



Vicarious motor activation during action perception: beyond correlational evidence

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Neurophysiological and imaging studies have shown that seeing the actions of other individuals brings about the vicarious activation of motor regions involved in performing the same actions. While this suggests a simulative mechanism mediating the perception of others' actions, one cannot use such evidence to make inferences about the functional significance of vicarious activations. Indeed, a central aim in social neuroscience is to comprehend how vicarious activations allow the understanding of other people's behavior, and this requires to use stimulation or lesion methods to establish causal links from brain activity to cognitive functions. In the present work, we review studies investigating the effects of transient manipulations of brain activity or stable lesions in the motor system on individuals' ability to perceive and understand the actions of others. We conclude there is now compelling evidence that neural activity in the motor system is critical for such cognitive ability. More research using causal methods, however, is needed in order to disclose the limits and the conditions under which vicarious activations are required to perceive and understand actions of others as well as their emotions and somatic feelings.

Keywords: action perception, action simulation, mirror neurons, brain lesion, transcranial magnetic stimulation (TMS)

VICARIOUS MOTOR ACTIVATIONS DURING ACTION PERCEPTION

There is now extensive neurophysiological evidence that monkeys—and possibly humans—are equipped with a particular class of neurons active during action execution and action perception (Cattaneo and Rizzolatti, 2009; Mukamel et al., 2010). These so called "mirror neurons" are thought to implement a mechanism matching perceived actions to one's own motor representation of similar actions (di Pellegrino et al., 1992; Gallese et al., 1996; Fogassi et al., 2005). By showing that action perception modulates activity within the motor system, the discovery of mirror neurons has provided direct neurophysiological evidence in favor of the older notion that action perception is inherently linked to action execution (Lotze, 1852; James, 1890; Prinz, 1997). This idea was further supported in humans by functional magnetic resonance imaging (fMRI) (Etzel et al., 2008; Gazzola and Keysers, 2009; Kilner et al., 2009; Oosterhof et al., 2010), electroencephalography (EEG) (Cochin et al., 1999; Lepage and Théoret, 2006; Arnstein et al., 2011), and magnetoencephalography (MEG) (Nishitani and Hari, 2002; Nishitani et al., 2004) evidence that the action observation network (AON), i.e., the neural network activated by seeing others' actions, largely overlaps with the brain network involved in action execution. This has supported the notion that perceiving and understanding others' actions may be based on their vicarious representations within the observer's motor system.

One of the most convincing evidence that action observation vicariously activates motor circuits involved in performing the observed action in humans comes from single-pulse transcranial magnetic stimulation (TMS) studies. This neurophysiological method implies that single magnetic pulses are administered over the participants' primary motor cortex to record motor-evoked potentials from the targeted muscles and assess the excitability of their corticospinal representation under different experimental conditions. Many studies have shown that observing others' actions increases the excitability of the observers' corticospinal motor system (Fadiga et al., 1995; Catmur et al., 2007; Enticott et al., 2010, 2011; Senot et al., 2011). This "motor resonance" appears to be present for both transitive and intransitive movements (Fadiga et al., 2005; Romani et al., 2005; Borgomaneri et al., 2012) and is specific for the muscles involved in the observed action (Urgesi et al., 2006a; Alaerts et al., 2009; Candidi et al., 2010). Moreover, motor resonance is largely automatic and occurs early in time (Lepage et al., 2010; Barchiesi and Cattaneo, 2012). Furthermore, motor resonance is temporally coupled with the observed action when this is dynamically displayed (Gangitano et al., 2004) and seems to encode specific motor features such as the direction (Stefan et al., 2005; Barchiesi and Cattaneo, 2012) and the apparent effort of the action (Alaerts et al., 2010a,b; Tidoni et al., 2013). These findings demonstrate that action observation induces a dynamic simulation of the observed movement in the onlooker's motor system. Studies using cyclic movements

(Borrioni et al., 2005) or static images of actions (Urgesi et al., 2006b, 2010; Avenanti et al., 2013), however, also indicate that action simulation may be biased toward the future phases of the observed movements, suggesting the motor system is involved in the predictive coding of observed actions as also highlighted by intracortical recordings in monkeys' premotor cortex (Umiltà et al., 2001).

Interestingly, motor resonance appears to be sensitive to higher order aspects of others' actions, such as the goal or the intention of the actor (Cattaneo et al., 2009; Tidoni et al., 2013), suggesting that motor cortex activity is influenced by processing occurring in higher-order regions within the AON. In keeping, there is now direct evidence that resonance in the motor cortex reflects computations carried out in the inferior frontal cortex (IFC, including the ventral premotor cortex and the posterior part of the inferior frontal gyrus) and the inferior parietal lobule (IPL). This is demonstrated by perturb-and-measure studies (Paus, 2005; Avenanti et al., 2007) in which off-line suppression of neural activity in IFC disrupts the motor facilitation induced by action observation (Avenanti et al., 2007, 2013; Enticott et al., 2012) and dual coil studies in which stimulation of IFC and IPL modulates motor cortex reactivity to observed actions (Koch et al., 2010; Catmur et al., 2011).

BRAIN STIMULATION AND LESION METHODS TO HIGHLIGHT CAUSAL LINK BETWEEN AON AND ACTION PERCEPTION

While neurophysiological and brain imaging techniques have been essential in highlighting that action simulation is automatically triggered by action observation, it should be noted that these approaches only provide correlational evidence and cannot establish whether neural activity in motor regions is necessary for action perception. Behavioral studies have shown that action execution affects the perception of others' actions, suggesting a close link between motor and perceptual processing in social interactions (Kilner et al., 2003; Hamilton et al., 2004; Schütz-Bosbach and Prinz, 2007a,b; D'Ausilio et al., 2010; Sacheli et al., 2012, 2013). Motor experts present superior perceptual abilities in the prediction of others' actions (Abernethy et al., 2008; Aglioti et al., 2008) and short-term action execution training improves perception of full (Hecht et al., 2001; Urgesi et al., 2012) and point-light (Casile and Giese, 2006) displays of the same action even if no visual feedback is provided during the execution phase. On the other hand, non-use of specific body parts, following massive deafferentation of lower limbs in spinal cord injury patients, leads to impaired recognition of their movements depicted in static images (Pernigo et al., 2012) and point-light (Arrighi et al., 2011) displays.

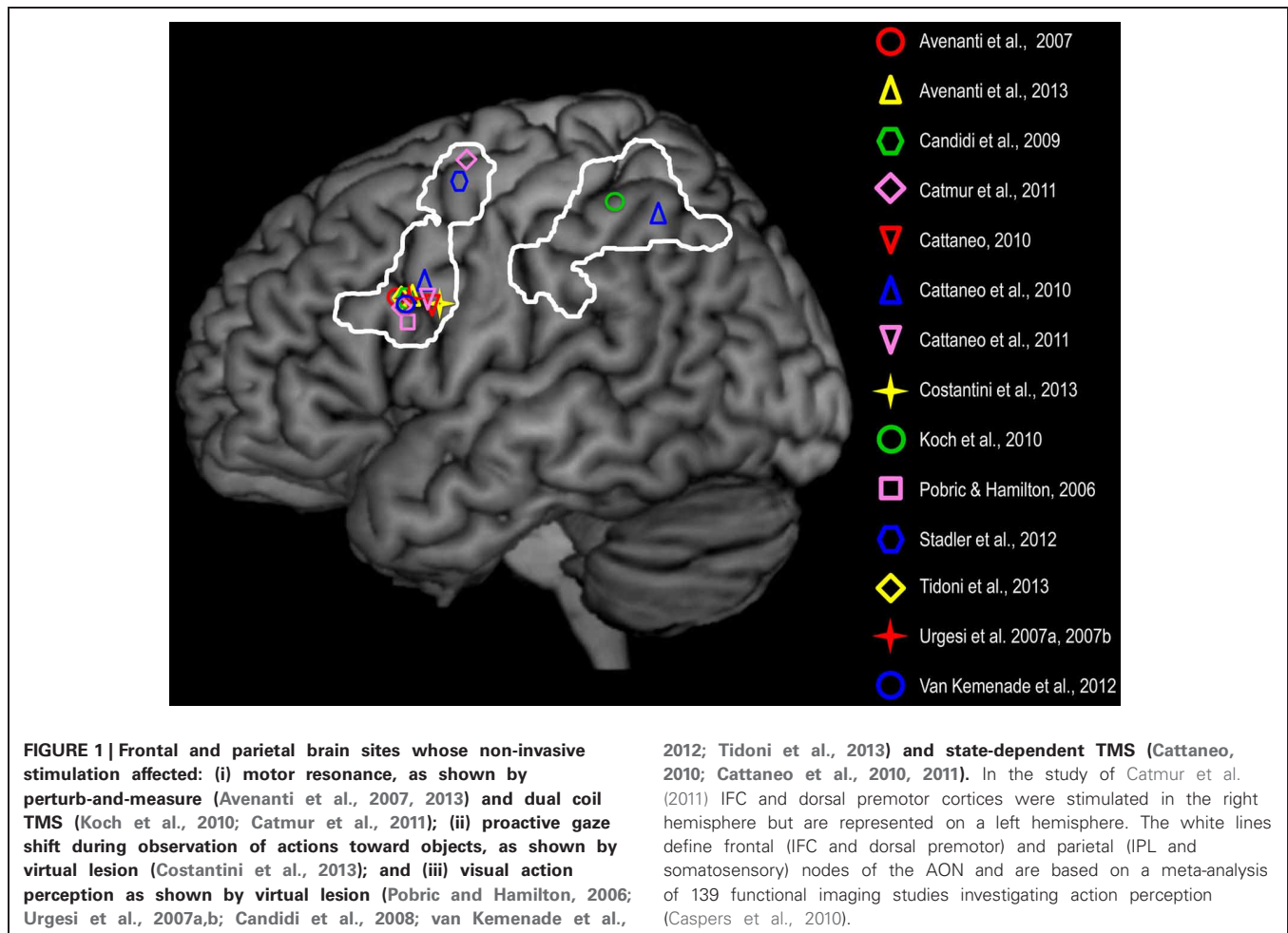
While behavioral studies have shown an influence of action execution on action perception these approaches do not tell "where" in the brain these two functions interact. Thus, to test the causal role of specific visuo-motor nodes of the AON in action perception is fundamental to recur to causal methods, i.e., investigating the effect of brain damage or non-invasive brain stimulation of parieto-frontal AON regions on the ability to perceive and recognize others' actions (Avenanti and Urgesi, 2011).

Mounting evidence suggests that IFC and IPL are critical for action perception. In two studies participants were presented with videos of an actor lifting and placing a box that could be of different weights and were asked to estimate the weight of the box (Pobric and Hamilton, 2006) or to recognize whether the actor was trying to provide deceiving information about the weight of the box (Tidoni et al., 2013). It was found that online repetitive TMS over IFC but not over occipital cortex or temporo-parietal junction worsened participants' performance in such tasks that required to monitor spatio-temporal features of seen actions (e.g., arm acceleration). Notably, no change in performance was found in "temporal" control tasks requiring to estimate how long the actor's hand was visible (Pobric and Hamilton, 2006) or in a "spatial" control task requiring to monitor the hand path during lifting and placing (Tidoni et al., 2013). Taken together these studies suggest that IFC is actively involved in processing seen kinematics and in particular in integrating their spatial and temporal features, which may be important to predict others' actions (see also Stadler et al., 2012; Avenanti et al., 2013; Costantini et al., 2013).

The integration of spatio-temporal features is critical for biological-motion perception in order to blend the coherent motion pattern of a series of point-lights into a unitary perception of a moving individual. While voxel-based morphometry (Gilaie-Dotan et al., 2013) and fMRI studies (Saygin et al., 2004) suggest a relation between IFC and biological motion perception, causal methods have recently demonstrated that off-line TMS suppression of IFC activity (van Kemenade et al., 2012) or vascular lesion to IFC (Saygin, 2007) impairs the ability to detect biological motion from point light displays.

Another group of studies has suggested a role of IFC in processing configurational aspects of observed actions (e.g., limb displacement, postures). In such studies participants were presented with static images showing hand grips (Jacquet and Avenanti, 2013), upper or lower limb actions (Urgesi et al., 2007b) or whole body movements (Urgesi et al., 2007a). In all the studies it was found that stimulation of IFC but not of control regions impaired the ability to visually discriminate between pictures depicting two slightly different actions. Notably, brain damage patients with lesions occurring in IFC but not in posterior regions were also impaired in similar tasks (Moro et al., 2008). Interestingly, these impairments in processing configurational aspects of others' actions appear specific for biological movements because IFC stimulation does not impair visual discrimination of images implying biomechanically impossible body movements (Candidi et al., 2008).

While brain stimulation studies suggest a role of the AON, and of IFC in particular (**Figure 1**), in processing specific spatio-temporal and configurational features of seen actions, neuropsychological evaluation of brain damage patients shows that lesions in IFC and premotor cortices may lead to more global deficits in action perception and understanding. Lesion in IFC and premotor cortices reduces the ability to: (i) associate pictures of pantomimes (e.g., licking) to the corresponding appropriate object (ice cream) (Saygin et al., 2004); (ii) judge whether a transitive action or an intransitive gesture is correctly performed (Pazzaglia et al., 2008a); (iii) associate the sounds evoking human actions



with pictures representing the same actions (Pazzaglia et al., 2008b); (iv) or re-order pictures of human actions compared to physical events (Fazio et al., 2009). On the other hand, lesion of the IPL impairs the recognition of transitive gestures (Buxbaum et al., 2005; Weiss et al., 2008; Kalénine et al., 2010) and of biological motion (Battelli et al., 2003). Moreover, Tranel et al. (2003) showed that patients with lesions in both IFC and IPL were impaired in tasks involving recognition of action from static pictures. Interestingly, there is a specific relation between the motor deficits shown by brain lesion patients and their impairment in action recognition (Eskenazi et al., 2009; Serino et al., 2010). For instance, patients with fronto-parietal lesions who were impaired in performing limb (limb apraxia) or mouth gestures (buccofacial apraxia) were also impaired in the audio-visual matching of hand and mouth actions, respectively (Pazzaglia et al., 2008b). Although the clinical pattern of apraxic patients is complex and cannot be reduced to the dysfunction of the AON visuo-motor nodes, the effector-specific correspondence between their motor and perceptual deficits further hints at the strict link between action execution and perception. In sum, there is now strong evidence that the activation of parieto-frontal nodes of the AON is not merely associated to action observation, but it appears to be critical to perceive and understand the actions of others.

STATE-DEPENDENT BRAIN STIMULATION IN ACTION PERCEPTION

One important limitation of causal approaches is that brain damage or non-invasive brain stimulation have remote effects. Although TMS is more focal than other non-invasive brain stimulation methods (i.e., transcranial direct current stimulation), and provides extremely high time-resolution, it modulates activity not only in the neurons under the coil but also in interconnected regions (Ruff et al., 2009; Siebner et al., 2009; Avenanti et al., 2012a,b; Arfeller et al., 2013). Thus, impairment of action perception due to vascular or “virtual,” TMS-induced lesions over specific motor regions may be at least partially due to the disconnection of a larger circuit (i.e., the AON) or the spread of the TMS-induced excitation along its connections (Valero-Cabré et al., 2005, 2007). The simultaneous combination of TMS with functional imaging promises to be of especially great value to tease apart the functional relevance of TMS-induced local and remote neural effects.

Moreover, one should notice that classical virtual lesions approaches do not elucidate how distinct neural populations within the stimulated area interact to give rise to perception and behavior (Silvanto et al., 2008; Avenanti and Urgesi, 2011; Silvanto and Pascual-Leone, 2012). Recently, the TMS-adaptation

and TMS-priming paradigms have been developed to tackle such limitation. The paradigms are based on the well-established notion of state-dependency, i.e., that TMS effects depend on the initial state of the stimulated neurons (Lang et al., 2004; Siebner et al., 2004, 2009; Bestmann et al., 2010). In such paradigms the functional state of the neurons is manipulated by means of perceptual (or motor) adaptation or priming. Although the underlying neurophysiological mechanisms are not well understood (Ruzzoli et al., 2011; Schwarzkopf et al., 2011; Perini et al., 2012), the phenomenology of TMS-adaptation and TMS-priming is very robust and consists in a TMS reduction or reverse of the behavioral effects classically induced by perceptual adaptation or priming. These effects unambiguously indicate the presence of neurons encoding for the adapted/primed feature in the stimulated area and their relevance for perceptual processing.

To date, state-dependent TMS has been used to explore perceptual encoding of goal and grip configurations in frontal, parietal, and visual nodes of the AON. For example, in a TMS-priming study of Cattaneo (2010) participants were presented with target pictures showing a hand grasping an object and were asked to judge whether the movement was fast or slow. Observed grasp types varied from precision (index finger and thumb involved only) to whole-hand grasp. Target pictures were preceded by similar prime pictures. Without TMS and with sham stimulation, a clear priming effect was observed as a shortening of reaction times and as a bias toward the priming grasp type in the classification responses. The perceptual advantage of priming was reversed by TMS over IFC, suggesting that distinct populations in such regions are tuned to different observed grasp types and are critical for perception. In a recent TMS-adaptation study, Cattaneo et al. (2010) used perceptual adaptation to goal-directed actions and showed that IFC and IPL contain distinct populations encoding the goal of observed action (i.e., grasping or pulling) independently from the effector (i.e., hand or foot) used to perform such actions. To test whether the same motor neurons involved in performing an action are critical for visual perception of the same action, Cattaneo et al. (2011) used cross-modal motor-to-visual TMS-adaptation. They asked participants to repeatedly perform an action (pushing or pulling) and then to categorize static images showing an actor's hand displacing a ball as pushing or pulling actions. Repeated motor performance induced a visual aftereffect when categorizing action stimuli, with a bias toward pulling after execution of pushing and a bias toward pushing after execution of pulling. Thus, the aftereffect following motor adaptation was a bias toward the action opposite to the one that had been trained, suggesting a motor-to-visual adaptation of the same visuo-motor neurons involved in action execution and observation. Notably, TMS over IFC but not over control regions disrupted such visuo-motor aftereffects. Thus, cross-modal TMS-adaptation provides complimentary evidence to fMRI adaptation studies investigating the attenuation of hemodynamic responses in AON regions after repeated execution and observation of actions. These studies reported action-specific cross-modal adaptation in fronto-parietal AON areas (Chong et al., 2008; Kilner et al., 2009; Lingnau et al., 2009), suggesting the same neural populations are activated in response to specific actions that are either observed or executed. Using the

TMS-adaptation paradigm allowed documenting that the same populations of neurons involved in action execution are also critical for action perception.

CONCLUSIONS AND FUTURE DIRECTIONS

In conclusion, the studies reviewed here provide striking evidence that action perception not only correlates with motor activations in the observer's brain, but also requires these activations for allowing dynamic representations of others' actions. Successful social interactions, however, require motor, sensorial, cognitive, and emotional representations of the behavior of conspecifics. There is now substantial evidence that perceiving the emotions (Carr et al., 2003; Gallese et al., 2004; Dapretto et al., 2006; Bastiaansen et al., 2009) as well as the bodily sensations of others such as touch (Keysers et al., 2004; Blakemore et al., 2005; Bufalari et al., 2007; Ebisch et al., 2008; Schaefer et al., 2009; Gazzola et al., 2012) or pain (Singer et al., 2004, 2006; Avenanti et al., 2005, 2009a; Valeriani et al., 2008; Lamm et al., 2011; Voisin et al., 2011) vicariously activates those brain regions involved in the first hand experience of such emotions and bodily sensations. Although it is held that the mechanism underlying perception of others' sensory or emotional feelings is similar to that underlying action perception (Gallese et al., 2004; Keysers et al., 2010; Gallese and Sinigaglia, 2011), fewer studies have addressed the issue of causality in the former relative to the latter case. However, some of these studies have been important in clarifying that, for example, somatosensory cortices are not only active but are also critical for recognition of others' emotional expressions (Adolphs et al., 2000; Pitcher et al., 2008; Banissy et al., 2010) and others' tactile experiences (Bolognini et al., 2011, 2012, 2013; Rossetti et al., 2012). Further studies, however, are needed to corroborate the causal link between vicarious activations and the understanding of others' sensorial and emotional states.

One critical question for future research concerns the degree to which vicarious activations interact with other mechanism to give rise to perception and understanding of others' actions and feelings. Mirroring and simulating others' actions and feelings may be just one strategy amongst many to gain knowledge of others' mental states. There may be inter-individual differences in the extent to which this strategy is deployed as well as some modulatory effect of social context and previous experience. Vicarious somatomotor activations are often correlated with interindividual differences in personality (Gazzola et al., 2006; Avenanti et al., 2009b; Minio-Paluello et al., 2009; Schaefer et al., 2012) and are influenced by previous experience with the same situation (Calvo-Merino et al., 2006; Cross et al., 2006; Cheng et al., 2007; Fourkas et al., 2008; Abreu et al., 2012; Candidi et al., 2012; Tomeo et al., 2012), and social group belonging (Xu et al., 2009; Avenanti et al., 2010; Hein et al., 2010; Azevedo et al., 2012). They are modulated also by a number of other factors ranging from body ownership (Schütz-Bosbach et al., 2006, 2009) to social tasks and contexts (Kokal et al., 2009; Donne et al., 2011; Sartori et al., 2011). It is thus fundamental to understand the functional significance of such differential activations and causal methods may provide direct information about how and when simulation plays a critical role in our understanding of others' mind.

ACKNOWLEDGMENTS

Alessio Avenanti, Matteo Candidi, and Cosimo Urgesi are funded by grants from the Istituto Italiano di Tecnologia SEED 2009 (Prot. 21538). Alessio Avenanti is also funded by grants from the Ministero della Salute (Bando Ricerca Finalizzata Giovani Ricercatori 2010, protocol number: GR-2010-2319335) and the Università di Bologna (Ricerca Fondamentale Orientata). Alessio Avenanti and Cosimo Urgesi are also funded by grants from the Ministero Istruzione,

Università e Ricerca (Futuro in Ricerca 2012, protocol number: RBFR12F0BD). Matteo Candidi is funded by the University of Rome “Sapienza” Ricerche Universitarie, Progetti di Ricerca 2012 (Prot. C26A122ZPS). Cosimo Urgesi is funded by grants from the Ministero Istruzione Università e Ricerca (Progetti di Ricerca di Interesse Nazionale, PRIN 2009; Prot. 2009A8FR3Z) and the Istituto di Ricovero e Cura a Carattere Scientifico “E. Medea” (Ricerca Corrente 2009, Ministero della Salute).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 16 March 2013; accepted: 23 April 2013; published online: 14 May 2013.

Citation: Avenanti A, Candidi M and Urgesi C (2013) Vicarious motor activation during action perception: beyond correlational evidence. *Front. Hum. Neurosci.* 7:185. doi: 10.3389/fnhum.2013.00185

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