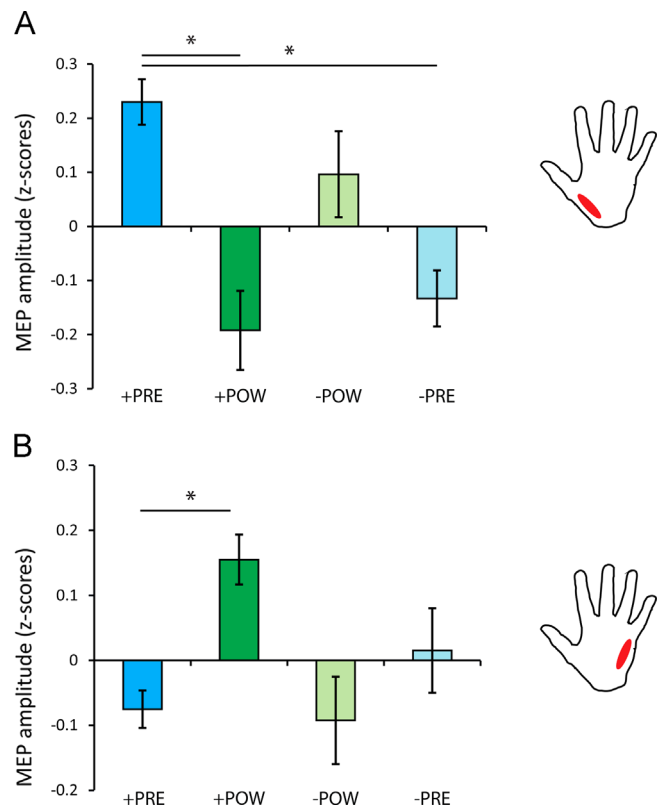


Fig. 2. MEPs results. Motor evoked potentials (MEPs) peak-to-peak amplitude (z-scores) for the four combinations of the experimental factors. The asterisks represents a statistically significant difference in the post-hoc analysis ($p < 0.0125$, true alpha level with Bonferroni correction). The bars represent standard error of the means. Panel A show the results for the APB muscle and Panel B those of the ADM muscle. On the right side of each panel muscles are schematically represented as red ellipsis on a hand shape.

adaptation (+POW: -0.199 ± 0.076) ($t(12)=4.9761$, $p=0.00032$) as well as precision grip affordance with mismatching adaptation ($-PRE$: -0.137 ± 0.050) ($t(12)=5.1839$, $p=0.00022$), whereas it was not significantly different from mean z-score of power grip affordance with mismatching adaptation ($-POW$: 0.102 ± 0.083) ($t(12)=1.3083$, $p=0.21$). In addition, the difference between the two mismatching conditions ($-PRE$ and $-POW$) did not reach statistical threshold ($t(12)=-2.0328$, $p=0.0648$).

3.3.2. ADM

The ADM muscle showed a significant interaction between *affordance* and *congruency* ($F(1,12)=5.99$, $p=0.0307$, $\eta^2=0.33$) whereas the main effect of *affordance* ($F(1,12)=0.536$, $p=0.47$) and of *congruency* ($F(1,12)=2.642$, $p=0.131$) did not reach significance threshold (Fig. 2, panel B). Post-hoc comparisons revealed that the mean z-score for the power grip affordance with matching adaptation (+POW: 0.142 ± 0.036) was significantly higher than mean z-score for precision grip affordance with matching adaptation (+PRE: -0.069 ± 0.028) ($t(12)=4.2045$, $p=0.0012$), just a trend toward a difference could be identified for power grip affordance with mismatching adaptation ($-POW$: -0.091 ± 0.068) ($t(12)=2.7868$, $p=0.0164$), whereas it was not significantly different from mean z-score of precision grip affordance with mismatching adaptation ($-PRE$: 0.023 ± 0.064) ($t(12)=1.4458$, $p=0.17$). In addition, the difference between the two mismatching conditions ($-PRE$ and $-POW$) did not reach statistical threshold ($t(12)=-0.9243$, $p=0.3735$).

3.4. Motion capture recordings

In this section, we report the results relative to z-transformed peak distance between the marker placed on the center of the metacarpus and the markers placed on the first, second, third, fourth and fifth finger (see Fig. 3, panel A). The other markers recorded were not further analyzed since the objective was to study changes in finger position following transcranial magnetic stimulation evoked movement. The z-scores reflected the changes associated with the experimental manipulation on the average movement evoked by stimulation, which in the present experiment was characterized by an overall flexion of the fingers. Thus, positive z-score values characterized a finger displacement which resembled an opening movement with respect to the average evoked movement. Descriptive statistics based on raw data (i.e. the relative displacement of the finger with respect to rest position in centimeters) were added following the analysis on standardized data in order to show more directly the effect of experimental manipulation on the features of evoked movement (for complete analysis on raw data see Appendix A). The results for each finger are reported separately below.

3.4.1. First finger

The peak distance for the first finger and the marker at the center of the metacarpus was not modulated by experimental manipulation (main effect of *affordance* $F(1,9)=0.127$, $p=0.73$, main effect of *congruency* $F(1,9)=0.022$, $p=0.89$, interaction *affordance*congruency* $F(1,9)=0.343$, $p=0.57$).

3.4.2. Second finger

The peak distance between the second finger and the metacarpus demonstrated significant *affordance*congruency* interaction ($F(1,9)=9.008$, $p=0.0149$, $\eta^2=0.50$), with no significant results relative to the main effects (main effect of *affordance* $F(1,9)=0.204$, $p=0.662$; main effect of *congruency* $F(1,9)=0.01$, $p=0.92$). The results on the index finger indicated an increase in the peak distance of the evoked movement during the observation

of the precision grip affordance, which in turn was related to an opening movement of the index, (z-scores mean +PRE: 0.113 ± 0.046 , raw mean +PRE: 0.549 ± 1.418 cm) with respect to the condition of power grip affordance (z-scores mean +POW: -0.106 ± 0.079 , raw mean +POW: -1.693 ± 1.311 cm) after a matching adaptation phase, with a pattern closely resembling the one obtained on APB muscle. Post-hoc comparisons (true alpha level= $=0.0125$) revealed that the mean z-score for the precision grip affordance with matching adaptation (+PRE) was significantly higher than mean z-score for power grip affordance with matching adaptation (+POW) ($t(9)=3.3222$, $p=0.0089$) whereas it was not significantly different from mean z-score for precision grip affordance with mismatching adaptation ($-PRE$) ($t(9)=0.3267$, $p=0.75$) and for power grip affordance with mismatching adaptation ($-POW$) ($t(9)=1.7639$, $p=0.11$). In addition, the difference between the two mismatching conditions ($-PRE$ and $-POW$) did not reach statistical threshold ($t(9)=-1.8373$, $p=0.09934$; Fig. 3, panel B).

3.4.3. Third finger

The peak distance for the third finger was not modulated by experimental conditions (main effect of *affordance* $F(1,9)=0.294$, $p=0.60$, main effect of *congruency* $F(1,9)=0.413$, $p=0.54$, interaction *affordance*congruency* $F(1,9)=0.46$, $p=0.52$).

3.4.4. Fourth finger

The peak distance for the fourth finger was significantly modulated by the *affordance* factor (main effect of *affordance*: $F(1,9)=5.724$, $p=0.0404$, $\eta^2=0.38$), due to an increase in mean z-score in the power grip affordance (POW: 0.109 ± 0.045) with respect to precision grip affordance (PRE: -0.108 ± 0.046). This was due to a reduced closure of the fourth finger when observing power grip objects (POW: -1.827 ± 0.796 cm) in contrast to an increase in the closure of this finger when observing precision grip objects (PRE: -3.144 ± 1.01 cm) with respect to average evoked movement. No other effect reached significance (main effect of *congruency*: $F(1,9)=0.096$, $p=0.76$; interaction *affordance*congruency*: $F(1,9)=0.172$, $p=0.69$; Fig. 3, panel C).

3.4.5. Fifth finger

The peak distance for the fifth finger revealed a significant *affordance*congruency* interaction ($F(1,9)=9.013$, $p=0.0149$, $\eta^2=0.50$) and a trend toward the main effect of *affordance* ($F(1,9)=5.109$, $p=0.0501$, $\eta^2=0.36$), whereas no significant effect was found in relation to *congruency* ($F(1,9)=0.959$, $p=0.35$). An increase in the peak distance of the evoked movement was revealed during the observation of the power grip affordance (z-scores mean +POW: 0.167 ± 0.041) with respect to the precision grip-affordance (mean +PRE: -0.234 ± 0.052) after a matching adaptation phase thus resembling the result found on ADM muscle. In terms of actual movement, this was reflected by an opening movement of the fifth finger in the power grip condition (raw mean +POW: 0.168 ± 0.782 cm) in contrast to a closure of this finger in precision grip condition (+PRE: -1.755 ± 0.930 cm). Post-hoc comparisons revealed that the mean z-score for the power grip affordance with matching adaptation (+POW) was significantly higher than mean z-score for precision grip affordance with matching adaptation (+PRE) ($t(9)=-6.4263$, $p=0.0001215$), whereas the difference from mean z-score of power grip affordance with mismatching adaptation ($-POW$) ($t(9)=1.0163$, $p=0.34$) and precision grip affordance with mismatching adaptation ($-PRE$) ($t(9)=2.2468$, $p=0.051$) failed to survive the Bonferroni correction for multiple comparison (true alpha level= $=0.0125$; Fig. 3, panel D), as did the difference

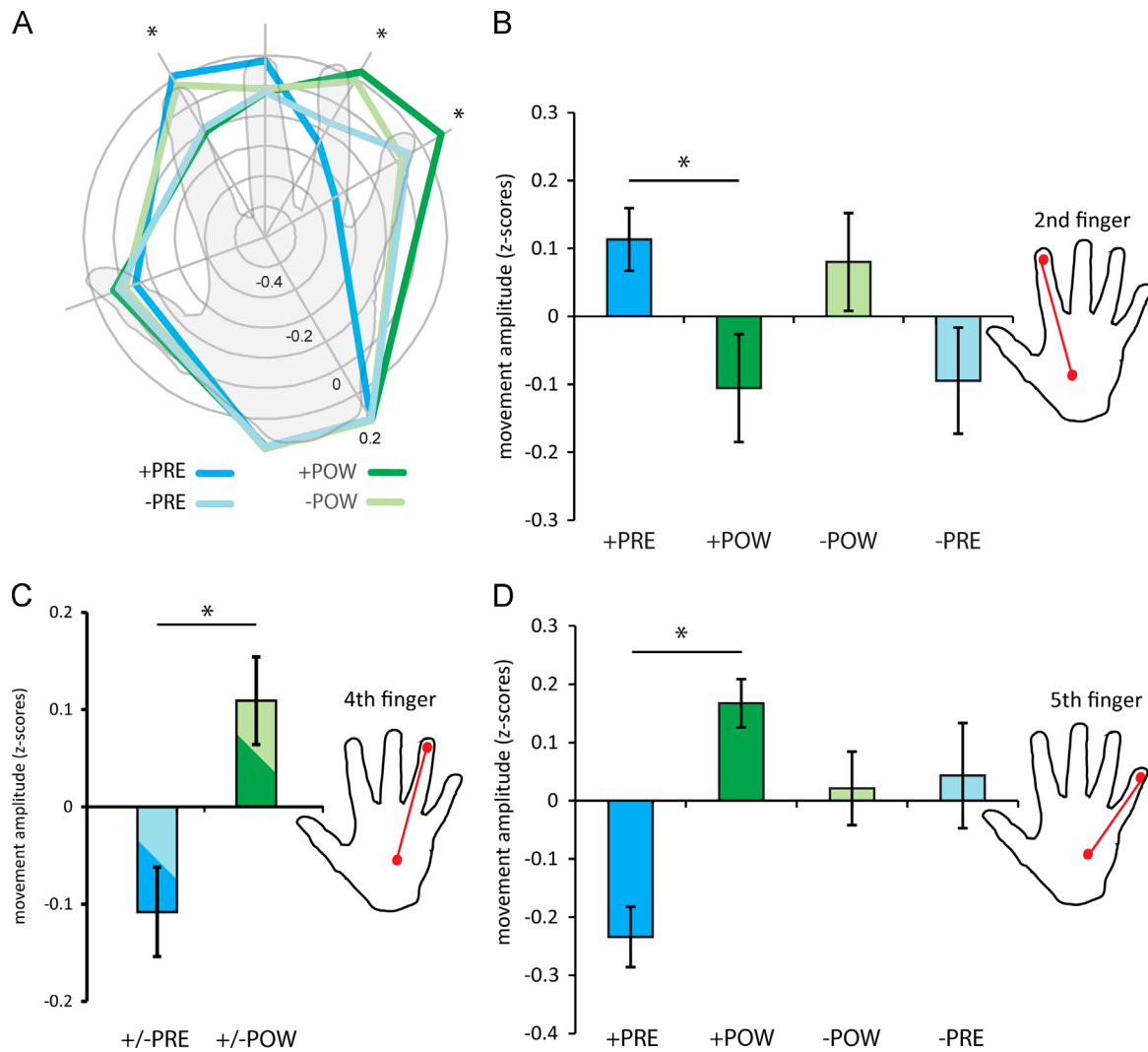


Fig. 3. Finger movement results. Panel A. Schematic representation of each finger movement amplitude evoked by TMS. Lines in different colors (color legend below the graph) connecting the fingers represent mean movement amplitude (z-scores) for each condition (+PRE: matching adaptation-precision affordance; +POW: matching adaptation - power affordance; -POW: mismatching adaptation - power affordance; -PRE: mismatching adaptation-precision affordance) for each finger. The asterisk represents a statistically significant difference ($p < 0.05$) according to experimental manipulation. Panel B and D. Peak distance between the second (panel B) and fifth (panel D) finger and the metacarpus (z-scores) for the four combinations of the experimental factors. The peak distance is schematically represented as a red line connecting the markers on a hand shape on the right side of each graph. The asterisks represents a statistically significant difference in the post-hoc analysis ($p < 0.0125$, true alpha level with Bonferroni correction). The bars represent standard error of the means. Panel C. Peak distance between the fourth finger and the metacarpus (z-scores) for the affordance factor (+/- PRE: precision affordance; +/- POW: power affordance). The asterisk represents a statistically significant difference (main effect of affordance $p < 0.05$). The bars represent standard error of the means.

between the two mismatching conditions (-PRE and -POW: $t(9) = 0.1544$, $p = 0.8807$).

4. Discussion

In the present study we investigated early cortico-spinal facilitation and hand movements' synergies evoked by the observation of tools. From the evidence present in the literature, we predicted that a fine-grained motor representation of the visual properties of affordable objects should be present in an early time window. Indeed, cortico-spinal excitability of hand muscles showed an extremely detailed pattern of modulations, matching tools' affordances. Similarly, TMS-induced twitches showed a pattern of grip-specific whole hand synergies. The results support the presence of early and specific visuomotor transformations, which we were able to evidence through the use of a state-dependent approach, by exploiting an adaptation-stimulation paradigm.

Neuroimaging and neurophysiological experiments in humans delineated a specific parieto-frontal circuit devoted to the processing of objects geometric properties that is in service of action planning (Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005; Chao & Martin, 2000). This circuit is believed to subtend the visuomotor transformations necessary for object-directed actions (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). In principle TMS can distinguish cortico-spinal activity for muscles involved in precision or power grip, thus allowing researchers to investigate the level of detail that characterizes the motor activity in response to the different affordances offered by the objects. Previous studies employing such technique show that object motor coding appears very early after visual presentation (Franca et al., 2012; Buccino et al., 2009). Others added to this account the demonstration that motor activities are somatotopically highly specific (Makris et al., 2013). In fact, single pulse TMS applied at 300, 600 and 900 ms showed a general effect appearing at 300 ms (specific muscle recruitment only for precision grip but not for power grip in Makris et al. (2011)) that in a subsequent study was shown to

somatotopically dissociate between affordances at 450 ms (Makris et al., 2013) and only partially at 300 ms (only precision grip at 300 ms, whereas dissociation for power grip was not present until 450 ms from visual presentation of the three-dimensional object). On the other hand, Franca et al. (2012) investigated the earlier phases after object presentation showing clear cortico-spinal modulations at 120 ms, but lacking specificity. It is important to note that somatotopic specificity and early recruitment are the defining features of canonical neurons as observed in monkeys (Murata et al., 1997), and more generally of the concept of affordance (Gibson, 1977). In general agreement with an early recruitment of the motor system after graspable object presentation, EEG potentials were affected as early as 180–280 ms (Petit et al., 2006; Proverbio et al., 2011) and monkey canonical neurons showed phasic peak of firing very soon after object presentation (Murata et al., 1997). Therefore, it is possible to predict that cortico-spinal excitability modulations should appear in an early time window after visual stimuli presentation. Indeed, later modulations cannot be univocally interpreted as automatic visuomotor transformation without considering spurious effects arising from secondary cognitive processes, as motor imagery. In fact, motor imagery, defined as the voluntary mental representation of movements, is known to modulate cortico-spinal excitability (Fadiga et al., 1999) and may constitute a major confounding in late motor modulations. In the present study, we stimulated 150 ms after object presentation, in order to bridge results between previous neurophysiological experiments. We report, for the first time, early differential patterns of cortico-spinal excitability characterized by somatotopic specificity with respect to the observed action-object pairs. In addition, by recording fingers movements induced by TMS, we show patterns of hand configurations resembling specific motor synergies. Our results suggest that visuomotor transformations occurring during the vision of graspable objects elicit specific motor synergies, which can be evidenced through cortico-spinal excitability and fingers' movement measures. TMS-evoked hand motor synergies (Gentner and Classen, 2006) have shown modulation by short motor training (Classen et al., 1998), short sessions of action observation training (Celnik et al., 2006), as well as long-term plasticity (Gentner et al., 2010). Here we show that passive visual presentation of action-object pairs selectively primes a coherent pattern of finger movements which is present in the individual motor repertoire, thus with no need of any training or explicit performance of an overt object-directed movement.

TMS timing after object presentation (here 150 ms) could be critical for the efficacy of single pulse TMS stimulation in testing responses evoked by different population of canonical neurons and eventually explain why some studies found significant but unspecific effects. Alternatively, one possibility is that the proportion of canonical neuron cells and their spatial distribution doesn't allow large modulations of the descending volley generated by the relatively large TMS cortical stimulation area. Here, to counteract this possibility, we employed a state-dependent TMS design to amplify affordance-related responses. State-dependency refers to the fact that the cortical response to an external stimulus depends on the previous ongoing activity (Thut & Miniussi, 2009). The functional state of the target neural system can be manipulated by means of perceptual adaptation, as in the present experiment. Importantly, the use of different adaptation stimuli enables the selection of a specific sub-population of neurons in the target area (Silvanto et al., 2008; Lang et al., 2004; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009). The TMS stimulation preferentially boosts the activity of the adapted population and therefore facilitation should be detected on a task, which, for its performance, recruits that very same population of neurons (Silvanto & Pascual-Leone, 2008; Cattaneo & Silvanto, 2008; Cattaneo,

Sandrini, & Schwarzbach, 2010; Cattaneo et al., 2011). State-dependency has mostly been employed in perceptual tasks (Cattaneo & Silvanto, 2008; Silvanto et al., 2008) and more recently in the study of the action observation domain (Cattaneo, 2010; Cattaneo et al., 2010, 2011). By exploiting an adaptation-stimulation paradigm, we were able to selectively test the early-stage activity of the population of neurons coding for a given grasp type by specifically adapting it through action observation. We evaluated the modulations in response to the presentation of tools, requiring the same or different finger affordances. By applying single-pulse TMS in primary motor cortex and recording hand MEPs as well as movement of the fingers evoked by the stimulation, we could investigate grasp synergies associated with the processing of tools and the interaction with the processing of hand movements, occurring upstream with respect to primary motor cortex. Our results show early (150 ms) and dissociable motor synergies evoked by the presentation of action-object pairs offering a precision or a power grip affordance. The pattern of activity, evoked under passive object observation, was coherent with that during the interaction between the agent and the geometric-functional features of the same object. Indeed, the cortico-spinal facilitation on the muscle recorded from the thumb (APB) and the index finger movement were increased by the precision grip affordance presentation, whereas the observation of a power grip affordance increased motor recruitment of the little finger muscle (ADM) as well as the movement of the little and ring finger. The combination of adaptation phase with the object was critical in the emergence of the specificity of the effects. Matching adaptation was the driving factor in the emergence of the somatotopic effect, given its role in selecting the population of neurons coding for the grasp type. Anyhow, the type of adaptation alone was not able to induce the observed cortico-spinal excitability patterns, as it can be deduced by the absence of difference between the two mismatching conditions. When the adapting action and the object were not matching, no difference could be detected between the patterns, thus supporting an interaction between the systems processing hand actions and objects during observation. Indeed, only matching action and objects caused significant dissociations, whereas mismatching associations did not. Together, our data offers the first clear demonstration that action-object observation elicits an early and specific pattern of motor synergies, matching the geometrical properties of the objects.

This result can be further interpreted as a neurophysiological evidence of a cross-talk between mirror and canonical neuron systems. The action (with the so called mirror neurons) and object (with the so called canonical neurons) systems encode for similar object-directed action execution but they differ in visual response properties (Rizzolatti & Craighero, 2004). The action system encodes the visual appearance of object-directed actions performed by others (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Umiltà et al., 2001). The object system encodes the visual appearance of the objects (Murata et al., 1997). Notwithstanding the clear functional connection between the two systems, very few studies have been conducted on the relation between the action observation system and the object affordance system. No monkey neurophysiology study has tried to study the functional relations of these two systems. In humans, several sparse reports appeared showing partially segregated parieto-premotor networks for canonical and mirror circuits (Grèzes, Tucker, Armony, Ellis & Passingham, 2003b) or suggested interaction when observing object-directed actions (Iacoboni et al., 2005). Here, we intentionally used a cross-system adaptation protocol, letting the subject observe intransitive actions (finger movements resembling precision or power grip) before the experimental presentation of objects offering different affordances. Subjects were also explicitly asked to detect the congruency between the hand movement in

the adaptation phase and the object subsequently presented. By performing an explicit task we could directly test the encoding of the critical information present in video-clips and pictures and it allowed us to compare the results to the well-established literature on match-mismatch effects in visuomotor domain. Mismatch induced larger reaction times, suggesting a cross-system transfer of information between the observation of a hand action and of the object in agreement with previous behavioral reports (Ellis & Tucker, 2000). No differences in reaction times were found for the two objects or the combination of objects and adaptation movements, thus suggesting, together with the very high accuracy, that there were no confounding effects related to the processing and/or identification of the pictures. Behavioral research already showed information transfer between the action and object processing system (Craighero et al., 1999) and stimulus-response compatibility effects (Hommel, Müssele, Aschersleben, & Prinz, 2001; Tucker & Ellis, 2004; Grèzes, Armony, Rowe & Passingham, 2003a). Such information transfer, measured in terms of behavioral facilitation when action and object match, suggests that some common neural overlap between the two systems might exist. In the present study, we show the neurophysiological interaction between the action and object systems. In fact, action-object matching induced specific cortico-spinal excitability modulations as well as larger affordance-specific finger displacements. Mismatching action-object observation, as expected, erased the specificity of the effects on most variables, with the exception of ring finger excursion, which was influenced only by the object presentation and did not show any interaction with the adaptation phase. This points out that the congruency of the adapting movement and the object was crucial to select the correct neural population, specific for encoding that affordance. Noteworthy, this is the first study employing a cross-system adaptation-stimulation protocol between action and object systems.

Although no one before has shown neurophysiological interaction between the “action” and “object” systems, this should come as no surprise since affordance encoding requires the tight integration of action and object representations. In fact, following an enactivist perspective, objects gain a special new status when they can be part of our action space. By action space we refer to the potentiality for action given contextual information and a desired state to be obtained. In agreement with this idea, cortico-spinal excitability modulation has been shown during the observation of graspable objects falling within the reachable space. Instead, observation of either a non-graspable object (Buccino et al., 2009) or a graspable object falling outside the reachable space (Cardellicchio, Sinigaglia, & Costantini, 2011) led to no significant affordance-related modulations. Therefore, objects may gain specific motor properties only if they can be part of an action and thus if they are part of our action space.

5. Conclusions

Our results support a somatotopic congruency between the induced motor synergies investigated through the magnetic stimulation of primary motor cortex and the visuomotor information contained in the graspable objects. The possibility of an early modulation of the cortico-spinal excitability to prime a specific hand muscular pattern is a well-established result during object observation requiring a subsequent action preparation (Prabhu et al., 2007a, 2007b). However, a major characteristic of the monkey canonical neurons activity is that they discharge even in absence of a required response (Murata et al., 1997). Along these lines, some experimental evidence in this sense has been shown in humans (Buccino et al., 2009; Franca et al., 2012; Makris et al., 2011, 2013). Exploiting the paradigm of adaptation-stimulation,

we were able to induce early and somatotopic-specific motor synergy modulations in response to the observation of hand movements combined with tools. These results suggest that tools may be automatically coded as hand movements, even if no action has to be planned on them.

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Appendix A

We analyzed raw distance measures (i.e. the displacement in centimeters with respect to rest distance between the markers of interest, as written in Section 2.6, before the z-transformation) to show the consistency of the direction of the effects and of their significance with respect to standardized data analysis (see Section 3.4). Descriptive statistics on raw measures are reported in the Section 3.4 following descriptive statistics on z-transformed measures to allow a more direct understanding of the interpretation of the z-scores in terms of actual movement features.

The peak distance for the first finger and the marker at the center of the metacarpus was not modulated by experimental manipulation (main effect of *affordance* $F(1,9)=0.712$, $p=0.72$, main effect of *congruency* $F(1,9)=0.254$, $p=0.63$, interaction *affordance*congruency* $F(1,9)=0.196$, $p=0.67$).

The peak distance between the second finger and the metacarpus demonstrated significant *affordance*congruency* interaction ($F(1,9)=7.159$, $p=0.0254$, $\eta^2=0.44$), with no significant results relative to the main effects (main effect of *affordance* $F(1,9)=0.007$, $p=0.94$; main effect of *congruency* $F(1,9)=0.026$, $p=0.88$). Post-hoc comparisons (true alpha level= $=0.0125$) revealed that the average displacement for the precision grip affordance with matching adaptation (+PRE) was significantly different from the average displacement for power grip affordance with matching adaptation (+POW) ($t(9)=3.157$, $p=0.0116$) whereas it was not significantly different from precision grip affordance with mismatching adaptation (−PRE) ($t(9)=1.859$, $p=0.10$) and for power grip affordance with mismatching adaptation (−POW) ($t(9)=−1.106$, $p=0.30$). In addition, the difference between the two mismatching conditions (−PRE and −POW) did not reach statistical threshold ($t(9)=−1.908$, $p=0.089$).

The peak distance for the third finger was not modulated by experimental conditions (main effect of *affordance* $F(1,9)=0.256$, $p=0.63$, main effect of *congruency* $F(1,9)=0.577$, $p=0.47$, interaction *affordance*congruency* $F(1,9)=0.002$, $p=0.97$).

The peak distance for the fourth finger was significantly modulated by the *affordance* factor ($F(1,9)=6.243$, $p=0.0339$, $\eta^2=0.41$). No other effect reached significance (main effect of *congruency*: $F(1,9)=0.107$, $p=0.76$; interaction *affordance*congruency*: $F(1,9)=0.036$, $p=0.85$).

The peak distance for the fifth finger revealed a significant *affordance*congruency* interaction ($F(1,9)=9.62$, $p=0.0127$, $\eta^2=0.51$) and a significant main effect of *affordance* ($F(1,9)=8.42$, $p=0.0175$, $\eta^2=0.48$). The latter effect was the only one that differed from the results on z-transformed data given that such main effect did not reach statistical threshold in the analysis on z-transformed data (see Section 3.4.5). No significant effect was found in relation to *congruency* ($F(1,9)=0.237$, $p=0.64$). Post-hoc comparisons revealed that the average distance measure for the power grip affordance with matching adaptation (+PRE) was significantly different from the distance related to precision grip affordance with matching adaptation (+PRE) ($t(9)=−4.712$,

$p=0.001102$), whereas the difference from average distance of power grip affordance with mismatching adaptation ($-POW$) ($t(9)=1.991$, $p=0.078$) and precision grip affordance with mismatching adaptation ($-PRE$) ($t(9)=1.729$, $p=0.12$) failed to survive the Bonferroni correction for multiple comparison (true alpha level = 0.0125), as did the difference between the two mismatching conditions ($-PRE$ and $-POW$: $t(9) = -0.387$, $p=0.71$).

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