Attention and cognitive load modulate motor resonance during action observation

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ABSTRACT

Observation of others' actions evokes a motor resonant (MR) response, in the parieto-frontal Action Observation Network (AON, comprising BA40, BA6, BA4). In order to investigate the effect of cognitive processes on the AON we manipulated attention and cognitive load during central and peripheral observation of hand grasping actions with three experiments. Motor Evoked Potentials (MEPs) were elicited in the opponent of the thumb (OP) and abductor of the little finger (ADM) by Transcranial Magnetic Stimulation (TMS) of the primary motor cortex. First, we investigated the role of selective attention by asking subjects to focus their attention on the thumb of the moving hand in central vision. A selective facilitation of OP MEPs was recorded, without the expected ADM MEPs modulation. Second, a "covert attention" paradigm was used to investigate the role of attention in peripheral vision. Surprisingly, MEP modulation was virtually abolished. In the third experiment we tested the hypothesis that the higher cognitive load introduced by the covert attention instruction had interfered with MR. We allowed subjects to view the action before its peripheral presentation with covert attention, thereby decreasing the cognitive effort necessary to decode the grasping action. The accuracy of motor resonant response was restored.

1. Introduction

Living in a complex social context, human beings have evolved a keen sensitivity to movement parameters that can be instructive of others' behavior and inform elaborate active interactions. Remarkably, at the neural level the ability to code others' action is not just related to classical posterior/parietal areas subserving visuospatial decoding but, in fact, cortical motor areas, typically responsible for programming the execution of movement, have been shown to also be involved in the perception of actions (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). In the past two decades much effort has been devoted to the study of motor resonance, the subliminal activation of the motor system during observation of actions performed by others. The first evidence of this mechanism was described in macaque monkeys, where the activity of single neurons in premotor cortex (mirror neurons) was recorded when animals were both actively performing and observing a grasping action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996, Fogassi & Simone,

2013). In humans, observation of others' actions evokes a motor resonant response, at many different levels of the Action Observation Network (AON, proposed as homologue of the monkey mirror neuron system, (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009)). During action observation, visual information travels from the occipital cortex, reaches Extrastriate Body Areas (EBA) and Superior Temporal Sulcus (STS) where a visual description of the relevant action (Miall, 2003; Rizzolatti, Fogassi, & Gallese, 2001) is represented and then proceeds through the parieto-frontal network formed by the inferior parietal (BA40) and premotor (BA6) areas (Cabinio et al., 2010; Cerri et al., 2015; Grèzes et al., 2001; Rizzolatti et al., 1996) where visuo-motor information is shaped, which then continues to the primary motor cortex (M1), and all the way to the spinal cord (Borroni & Baldissera, 2008; Borroni, Montagna, Cerri, & Baldissera, 2005; Rizzolatti & Craighero, 2005; Rizzolatti & Sinigaglia, 2010). In M1 this activation reflects the motor program encoding kinematic parameters of the observed actions and is characterized by a high level of muscular and temporal specificity. Specifically, studies with transcranial magnetic

stimulation (TMS) have shown that observation of a hand grasping an object elicits a pattern of motor-evoked potential (MEP) facilitation of the same muscular groups, with the same time course, as when actually executing grasping of that object (Cavallo, Becchio, Sartori, Bucchioni, & Castiello, 2012; Cavallo, Bucchioni, Castiello, & Becchio, 2013; Gangitano, Mottaghy, & Pascual-Leone, 2001; Mc Cabe, Villalta, Saunier, Grafton, & Della-Maggiore, 2015; Montagna, Cerri, Borroni, & Baldissera, 2005; Naish, Houston-Price, Bremner, & Holmes, 2014; Press, Cook, Blakemore, & Kilner, 2011). Several hypotheses have been proposed about the functional significance of motor resonance, ranging from action recognition and understanding to imitation, cooperation and motor learning (Catmur, 2015; Kilner & Frith, 2007; Quadflieg & Koldewyn, 2017; Rizzolatti & Craighero, 2004). Although these are all attractive hypotheses, in part confirmed by numerous behavioral experiments, many physiological mechanisms underlying motor resonance, as well as how these mechanisms are modulated in the different cognitive and perceptual conditions under which the resonant response can occur, are still poorly understood. For example, attention has been shown to have a profound influence in shaping the resonant activation of motor circuits during action observation (Bach, Peatfield, & Tipper, 2007; Chong, Williams, Cunnington, & Mattingley, 2008; Gowen, Bradshaw, Galpin, Lawrence, & Poliakoff, 2010; Muthukumaraswamy & Singh, 2008; Perry & Bentin, 2010; Puglisi et al., 2017; Woodruff & Klein, 2013). Often in action observation studies subjects are allowed or even required to pay full attention to the observed action, viewed in central vision, though from a more naturalistic point of view this is not the most common circumstance. In daily life people are often exposed to several simultaneous actions, which cannot all be in central vision or equally relevant or interesting to them, and thus will not receive the same amount of their attentive resources. Thus, the present study is an initial attempt to sort out the relative involvement of vision, attention and cognitive effort in motor resonance response; we explore these naturally entangled variables with three specific experimental manipulations asking subjects to focus their attention (selective or covert) during action observation in central or peripheral vision and, in doing so, also manipulating the cognitive load of their tasks.

Evidence from behavioral experiments shows that attention has a critical role in shaping "automatic imitation" - i.e. the automatic facilitation in the observer of motor pathways normally involved in the execution of the observed action (for reviews see Heyes, 2011; Cracco et al. 2018). Adding a demanding perceptual secondary task can have a profound influence on the coding of the observed action, resulting in the modification (Catmur, 2016) or even in the elimination (Bach et al., 2007; Gowen et al., 2010; Chong, Cunnington, Williams, & Mattingley, 2009) of its automatic imitation. Neuroimaging studies have shown that even in central vision the activation of the motor cortex during action observation is not an automatic event, occurring every time an action falls in the visual field of an observer, but it varies in scale and shape according to attentive resources available to the observer (Bach et al., 2007; Chong, et al., 2008; Muthukumaraswamy & Singh, 2008; Perry & Bentin, 2010; Woodruff & Klein, 2013). Electrophysiological experiments in our lab have demonstrated that partially diverting attention from an action observation task with a second cognitive task, affects different parameters of the resonant response, preserving time course and muscle selection, while reducing dramatically the excitability of cortical and spinal motor neurons innervating the muscles involved in the observed action, and the kinematic specificity of the response (Puglisi et al., 2017). Motor resonance therefore appears to be a composite phenomenon, with different components that are differently susceptible to cognitive manipulation and may constitute parallel motor representations of the same observed action, utilized for different purposes by the central nervous system (Sartori, Betti, Chinellato, & Castiello, 2015). It is reasonable to assume that attention might have a role in modulating the activity of the AON by affecting early visual processing (Beck & Kastner, 2009; Kastner & Ungerleider, 2000) and

then the activation of motor areas related to the execution of the observed action. Bach et al., (Bach et al., 2007) utilized a visuomotor priming task in order to evaluate behaviorally whether attention has a role in selective motor facilitation of the hand or the foot during an action observation task. They found an effective priming effect when participants' attention was directed toward the corresponding limb in the displayed image, with faster foot responses as they payed attention to the leg and faster hand responses as they pay attention to the hand, compared to conditions in which subjects were focused on the head of the observed model. The first goal of the present study is to investigate the effect of selective attention on the activation of specific motor pathways during action observation tasks.

A closely related issue is whether and how attention can shape motor resonant responses to actions located in different sections of the visual field. It is well known that peripheral vision plays a fundamental role in the recognition of general aspects of a visual scene as well as of biological motion (Gibson, Sadr, Troje, & Nakayama, 2005; Gurnsey, Roddy, Ouhnana, & Troje, 2008; Larson & Loschky, 2009; Thompson, Hansen, Hess, & Troje, 2007). In recent years the possibility that actions viewed in peripheral vision may be effective stimuli for the AON has become subject to investigation, and modulation of resonant motor circuits by actions located in the peripheral field have recently been described (Cavallo et al., 2012; D'Innocenzo, Gonzalez, Nowicky, Williams, & Bishop, 2017; Donaldson, Gurvich, Fielding, & Enticott, 2015; Leonetti et al., 2015; Maranesi et al., 2013). In the study by Leonetti (2015) we have shown that during observation of grasping actions in periphery the reduction of visual resolution induces a resonant pattern of activation of motor circuits with much lower kinematic specificity compared to observation of the same action in central vision. Although in that study the analysis was focused on the visual limits imposed on the development of resonant responses by the low resolution of peripheral vision, in fact, in addition to the intrinsic reduction of visual acuity, stimuli receive fewer attentive resources, simply because attention is automatically deployed to items viewed in central vision (Liversedge & Findlay, 2000; Smith & Schenk, 2012). The second goal of the present study is to investigate the role of attention and cognitive load in affecting motor pathways during the peripheral vision. To this end we utilized the same experimental paradigm as in Leonetti et al. (2015), which included observation of actions that are very similar but burden the AON with different levels of cognitive effort: one was a natural grasping action, while the other was an impossible grasping action, i.e. an action that violates the biomechanical constraints of the human body, and which is not as immediately familiar. The ability to resonate indeed extends also to actions that don't belong to the observer's natural repertoire, such as mechanically impossible ones (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005). In a previous study we have shown that when subjects observed a grasping action performed with an impossible sequence (fingers flexing towards the back of the hand), MEPs in the Opponent Pollicis (OP) and Abductor Digit Minimi (ADM) muscles were facilitated, as in the observation of the natural movement (fingers flexing towards the palm of the hand), but with a different pattern, consistent with the observed kinematic details. In other words, excitability modulation of the cortical motor areas involved in the control of these muscles reproduced faithfully their activation during the execution of the feasible movements within the impossible action (Borroni, Gorini, Riva, Bouchard, & Cerri, 2011). This has become a useful protocol to evaluate the specificity of motor resonance in different experimental conditions and will be utilized in the present study

The overall aim of the study was to assess how three interacting parameters, namely attentive processes, cognitive load and location of the action in the observer's visual field, affect the activity of motor areas during the observation of a grasping action. We manipulated these parameters with three different experiments utilizing: 1) a selective attention paradigm, in which subjects' attention is explicitly directed to only one portion of the action observed in central vision

(Expt1); 2) a covert attention paradigm (Posner, 1980), in which subjects are instructed to pay attention to the action shown in peripheral vision, while maintaining fixation on a spot in central vision (Expt2); and 3) a cognitive load paradigm, in which attention is modulated by manipulating the cognitive effort necessary to complete the task in peripheral vision (Expt3). The general hypothesis of the three experiments is that different combinations of visual and attentive parameters will affect the motor resonant response in different ways; the detailed hypothesis of each experiment is presented below, in each specific section of the paper.

2. General methods

A total of 64 healthy adult volunteers (average age 23 ± 1.2; 34 females) took part in the study, composed of three different action observation experiments. Different subjects participated in the different experiments: 19 in Expt1, 29 in Expt2, and 16 in Expt3. Expt2 had a between-subject design, in which two different groups of subjects observed two different actions (natural and impossible, see below). In order to compute the sample size, a statistical power analysis (GPower 3.1) for Repeated Measures ANOVA-within factor, was performed based on data from the published study (Borroni et al. 2011). The effect size (ES) for muscle (OP and ADM) and delay interaction ($\mu2 = 0.5$) in central vision condition was used, with an alpha = 0.05 and power = 0.95. The expected sample size needed with this effect size is approximately n = 10. Thus, we choose 10 as minimum sample size for each experimental condition (selective attention, covert possible, covert impossible, load condition). In order to achieve a more than adequate sample, a total of 80 subjects (20 per condition) were initially recruited. In 13 of these, MEPs were not evocable and 3 felt the stimulation painful, so that the experiment was aborted.

Subjects were fully informed about the experimental procedures and signed a written consent. Experimentation was conducted in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee. All subjects had normal or corrected-to-normal vision, no history of neurological disorders or contraindication to TMS. All were right handed according to the standard Edinburgh Handedness Inventory (Oldfield, 1971).

All subjects, sitting in a comfortable armchair with prone hands resting on lateral supports, were asked to observe, without moving, a 5 s video clip showing either a natural or impossible grasping action performed by a male avatar. The room was quiet and lights were dimmed to minimize acoustic and visual distractions. Before the first trial, a short introductory video was shown, zooming on the avatar standing near a table where a red ball was resting; this scene was shown in central vision in order to familiarize subjects with the context of the action. Subsequently, during the experimental trials, the hand action video was shown either in central or in peripheral vision, consisting of a close-up of the avatar's hand grasping the ball. This video started with the right hand moving from its resting position, along the avatar's body, to the ball. Then, in the natural grasping video, the hand opened with a finger extension and grasped the ball with a normal "palmar" finger flexion (fingers flexing towards the palm of the hand), while in the impossible grasping video the hand was supinated while opening with finger extension and grasped the ball with an abnormal "dorsal" finger flexion (fingers flexing towards the back of the hand); after a brief lifting phase the sequence was concluded. The video was presented on a 19" high-resolution computer screen placed at eye level at a distance of 1 m, while the excitability modulation of cortical and spinal motor neurons controlling finger muscles was measured. In central vision observation (Exp1), the ball was centered on the screen, right in front of subjects, and subjects were instructed to focus their attention on the thumb during the observation of the grasping action (Fig. 1A). In peripheral vision observation (Exp2 and 3), subjects were instructed to fixate a red cross (about 4 cm in size) on the left side of the computer screen, while the video with the hand action appeared on the right side
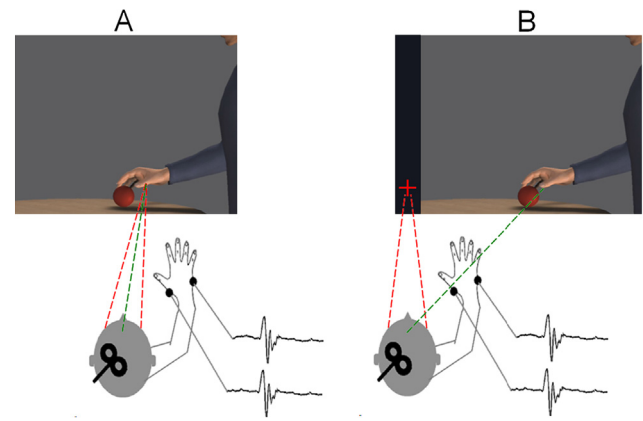

Fig. 1. Experimental settings. Panel A, setting for Expt1. Subjects were instructed to observe the video, looking at the hand action (dashed red line) and paying close attention to the movement of the thumb, shown in central vision (dashed green line). Panel B, setting for Expt2 and Expt3. Subjects were asked to observe the video, looking at the red cross (dashed red line) and paying close attention to the movement shown in peripheral vision (dashed green line). In all experiments, MEPs were evoked by TMS focal stimulation of M1 and recorded from OP and ADM muscles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the screen (Fig. 1B). The center of the ball, focus of the grasping action, was placed at 17 cm to the right of the fixating point, i.e. at about 10° of eccentricity on the horizontal plane with respect to central vision. In peripheral vision experiments, to verify that subjects maintained their gaze on the fixation point, eye position was continuously monitored during video presentation with electro-oculogram recordings (EOG) obtained with self-adhesive monopolar surface electrodes placed laterally to each eye. Subjects were compliant with the instruction for the short duration of each trial (5 s) and no trial was excluded because of undesired eye movement.

In all experiments, motor-evoked potentials (MEPs) were used to measure the excitability modulation of cortical and spinal motor neurons during observation of the grasping action. MEPs were evoked by single-pulse TMS of the hand area in the left M1 and recorded simultaneously, using self-adhesive bipolar surface electrodes placed on each muscle belly, from the right Opponens Pollicis (OP) and Abductor Digiti Minimi (ADM), two muscles normally utilized during the grasping action for thumb closing and little finger opening respectively. Electromyographic signals were amplified, filtered (10 Hz to 1 kHz) and digitally converted (sampling rate 5 kHz). A mechanical arm held a figure-of-eight-shaped coil connected to a magnetic stimulator (Magstim 200, Magstim Company Limited, Whitland, Wales, UK; maximal power 2.2T). The head of subjects was restrained by a comfortable pillow wrapping around the neck and supported by a fixed headrest, the coil was positioned and fixed on the left M1 so as to activate both selected muscles, and the stimulator output was set at about 110% of the motor threshold of the less excitable muscle (defined as the intensity giving 3 MEP responses out of 6 stimuli, Rossini et al., 1994; Borroni et al., 2008). MEPs of amplitude lower than 50 μV were discarded online during the experiment (in all the different experiments, a total of 346 discarded MEPs out of 5120 recorded).

The excitability time-course was explored at four relevant randomized delays from the onset of the video: d1 = 0 s Baseline, avatar's hand just beginning to move; d2 = 1 s Opening phase, moment of maximal finger aperture during the grasping action; d3 = 1.6 s Grasping phase, moment in which the avatar's fingers grasp the ball and d4 = 3 s Holding phase, moment in which the avatar's hand lifts the ball and then places it back on the table. For each subject a total of 40 presentations were obtained, so that overall 10 MEP responses were recorded at each of the 4 delays. Presentations were grouped in 2 blocks of 20 trials, and subjects were instructed that they could rest at the end

of each block. Within each block of 20 trials, MEPs were evoked and recorded 5 times at each specific delay, chosen in a semi-random order (completing a set of 4 delays before starting the next set) by the data acquisition program. In order to do this, at the very first frame of the close-up video a synchronizing signal was fed into the computer, which triggered both TMS stimulator and acquisition program at one of the selected delays. Presentations were spaced by 8 s dark screen intervals. To exclude the possibility of voluntary or involuntary mimic activity of the observer, the background electromyographic activity was monitored in the two muscles throughout the whole video presentation. In order to investigate the conscious perception of actions observed in peripheral vision, at the end of the experiments all subjects answered a questionnaire asking to describe with words what they had seen and then to physically repeat it as accurately as possible.

Data analysis. Data were acquired and recorded using a custom program written in LabView11 and stored for later analysis. In each subject, MEP responses were measured as peak-to-peak amplitude; for each muscle, MEP values in all 4 delays were normalized to the average of values in d1 (Baseline, time = 0 s, avatar's hand just beginning to move) and then averaged across all subjects. Average values of MEPs in the first delay are shown in Table 1. Because of the presence of not normally distributed residuals, a square root transformation was applied to normalized data and an ANOVA for repeated measures was run to determine if there were differences in MEP facilitation at different delays in the different muscles. Significance of multiple pairwise comparisons was established after Bonferroni correction; statistical analysis was conducted using SPSS software (SPSS Inc, Chicago, USA).

3. Experiment 1: Selective attention

In Expt1 the subjects' selective attention was explicitly directed to the thumb during the observation of the grasping action. We hypothesized that by focusing the attention of subjects to only one effector of the observed action, resonant response to that effector, measured as the amplitude modulation of MEPs in the OP muscle, would be enhanced. The goal of the experiment was to demonstrate a neurophysiological priming effect on the resonant activation of motor pathways induced by selective attention, inspired by the study by Bach et al. (2007), which demonstrated a behavioral priming effect (faster response reaction time) in a given limb when the selective attention of subjects was directed toward that limb, during the observation of a whole-body action.

Experimental paradigm. In Expt1, right-handed subjects (n = 16) observed the 5 s video showing the natural grasping motor sequence and were instructed to pay close attention to the movement of the thumb, while observing the grasping action performed by the avatar's right hand (Fig. 1A). MEPs were recorded in the OP and ADM muscles of their right hand, at four relevant delays from the onset of the video. All experimental details are described in Section 2.

3.1. Selective attention: Results and discussion

A 4x2 two-way repeated-measure ANOVA with delay (1,2,3,4) and muscle (OP-ADM) as within-subject factors was run to determine whether MEP facilitation of the ADM and OP muscles was significantly different from the baseline delay (d1). No main effects were found for muscle factor $(F(1,15) = 2.428, p = 0.140)$ nor delay factor $(F(3,45) = 2.403, p = 0.80)$, while there was a statistically significant interaction between the muscle and delay factors $F(3,45) = 4.206, p = 0.010$. Multiple comparisons of OP MEPs amplitude among the baseline delay (delay 1) and the three different dynamic delays, (paired *t*-test, Bonferroni-corrected level of significance $p < 0.01$), revealed statistically significant differences between d1 and d3 $(p = 0.003)$ and between d1 and d4 $(p = 0.009)$ while no statistical difference was found between d1 and d2 $(p = 0.469)$. The same analysis for ADM muscle did not reveal any statistical differences (d1 vs d2: $p = 0.744$; d1 vs d3: $p = 0.774$; d1 vs d4: $p = 0.529$).

Observation of the natural hand grasping action, with selective attention focused only on the thumb, evoked a MEP facilitation only in the OP muscle, in d3 and in d4 of the observed action time course, i.e. the hand Closing and ball Holding phases, when this thumb muscle is normally active (Fig. 2, panels A and B). However, the modulation of MEPs in the ADM muscle, typically measured during observation of the grasping action when attention is spontaneously focused on the whole hand, was completely abolished (Fig. 2, panels A and B, see Supplemental statistical analysis (1) for a direct statistical comparison with data from Borroni et al. 2011 shown in panel B). ADM MEPs should have been facilitated in d2 i.e. the hand Opening phase, when this muscle opening the little finger is normally active.

The first interesting result of this experiment is that selective attention enhanced the resonant activity in motor pathways to the OP muscle to the expense of the modulation of other effectors active in the grasping action, in this case the ADM muscle. This evidence suggests that through the attentional manipulation, the portion of primary motor cortex controlling the descending pathways to the ADM muscle might receive less input from the rest of the AON (primarily from premotor cortex), resulting in a reduced activation of corticospinal motoneurons and thus in a decreased amplitude modulation of ADM MEPs. This finding is consistent with the large literature on selective attention showing clearly how attention can enhance the salience of an attended stimulus or feature and at the same time inhibit the relevance of the unattended ones (Carrasco, 2011; Driver & Frackowiak, 2001). At the neurophysiological level such a selective mechanism would increase the activity of visual cortices coding an attended stimulus or feature and at the same time inhibit the visual cortices related to the unattended ones (Tompary, Al-Aidroos & Turk-Browne, 2018; Beck & Kastner, 2009; Maunsell & Treue, 2006; Mirabella et al., 2007; Saenz, Buracas, & Boynton, 2002). A similar process might be active also during our experimental manipulation making the resonant response in the ADM muscle to the little finger's movement (unattended stimulus) disappear completely.

A second, unexpected, result is that by instructing subjects to maintain their attention focused on the thumb, a resonant response was also measured in the last delay of the action time course. In conditions of spontaneous observation of the grasping action, and of spontaneous allocation of attention to the whole hand, there is normally no facilitation of the OP resonant response at this delay (Holding phase) (Fig. 2, OP panel B). In past experiments, we interpreted the absence of MEP modulation in the OP during observation of the Holding phase, even though the thumb is still actively contracted during this phase of the natural action, as a consequence of the fact that this is not a critical, dynamic phase of grasping *per se*. But in this experiment, selective attention unlocked the facilitation of OP MEPs also in the last delay which, though non-essential to grasping, is still characterized by active contraction of this thumb muscle, necessary to hold and lift the ball from the table. This unexpected result suggests that it is possible to
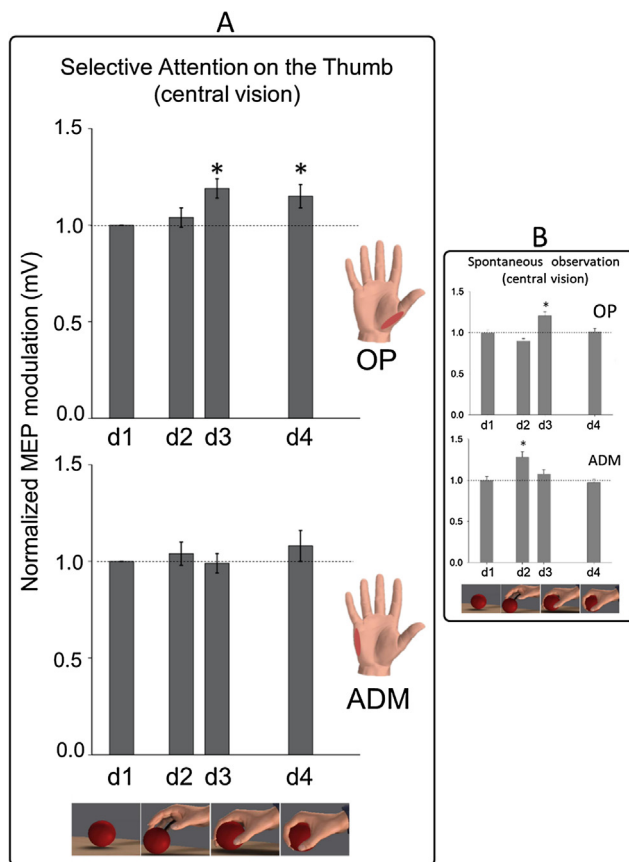
Table 1
Mean MEP amplitudes (μV) and SD of the first delay (Baseline = 0 s) in all the different experimental conditions.

		OP1	ADM1
Selective (natural)	MEAN	690	545
	SD	460	372
Covert (natural)	MEAN	859	308
	SD	703	129
Covert (impossible)	MEAN	694	574
	SD	271	423
Load (impossible)	MEAN	867	660
	SD	442	338

Fig. 2. Selective attention. Panel A, MEP modulation during observation of the natural grasping action in central vision when subjects are asked to focus their attention on the thumb. MEP amplitude variations in OP and ADM muscles (vertical bars, means ± SE) recorded at four selected delays (d1 = 0 s, d2 = 1 s, d3 = 1.6 s and d4 = 3 s) during the observation in central vision of the natural grasping action. Small figures on the bottom are the video frames illustrating positions of the hand at the four delays. MEPs were significantly (*) facilitated only in the motor circuits controlling the OP muscle at d3 and d4 (Grasping and Holding phases of the action). Panel B, MEP modulation in OP and ADM muscles during spontaneous observation of the same video in central vision, modified with permission from Borroni et al., 2011 (Fig. 3). Note the significant (*) facilitation of circuits to the OP during hand Closing (d3) and to the ADM during hand Opening (d2).

modify the shape of the motor resonant response, by simply changing the observing instructions and introducing a new attentive filter. Finally, it is important to note that the OP resonant response, while being expanded by attention to include the last delay, remained specific, with no facilitation in d1, Baseline delay, or in d2, Opening delay, in which the OP muscle is not utilized.

4. Experiment 2: Covert attention

Expt1 showed how selective deployment of attentive resources can have a strong influence in shaping motor resonant responses. The aim of Expt2 was to tease apart the roles of vision and attention during observation of actions in peripheral vision, a condition in which the attention to the observed action is spontaneously reduced. With this experiment, we tested the specific hypothesis that the reduction in kinematic accuracy of resonant responses described with the same experimental protocol by Leonetti et al. (2015) and explained as the consequence of decreased visual acuity in peripheral vision, could also be due to decreased attention with respect to central vision. Since covert attention improves performance in peripheral vision (Hein, Rolke, & Ulrich, 2006; Yeshurun, Montagna, & Carrasco, 2008),

compensating for the low resolution of visual cortices coding the peripheral field, we expected that covertly attending an action unfolding in periphery might improve its visual perception, thus also improving the quality of the input from the rest of the AON toward motor areas and thus also the specificity of the resonant response (perhaps even restoring the accuracy measured in central vision). Specifically, we expected MEPs in the OP and ADM muscles to be facilitated only in the most salient phases of the grasping action (d2 = hand Opening and d3 = hand Closing), as measured during observation in central vision, instead of being unspecifically facilitated at all movement phases (Opening, Closing and Holding) as measured in peripheral vision. In fact, in the latter condition, MEP facilitation recorded in the OP and ADM muscles was found to be generalized in terms of muscle selection and timing of activation during the observation of the different phases of the grasping action: it was virtually identical at all interactive delays (d2, d3, and d4) irrespective of the muscle (flexor or extensor) (Leonetti et al., 2015). This MEP modulation is obviously not consistent with the motor program corresponding to the observed grasping, in which ADM and OP MEPs are correctly facilitated at different times during hand Opening and Closing respectively.

Experimental paradigm. In Expt2, subjects (n = 14) observed the 5 s video showing the natural grasping motor sequence, while different subjects (n = 15) observed the 5 s video showing the impossible grasping motor sequence. The two videos were identical, except for the frames in which the hand grasps the ball using either the natural or the impossible hand kinematic sequence. Utilizing the same experimental paradigm as in the previous experiment (Leonetti et al., 2015) in which subjects were asked to focus their attention on a central fixation point (red cross) while a grasping action was presented in their peripheral field of vision, in the present experiment subjects were instructed to actively pay close covert attention to the content of the video, i.e. without shifting their gaze from the same central fixation point (Fig. 1B). MEPs were recorded in the OP and ADM muscles of their right hand, at the four relevant delays from the onset of the video. All experimental details are described in Section 2. Eye movements were monitored by electro-oculography (EOG) throughout the whole video presentation (for details see Section 2). After the experiment, we also investigated whether subjects had recognized the movement by asking them to describe and reproduce what they had seen. It has been our experience from previous studies that the combination of this subjective evaluation with the objective physiological recordings offers the chance to obtain important information, often critical to the interpretation of results.

4.1. Covert attention: Results and discussion

A 4 × 2 × 2 three-way repeated-measure ANOVA with delay (1,2,3,4) and muscle (OP-ADM) as within-subject factors and movement (natural vs impossible) was run to determine whether MEP facilitation of the ADM and OP muscles in the different delays was different in the two movements. No main effects were found for muscle factor ($F(1,27) = 0.075$; $p = 0.787$), delay factor ($F(3,27) = 2.450$; $p = 0.069$), movement factor ($F(1,27) = 0.700$; $p = 0.410$) nor interaction effects for muscle * movement ($F(3,81) = 0.391$; $p = 0.537$), delay * movement ($F = 3,81) = 1.286$; $p = 0.285$), muscle * delay ($F(3,81) = 2.291$; $p = 0.084$), muscle*delay*movement ($F(3,81) = 0.891$; $p = .449$). Surprisingly, not only did observation during covert observation of the natural and impossible grasping actions in peripheral vision fail to replicate the excitability modulation of motor pathways to hand muscles measured during observation of the same actions in central vision, but it canceled even the modulation normally measured in spontaneous peripheral vision observation (Fig. 3 panels A and B, see Supplemental statistical analysis (2) for a direct statistical comparison with data from Leonetti et al. (2015) shown in panel B). While in the latter observation condition MEP facilitation was generalized to both OP and ADM muscles and to all dynamic delays of
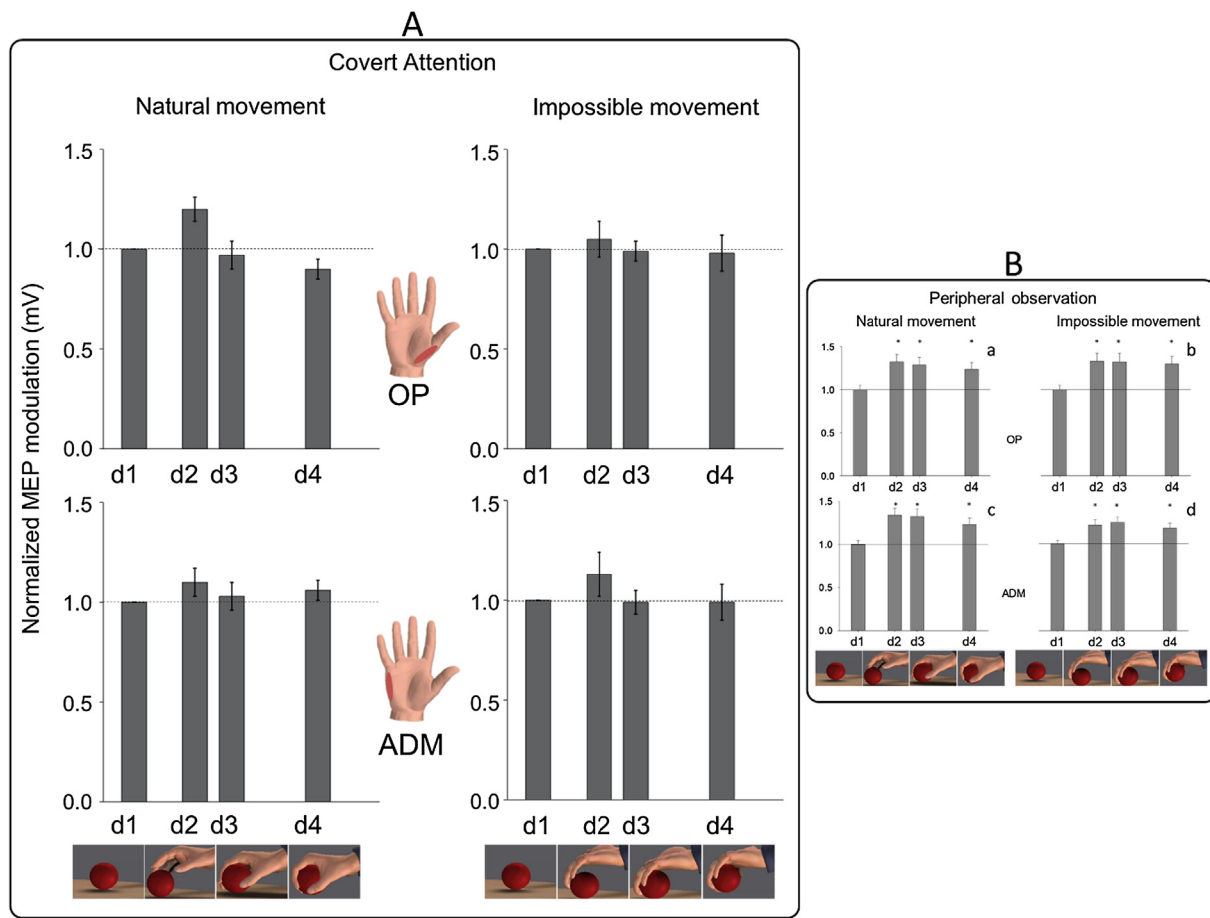
Fig. 3. Covert attention. Panel A, MEP modulation during observation of the natural and impossible grasping actions in peripheral vision when subjects are asked to pay covert attention. MEP amplitude variations in OP and ADM muscles (vertical bars, means ± SE) recorded at four selected delays (d1 = 0 s, d2 = 1 s, d3 = 1.6 s and d4 = 3 s) during the observation in peripheral vision of the avatar's natural or impossible grasping action. Small figures on the bottom are the video frames illustrating positions of the hand at the four delays. MEPs were not significantly modulated with respect to d1 (Baseline). Panel B, MEP modulation in OP and ADM muscles during spontaneous observation of the same video in peripheral vision, modified with permission from Leonetti et al., 2015 (Fig. 3). Note the significant (*) unspecific facilitation of circuits to both OP and ADM, at all dynamic delays (d2, d3, and d4).

both natural and impossible observed actions, in the covert attention condition MEP amplitude in both muscles were not significantly facilitated, compared to baseline, at any of the measured delays and during observation of either action sequences. Covert attention, therefore, did not improve or restore the resonant response and the results of this experiment do not support our starting hypothesis.

We interpret these data as the result of the high cognitive load introduced by the covert attention instruction which, instead of helping, prompts in subjects a new effort aimed at decoding the meaning of the scene viewed in periphery (since we asked them to pay particular attention to it). We suspect that this effort occupies much of their cognitive resources, thus less available for the normal development of the motor resonant response. This interpretation is consistent with our recent results on the importance of attention for action observation tasks (Puglisi et al., 2017) and with other reports in the literature describing the detrimental effects of subtraction of attentive resources from the process of motor resonance generation (Bach et al., 2007; Chong et al., 2008; Gowen et al., 2010; Muthukumaraswamy & Singh, 2008; Perry & Bentin, 2010; Woodruff & Klein, 2013). For instance, Chong and colleagues (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008) showed that when the attentive resources available to process the observed action are significantly reduced by adding a high cognitive load secondary task, the activity of a frontal AON node (near the Inferior Frontal Gyrus) decreases. These data suggest that when the coding of an observed action is hindered by adding a secondary task, so that few or no cognitive resource remain available to process the observed action,

the AON input toward motor areas involved in the execution of the observed action is reduced, preventing a proper motor facilitation effect.

In order to investigate the conscious perception of the actions observed in peripheral vision, at the end of Expt2 we asked all subjects to describe with words what they had seen, and then to physically repeat it. Results of this post-experimental questionnaire, especially when compared to answers given to the same questionnaire in our previous study with spontaneous observation of the same actions in periphery (Leonetti et al., 2015), indicate that observation of the impossible movement in peripheral vision is particularly challenging and susceptible to attention manipulation. Subjects observing the natural movement referred, with little hesitation, to having seen a hand grasping a ball and imitated fairly accurately the grasping action, while subjects observing the impossible movement while still reporting having seen a hand grasping the ball, had difficulties in identifying the exact manner in which the movement was performed. Interestingly, results of the questionnaire in our previous study had indicated that subjects who were not explicitly instructed to pay attention to the scene in their peripheral field, tended to accept a lower level of certainty about the goal of the observed impossible action: several subjects referred to having seen actions different from a grasping, such as bouncing or stroking. Instead, in the present experiment, despite expressing frequent doubts about movement kinematics, few subjects had doubts about the goal of the action they were observing, i.e. a grasping, denoting a stronger voluntary effort to understand, categorize and report

the action. These results suggest that subjects who observed the action in the covert attention condition (especially the impossible grasping) were performing a more demanding perceptual task than just observing it passively, which might have subtracted cognitive resources from the motor resonance process. In order to verify whether cognitive load was a suitable explanation of the present results, we carried out Expt3, in which the load of perceptual processing of the impossible movement in periphery was manipulated.

5. Experiment 3: Cognitive load

According to the interpretation of Expt2, the hypothesis of this third experiment is straightforward: if the cognitive load of the covert attention action observation task in peripheral vision can be reduced, the level of activation of motor circuits should increase, improving or even restoring the motor resonant response. In particular, if indeed the demand to pay covert attention to a scene viewed with poor definition, resulted in the subjects perceiving an increased pressure to decode the kinematics of the observed action and increased their cognitive effort to do so, then by revealing the action in advance we could expect to evoke a more accurate resonant response (consistent with the response in peripheral vision, or even in central vision). We decided to test this hypothesis utilizing the video of the impossible movement since, according to the results of the questionnaires, the cognitive effort appeared to be particularly demanding for this experimental condition. Specifically, the hypothesis can be articulated as follows: (1) if the typical resonant response in peripheral vision were to be restored, we expect MEPs to be facilitated in both the OP and ADM muscles, at all dynamic delays (Fig. 3, panel B); (2) if instead knowing in advance the precise movement, together perhaps with the enhanced processing of visual information thanks to covert attention, is sufficient to compensate for the decreased visual acuity of peripheral vision, we could even expect the correct resonant motor program, i.e. no modulation of OP MEPs, since the thumb is always extended in the impossible movement, and facilitation of ADM MEPs in the two interactive hand opening and closing delays, when the little finger is performing the grasping (Fig. 4, panel B).

Experimental paradigm. In Expt3, the cognitive load necessary for decoding the impossible grasping was lowered by allowing subjects (n = 19) to watch the video 10 times, in central vision, in order to familiarize themselves with the odd motor sequence. After that, they were asked to observe the same video in peripheral vision in the covert attention condition, with the identical protocol as in Expt2. Knowing the exact kinematics of the impossible movement before the peripheral presentation allows subjects to observe the stimulus without uncertainty about its nature. MEPs were recorded in the OP and ADM muscles. All experimental details as in Section 2. In order to confirm that subjects' gaze did not move from the fixation point, eye movements were monitored by elecro-oculography (EOG) throughout the whole video presentation.

5.1. Cognitive load: Results and discussion

A 4x2 two-way repeated-measure ANOVA with delay (1,2,3,4) and muscle (OP-ADM) as within-subject factors was run to determine whether MEP facilitation of the ADM and OP muscles was significantly different from the baseline delay. A main effect was found for muscle factor (F(1,18) = 6.639, p = 0.019) and delay factor (F(3,54) = 4,620, p = 0.006). Crucially a statistically significant interaction between the muscle and delay factors (F(3, 54) = 4.782, p = 0.005) was found. Multiple comparisons of ADM MEPs amplitude among the baseline delay (delay 1) and the three different dynamic delays (paired *t*-test, Bonferroni-corrected level of significance P < 0.01), revealed statistically significant differences between d1 and d2 (*p* = 0.003) and between d1 and d3 (*p* = 0.001) while no significant difference was found between d1 and d4 (*p* = 0.930). The same analysis for OP muscle did
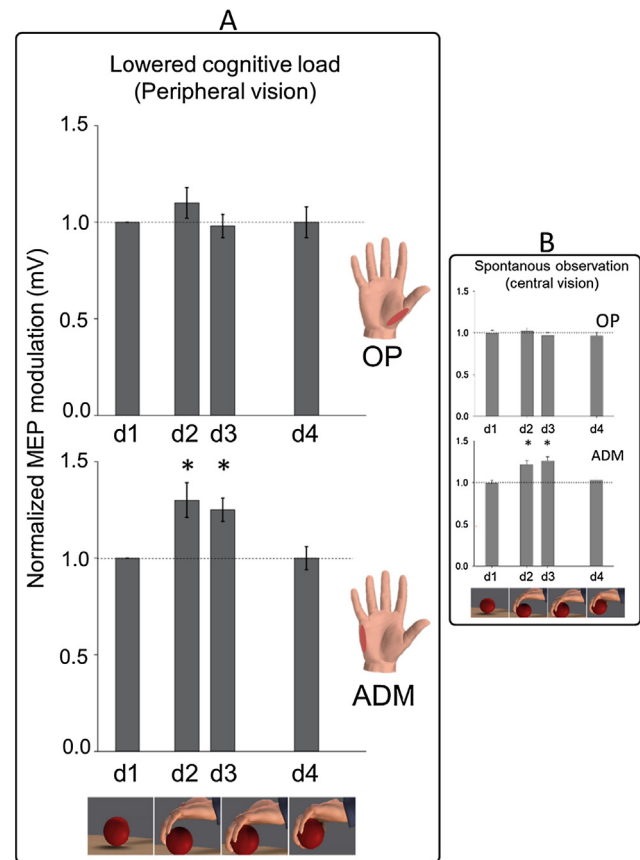

Fig. 4. Cognitive load. Panel A, MEP modulation during observation of the impossible grasping action in peripheral vision, when subjects are asked to pay covert attention, having lowered their cognitive load by previous familiarization with the complex action. MEP amplitude variations in OP and ADM muscles (vertical bars, means ± SE) recorded at four selected delays (d1 = 0 s, d2 = 1 s, d3 = 1.6 s and d4 = 3 s) during the observation in peripheral vision of the impossible grasping action. Small figures on the bottom are the video frames illustrating positions of the hand at the four delays. OP MEPs were not modulated, while ADM MEPs were significantly (*) facilitated during the central delays, d2 and d3 (Opening and Grasping phases), consistently with the modulation recorded in these muscles during observation of the same video in central vision, Panel B, modified with permission from Borroni et al., 2011 (Fig. 3).

not reveal any statistical difference (d1 vs d2 (p = 0.329), d1 vs d3 (p = 0.516), d1 vs d4 (p = 0.675).

Observation of the impossible grasping action in covert attention condition as in Expt2, but after lowering the cognitive load thanks to previous familiarization with the odd movement, confirmed our hypothesis in its second articulation, i.e. it restored the facilitation pattern in the ADM and OP MEPs normally measured in central vision (Fig. 4 panels A and B, see Supplemental statistical analysis (3) for a direct statistical comparison with data from Borroni et al. 2011 shown in panel B). This result confirms our hypothesis that decreasing the cognitive effort necessary to decode the impossible movement improves the accuracy of the motor resonant process and restore responses. Moreover, it confirms our interpretation of the results of Expt2 that the facilitation of motor pathways recorded during the peripheral action observation is actually hindered by deployment of covert attention, because this cognitive effort subtracts resources from the motor resonance process. A 4 × 2 × 2 three-way repeated-measures ANOVA with delay (1,2,3,4) and muscle (OP-ADM) as within-subject factors and condition (covert attention (Expt2) vs cognitive load (Expt3)) was run to determine whether MEP facilitation of the ADM and OP muscles in the different delays was different in the two experimental conditions.

There was a significant interaction among condition, muscle and delay factors $F(3, 96) = 2.795$, $p = 0.05$. Multiple comparisons of OP muscle MEP amplitude of the dynamic delays between the two conditions (independent-sample *t*-test), did not reveal statistically significant differences (d2: $p = 0.676$, d3: $p = 0.811$, d4: $p = 0.941$). The same analysis for ADM muscle reveals statistical difference for delays 2 and 3 ($p = 0.005$) but not for delay 3 ($p = 0.743$).

6. General discussion

The question of whether the motor resonant response, i.e. the resonant motor program subliminally mirroring an observed action, is automatically assembled by the observer's AON or whether it requires attentional resources, has important theoretical implications for the proposed role of motor resonance in cognitive functions such as action understanding, imitation, motor learning and rehabilitation (Bien, Roebroeck, Goebel, & Sack, 2009; Naish et al., 2014; Ubaldi, Barchiesi, & Cattaneo, 2013). Present knowledge indicates that biological movement is a powerful exogenous stimulus for the AON, so that motor resonant responses can develop even when an action, falling in the observer's field of view, is not the primary focus of his/her attention and even when it is irrelevant to a different main task simultaneously performed (Puglisi et al., 2017). But additional evidence shows that when attentional resources are not directly allocated to the observation of movement, the resulting activation of motor circuits is greatly weakened (Bach et al., 2007; Chong et al., 2008; Gowen et al., 2010; Muthukumaraswamy & Singh, 2008; Perry & Bentin, 2010; Puglisi et al., 2017; Woodruff & Klein, 2013) and loses much of its kinematic specificity (Puglisi et al., 2017).

The aim of this work was to define the extent to which the resonant response can be modulated by manipulating subjects' attention in different experimental conditions. Three different experiments were performed, in which selective and spatial attention were manipulated during action observation by giving specific instructions to observers regarding the allocation of their attention during the task, while placing the observed action either in central vision, or in the near periphery of their field of view, where it naturally would receive less attention compared to central vision (Chung, 2010; Larson & Loschky, 2009; Staugaard, Petersen, & Vangkilde, 2016).

Overall our results confirm and expand the notion that the motor resonant response is not an "all or nothing" event, which occurs every time an action falls in our visual field but, similarly to other visual processes, it can be modulated by top-down influences, such as attention (Beck & Kastner, 2009; Kastner & Ungerleider, 2000). For example, the first experiment showed that motor resonance is susceptible to the selective mechanism of attention (Carrasco, 2011; Chong et al., 2009; Driver & Frackowiak, 2001), so that a comprehensive resonant motor program, inclusive of the multiple effectors participating in the observed action, is not assembled when the observer's attention is selectively focused only on one of the effectors (the thumb). The role of selective attention was investigated by asking subjects to focus on a specific element (the thumb of the hand) of a grasping action observed in central vision. As a result of this attentional shift to the thumb, a motor facilitation was measured only in MEPs recorded from the opponent of the thumb (OP) and not in MEPs of the abductor of the little finger (ADM), which is normally also activated during natural observation of the grasping action. This evidence suggests that in this experimental condition the portion of primary motor cortex controlling the ADM received less input from the rest of the AON. We can speculate that attention could modulate the activity of the AON by affecting early visual processing: many studies show that the activity of visual cortex can be modulated by top-down factors by medial prefrontal and parietal areas (Tompary, et al., 2018; Beck & Kastner, 2009; Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000; Maunsell & Treue, 2006; Saenz et al., 2002). Following this initial modulation of visual information, all the subsequent processing stages would be influenced,

resulting in the corresponding modulatory effect on the activity of the motor cortex during action observation. Alternatively (or in parallel), an attention-modulated prefrontal input to premotor areas could exert a later more direct modulatory activity (Rizzolatti & Luppino, 2001), and in turn regulate the excitability of primary motor cortex during action observation. In addition, by virtue of the instruction to pay attention to the thumb throughout the experiment, the facilitation of the OP muscle was prolonged to include the last delay, beyond the actual grasping and into the holding and lifting movements, which is not measured during spontaneous observation. Overall the data suggest that the shape of the motor resonant response can be affected by selective attention, by automatically directing the selection of specific corticospinal pathways to specific muscular groups upon which attention is placed, enhancing their excitability to the expense of others not included in the attentive focus.

Furthermore, results of the second and third experiments suggest that the motor resonant response may not be the result of a unitary neural process, and support the possibility for a dual action representation mechanism (mirror and inferential) in which the default mechanism of action decoding mediated by motor simulation in the AON (mirror), in conditions of high perceptual complexity can be substituted or complemented by an inference-based mechanism probably mediated by mesial frontal areas and superior temporal areas (Brass, Schmitt, Spengler, & Gergely, 2007; Decety & Grèzes, 2006; Frith & Frith, 2006). Crucially, the switch between the two mechanisms seems to depend on the attentional load associated with action coding. In these experiments we moved the action to be observed in the subjects' peripheral vision and studied the effect of covert attention and cognitive load in modulating the resonant response. Having previously demonstrated that observation of the same grasping action located in the peripheral field produces a rough and inaccurate resonant response compared to observation in central vision (Leonetti et al., 2015), in the second experiment we tested the hypothesis that one of the causes of such inaccuracy might be the natural decrease of attentive resources in this visual location (in addition to a decrease of visual acuity). Excitability of motor pathways controlling the OP and ADM muscles was assessed in a condition of covert attention, i.e. after explicitly instructing subjects to focus their attention on the action viewed in their peripheral field without shifting their gaze from a fixation point in their central vision (Posner, 1980). Based on the literature (Carrasco, 2011; Carrasco & Yeshurun, 2009; Hein et al., 2006; Yeshurun et al., 2008), we expected that allocating covert attention would improve the accuracy of resonant responses perhaps even restoring the response measured in central vision but, surprisingly, responses were almost completely abolished. We attributed this effect, i.e. the interference with the normal development of motor resonance, especially when combined with the difficulty of decoding the unfamiliar grasping movement in peripheral vision, to the higher cognitive load introduced by the covert attention instruction, compared to spontaneous observation. The results of the second experiment suggest that when action decoding becomes difficult as in the case in which subjects are explicitly instructed to pay covert attention, the AON input toward motor areas involved in the execution of the observed action is reduced, preventing a proper motor facilitation effect because less attentive resources remain available for action observation, being redirected to inferential processes/neural network needed for action understanding (Brass et al., 2007; Catmur, 2015; Fecteau, Tormos, Gangitano, Théoret, & Pascual-Leone, 2010; Heyes, 2010; Moore & Haggard, 2008). The third experiment tested this hypothesis. We reasoned that lowering the cognitive load (by allowing subjects to view and familiarize with the impossible grasping movement before the covert attention experimental session) should restore the motor resonant response at least to the level of accuracy measured in peripheral vision. In fact, this cognitive manipulation was so effective as to fully restore the accuracy of the resonant subliminal motor program to that measured in central vision. We conclude that when the complexity of the action decoding process is high, the challenge posed

to this process requires attentional resources, and that when these resources are engaged by some other cognitive process motor resonance results impaired or fully abolished. On the other hand, if the observed action is fully known (as for familiar actions or actions observed in central vision), the action simulation mechanism underlying motor resonance requires less attentional effort and is therefore less susceptible to interference by other processes capturing cognitive resources.

Given that the protocol of Expt3 had to include both covert attention to the action observed in peripheral vision and previous familiarization with its kinematic details (to decrease cognitive load), we cannot attribute the return of the accurate resonant response to either cognitive manipulation. Whether previous knowledge is sufficient to generate the correct response, or whether covert attention is also necessary to potentiate perception of details lost with peripheral observation remains to be determined.

Declaration of interest

None.

Acknowledgments

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