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Neural correlates of human action perception: motor, semantic and social aspects

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Sedulo curavi humanas actiones non ridere, non lugere, neque detestari, sed intelligere.

Spinoza

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Abstract

In the last decades, human action processing has been the research focus of a series of studies aimed at investigating the brain mechanisms underlying this complex process. Converging neurophysiological and functional neuroimaging literature suggested that human actions processing is associated with a large scale network involving areas within the temporal, parietal and frontal cortices. Against the amount of literature available on the localization of these areas, the temporal course of their activations is poorly understood.

The purpose of the present project was to explore the temporal dynamics associated with human action perception investigating the neural responses to different aspects of human behavior by means of a series of high-density electrophysiological recording experiments combined with source localization methods.

Specifically, the motor (Chapter 1), the semantic (Chapter 2) and the social (Chapter 3) aspects were investigated.

Results highlighted a crucial role of the social/affective content, revealing a very early recognition (at 170 ms) operated by the temporal and limbic areas, of this aspect of the human behavior. Starting from 250 ms the processing of the different aspects occurs temporally aligned, involving firstly the mid-superior temporal sulcus (STS) and subsequently the fronto-parietal mirror (hMNS) circuit. Evidence from the source localization analysis suggested also a later involvement of the medial prefrontal cortex (mPFC), associated with mentalizing process.

A deepening of the social content of actions was then performed (Chapter 4). Specifically, the modulation of the neural response to particular social actions, that is the communicative actions, caused by the different role held by the observer was investigated using fMRI. Activations in the brain circuits associated with action perception, namely the STS, the hMNS and the mPFC, were recorded only when participants were the addressees of the communicative actions, clearly indicating the importance of social involvement in processing human actions.

All in all, the present results point toward a complex interplay of different brain networks to process in parallel distinct aspects of the human behavior in order to ensure a rapid and effective comprehension of the surrounding social environment. The prominent role of the social aspect in human action perception is also supported by the clear result of the prevalence of the affective/social content on the others.

Introduction

Humans are inherently a social species.

Humans live in groups, carve the company of others, share emotions with conspecifics and cooperate to reach a common goal. Humans suffer for being separated from important others, for being socially excluded and for solitude. Humans rarely survive alone.

Complexity of human societies is unique, being much larger and more composite than the societies of other social animals (Richerson & Boyd, 2001). Also, no other animal has such complex and various social relationships or is more dependent on them. Sophisticated mechanisms are needed to be successful engaged in these relationships (Iacoboni et al., 2004).

Despite the uniqueness of the human societies, the human species is not the only one to be socially organized. Social organizations are observable in a lot of other species, from insects to primates. Of special interest, on the evolution line, are the great apes that live in highly organized societies and present rudimental versions of sophisticated social behavior, such as tactical deception (Whiten & Byrne, 1988).

According to the social brain hypothesis (Dunbar, 1992; Dunbar, 1998), brain size and specifically the relative size of the isocortex, positively correlate with the size of groups primates live in. Based on this evidence, the social brain hypothesis' authors argued that larger brains and proportionately enlarged isocortices provide primates with amplified cognitive "computational power" to manage a greater amount of social interactions and relationships (Charvet & Finlay, 2012). Although other hypotheses have been formulated suggesting that brain size correlates with a number of other factors, including dietary foraging strategy (Dunbar, 1998), it's likely that large brain size is at least in part due to the complexity of primate social structure (Adolphs, 1999).

Thus, human brain seems to be highly specialized for solving social situations such as anticipate other people's behavior, chose the right person to form an alliance and to cooperate with, and also manipulate other people to own advantages. Therefore, humans appear to be expert in developing and using strategies to create and maintain several relationships and to manage complex social interactions.

Interacting with others is based on different processes including perceiving other emotions, understanding their actions and gestures, detecting social cues such as eye gaze, body language and non-verbal communication, comprehending others' intentions and mental states, and finally providing an appropriate response.

How our brain perfectly accomplishes all these activities is a matter of study of the social neuroscience. Social neuroscience is a recently developing area of research that endeavors to give responses to fundamental questions about the nature of human social cognition and behavior. It emerged from the union of the cognitive neuroscience with social psychology, joining the advanced techniques employed to explore how the brain works with the large amount of experimental methods employed by social psychologists and other social scientists to study these questions (Lieberman, 2005).

The work presented in this thesis regards one of the most intriguing topic this new discipline deals with. Specifically, the main theme of the studies described in the following chapters is the investigation of the neural bases of perceiving and understanding human actions, with particular attention focused to specific aspects, namely motor, semantic and social aspects.

Human action processing and underlying brain mechanisms

Comprehending human actions is a complex process that is based on the perception of different elements as the movements performed to execute the action, the presence or not of an object to which the action might be directed, the presence of other people as addresses of the action, the physical and the social environment where the action is played out. All these elements have to be integrated among themselves and with our stored knowledge, in order to have a sensible representation of the action.

Despite how humans understand each others' behavior has always been of interest for researchers, in the last decades an increasing and flourishing literature has been striving to explore and uncover the brain mechanisms underlying human action processing.

Considered the complexity of the process it's not surprising that studies centered on this topic have employed many different techniques such as functional Magnetic Resonance Imaging (fMRI) (Hamilton & Grafton, 2006; Iacoboni et al., 2005a), Electroencephalogram (EEG) and Event-related Potentials (ERPs) (Muthukumaraswamy et al., 2004; Proverbio et al., 2009), Magnetoencephalogram (Pavlova et al., 2006), electro-magnetic stimulation techniques as Transcranial Magnetic Stimulation (TMS) (Aglioti et al. 2008; Gangitano et al. 2004), and kinematics (Sartori et al., 2009). Various experimental designs and different type of stimuli have been also employed, including comparisons of moving with still bodies or limbs (Piefke et al., 2009), transitive vs. intransitive gestures (Enticott et al., 2010), meaningful vs. meaningless actions (Proverbio et al., 2010), action perception aimed to memorization vs. imitation (Decety et al., 1997), solo vs. joint actions (Newman-Norlund et al., 2007a).

As can be inferred by the quantity and the heterogeneity of the studies above cited, the complexity of the action comprehension process is reflected in the difficulty of defining in accurate way the neural underpinnings and mostly their roles and their reciprocal relationships.

Data now available are the results of years of studies that have their origin from three distinct lines of research: the perception of biological motion, the characterization of the mirror neurons and the neural bases of mentalizing, or theory of mind.

Biological motion and the Superior Temporal Sulcus (STS)

Humans, and indeed all creatures, need to rapidly detect and process sensory cues that suggest the presence of another living entity. Plausibly, one of the richest sources of such information comes from visual processing of the movements of others, commonly known as biological motion (BM) (Krakowski et al., 2011).

Biological motion is a term employed to indicate the motion produced by living organisms.

Traditionally, in the literature studying the perception of biological motion, this term is associated with a specific type of stimulus, the Point Light Displays (PLDs). These stimuli were created for the first time in the 1973 by the young Swedish researcher Gunnar Johansson (Johansson, 1973). He filmed walking actors wearing black clothes with white dots attached to their joints on a completely black set. The result was a display where it’s possible to identify a walking man just from the lights placed on his joints. In the following years this kind of stimuli were reproduced to represent various different actions by several research groups and also created by means of graphic software.

Lots of studies were conducted employing the PLDs to explore and delineate the motion perception process, the factors influencing it and the information humans can infer just from motion.

Studies proved that observers can easily recognize what a individual is doing in a given PLD (Dittrich, 1993), his/her identity (Loula et al., 2005) and gender (Troje, 2002). Even activities involving two or more individuals (Blake & Shiffrar 2007) and movements of singles limbs are identifiable (Pollick et al., 2001). Emotional content is detectable too, both from the whole body motion (Clarke et al., 2005) and from facial expression (Bassili, 1978).

Observers are also able to perceive human motion in non-optimal conditions, e.g. when a PL animation is presented for a short time as 100 ms (Johansson, 1973) or is embedded in a set of light dots forming a background noise (Ikeda et al., 2005).

Moreover, the ability to perceive biological motion from PL stimuli arises early in life: four months old infants prefer staring human motion sequences than random motions (Bertenthal 1993). However, this ability keeps improving during the first years of life, with adult levels of performance achieved by age five (Pavlova et al., 2010). On the other side, observers older than 60 years, show a good performance in discriminating among different forms of human motion even when under tough conditions, as brief PL sequences or partially covered dots (Norman et al., 2004).

Taken together, all these studies provide strong evidence that human brain is highly adapted and specialized for the perception and comprehension of other people’s motion and actions.

Evidence for this specialization comes also from neuropsychological lesion studies demonstrating dissociations between the ability to perceive biological motion and other kinds of motion: patients who couldn’t perceive any types of motion were able to perceive biological motion (Vaina et al., 1990) and conversely, patients with relative preserved ability to perceive motion were unable to perceive biological motion (Schenk & Zihl, 1997).

Converging evidence coming from human neuroimaging (Bonda et al., 1996; Grossman & Blake, 2002), electrophysiological (Hirai et al., 2003; Jokisch et al., 2005) and also non-human primates single-cells recording studies (Jellema et al., 2000) demonstrated that perception of biological motion is associated with brain activity in an area surrounding the

Superior Temporal Sulcus (STS). Specifically, perception of Biological Motion activates the posterior part of the STS (pSTS) with a right side preference (Pelphrey et al., 2003).

Activity in the pSTS is also evoked by movements of body parts, such as eye and mouth movements (Puce et al., 1998), and hand movements (Grafton et al., 1996). To this regard, it has been shown that STS is responsive not only to simple motion, but also to more complex movements, such as hand grasping (Grafton et al., 1996) and goal-directed actions (Grezes, 1998). Finally, the STS is resulted to be active during evaluation of the intentions behind other people’s actions (Pelphrey et al. 2004) and the processing of geometric shapes motion suggesting underlying intentional activity but do not actually contain biological motion (Castelli et al., 2000).

Overall, the STS has been recognized as playing a crucial role not only in the mere perception of human motion, but more broadly in processes associated with social cognition as perception of social cues and recognition of action goals and intentions (Allison et al. 2000).

Human Mirror Neuron System

Mirror Neurons are a set of neurons the properties of which were uncovered by a group of Italian researchers led by Rizzolatti, in the macaque brain, specifically in the premotor cortex and in the parietal cortex (Di Pellegrino et al. 1992; Gallese et al. 1996).

Single cells recording from the ventral premotor cortex (F5) and the inferior parietal lobule of the macaque brain revealed that these neurons discharge during both the execution of an action and the observation of the same action. Because of this property they have been called mirror neurons.

Since their discover, lots of studies have appeared in the scientific journals aiming at exploring, investigating, defining the existence of neurons with similar properties in the human brain and their functions in both human and monkey brain.

The first evidence of the existence of a mirror mechanism in the human brain was shown by Fogassi et al. (Fadiga et al. 1995) who applied Transcranial Magnetic Stimulation (TMS) to participants' motor cortex and recorded their MEP (Motor Evoked Potentials) during both the execution and the observation of arm movements and goal-directed actions. MEP significantly increased during the observation conditions reflecting the pattern of muscle activity recorded when participants were executing the same actions. The authors interpreted the increased MEP as an observation-execution matching system resembling the mirror properties of the macaque brain.

After this first study, converging evidence from brain imaging (Rizzolatti et al. 1996; Iacoboni et al. 2005), transcranial magnetic stimulation (TMS) (Enticott et al., 2010; Gangitano et al. 2001), electroencephalography (EEG) (Cochin et al. 1999; Cheng et al. 2008) and magnetoencephalography (MEG) (Hari et al. 1998; Kessler et al. 2006) studies came down in favor of the existence of a mirror mechanism also in the human brain.

In humans, mirror mechanisms were detected in brain areas corresponding to those found in the macaque's brain, namely the Inferior Frontal Gyrus (IFG) associated with the macaque ventral premotor cortex (F5) and the Inferior Parietal Lobule (IPL). Given that the large part of the studies with humans employed indirect measures of the mirror activity, when we deal with humans, it's commonly accepted to speak of a human Mirror Neurons System (hMNS).

Following studies (Gazzola & Keysers, 2009; Grèzes et al. 2003; Buccino et al. 2004; Hamilton & Grafton 2006; for a review see Caspers et al. 2010) revealed mirror mechanisms in other cortical areas such as the primary and the secondary somatosensory cortex (I and II), the primary motor cortex, the Supplementary Motor Area (SMA), the dorsal premotor cortex, the superior and the Intraparietal Sulcus (IaPS).

The finding of the existence of neurons that discharge both when we execute and when we observe an action has led to the idea that action understanding is supported by a mechanism of automatic simulation, transforming visual input into the motor vocabulary of our own actions (Rizzolatti & Craighero 2004; Keysers & Gazzola 2010).

A long debate that characterized research on mirror neurons since the earliest studies regard what really encode mirror neurons, whether motor acts (goal-directed behavior) or movements (motion without specific aim) (Rizzolatti & Sinigaglia 2010).

A number of studies provided evidence that the hMNS encodes the goal of motor acts.

For example, in an fMRI study, observation of an action having the same goal performed by humans and robots elicited an activation in areas belonging to the hMNN, despite differences in the effectors' kinematics (Gazzola et al. 2007). In another study by Gazzola et al. (2007), two aplasic patients, born without arms and hands, showed activation in the fronto-parietal mirror network during both the execution of feet and mouth movements and the observation of hand motor acts that they have never executed.

By contrast, literature exhibited also results in favor of movements coding by the hMNS. A TMS experiment revealed an activation of muscles involved in executing a movements when the same movement were observed (Lui et al., 2008). Also, EEG desynchronization of the μ-rhythm in the motor areas were recorded during the observation of movements without goal (Perry & Bentin 2009)

These and other studies led Rizzolatti (Rizzolatti & Sinigaglia 2010) to argue that human parieto-frontal mirror network encodes both movements and motor acts goal-directed.

The Action Observation Network

In the very last years (Grafton 2009; Turella et al. 2012; Gazzola & Keysers 2009; Avenanti et al. 2012), temporal regions sensitive to action observation and the fronto-parietal mirror network are considered together as being part of a widespread network of brain areas associated with the perception and the comprehension of actions. This brain network has been termed Action Observation Network (AON) and specifically refers to these areas: within the frontal cortex, the dorsal and ventral premotor cortex together with the inferior frontal gyrus; within the parietal cortex, both the superior and the inferior parietal lobules, the intraparietal cortex and the postcentral gyrus; within the temporal cortex, the superior and middle temporal gyri.

The Mentalizing System

Mentalizing is the ability to attribute mental states to other agents. This process is mostly made automatically, without any thought or deliberation (Frith & Frith 2006).

There are many different types of mental states that can drive or affect our and others' behavior. In their review Frith and Frith (2006) described long-term dispositions (e.g. to be trustworthy), short-term emotional states (e.g. to be anger), desires and associated goal-directed intention (to be hungry and desiring a sandwich), beliefs about the world and finally a different role is attributed to the communicative intent that prompts actions directed to social interactions.

The ability of mentalizing derived from the acquisition of the Theory of Mind (ToM), the capacity to attribute independent mental states to self and others in order to predict their actions (Castelli et al., 2000). ToM and mentalizing are terms now used to indicate the same social ability.

Acquisition of a Theory of Mind has been widely studied in children, particularly with the paradigm of the False Beliefs and it has been found that four years old children can separate their mental states from those of others and thus taking their perspective. Studies investigating ToM in children were prompted also by the consistent finding that this ability is impaired in the Autism Spectrum Disorder (Baron-Cohen et al. 1985; Baron-Cohen 1989; Colle et al. 2007), a syndrome characterized by impairment in social skills and communicative abilities.

In the last decades, the neural correlates of mentalizing have been the topic of several studies that employed different paradigms. Mentalizing system was investigated with stories of false beliefs (Saxe & Kanwisher, 2003), non-verbal cartoons depicting ToM vs. physical stories (Gallagher et al., 2000), geometric shapes interacting in socially meaningful ways (Castelli et al., 2000), and computerized interactive games (Rilling et al., 2004). Available literature shows a general agreement on the brain areas associated with the attribution of mental states and with thinking about others. These regions forms a common network including the medial Prefrontal Cortex (mPFC) including the Anterior Cingulate Cortex, the Temporo-Parietal Junction (TPJ), the posterior cingulate/precuneus (PCC/PC), and the anterior temporal poles (Gobbini et al. 2007; Frith & Frith 2006). The role held by the different brain areas has yet to be clarified, although it has been proposed that the TPJ is mainly associated with perspective taking and transient mental inferences about others such as people’s goals and desires, while the mPFC might subserve the attribution of long-term dispositions as traits and qualities about other people (Van Overwalle & Baetens, 2009).

Mirror or mentalizing?

The discovery of the mirror neurons with the following flourishing of inherent research and the contemporary growing interest in investigating the social cognition with neuroscience technique have revived the debate between simulation and inference theories.

Do we understand other people’s behavior by recognizing the goal of a perceived action by matching it on our motor vocabulary or by inferring the goal integrating the perceived action with our previous knowledge?

This question is still debated. However the most reliable hypothesis is that the mentalizing and the mirror systems are independent but complementary systems that underlying different process, namely mirror system underlies task and action goal recognition, while the mentalizing system underlies the comprehension of intentions and long-term dispositions (Rizzolatti & Sinigaglia 2010; Van Overwalle & Baetens 2009).

The aim of the present work

The brief overview on the data available to date about our knowledge on the brain mechanisms underlying human action processing illustrates the complexity of the theme and the difficulty to clearly define it. The different types of the involved techniques, the amount of the employed paradigms, and the number of tasks and stimuli used on one side help in increasing our knowledge exploring different aspects and testing diverse models; on the other side they make harder the overlapping of the results and the integration of data. Hence, it’s not surprising that they’re still open questions, weaknesses and deficiencies.

A noticeable gap in the available literature regards the temporal dynamics of brain processes at the base of the perception of actions. Indeed, against the countless neuroimaging and the discrete number of brain stimulation studies focused on localizing the cortical regions activated by the observation of actions, not enough effort has been put to explore the temporal course of action observation process.

Knowing the temporal dynamics of action perception is surely useful to deepen our understanding on how we comprehend human behavior and to help in clarifying the roles and the respective interactions of the different neural systems at the base of the human action understanding process.

Thus, the main goal of the present work consisted of investigating the temporal course of the neural responses to the observation of human behavior focusing our attention on different aspects characterizing actions. Specifically with this project we followed a route beginning from lower to get to higher levels aspects of actions: the motor side was first considered, the semantic aspects and the attribution of meaning were then contemplated and lastly the more complex social facet of actions was explored.

To inspect the temporal mechanisms we made use of one of the techniques characterized by the best level of temporal resolution (ms) to date available, namely the Event-Related Potential (ERP) technique.

In the experiment presented in the first chapter we'll focus our attention on the motor aspects of action perception. To deal with this topic we introduced a manipulation of the physical effort exhibited by actions employed as stimuli, thus comparing effortful and effortless actions.

With the second chapter, the focus of the experiment will shift to the semantic aspect in perceiving other people's actions. A linguistic paradigm, the N400, is borrowed by the electrophysiological literature to study the temporal dynamics of attributing meaning to daily actions.

In the third chapter the social meaning of human actions will be explored. Since social basically means to interact with other people, instead of presenting individual actions, pictures of interactions between two people were employed as stimuli. A manipulation of the interaction goal was introduced, explicitly we presented affective vs. cooperative interactions. To better specify the cortical areas involved in processing social interactions this study was conducted in collaboration with another research group (Canessa et al., 2012) who carried out the same experiment but employing fMRI. Results from both the ERP and the fMRI versions of the experiment will be presented.

Beyond the temporal course of action perception, a weakness of the current literature is reflected in the type of stimuli used and the paradigms employed. Quite often stimuli are very artificial consisting of pictures or movies depicting just the limb implicated in the action, that not rarely is just a grasping motion. Not really ecological are also the experimental paradigms that frequently consist of the passive viewing of human actions.

Therefore, the aim of the study described in the fourth chapter was to investigate the brain correlates of the perception of socially crucial human actions, namely communicative actions. Considered that data on communicative actions processing are sparse and lacking, few dedicated neuroimaging data were available. Hence, this study was conducted with the fMRI technique. To carry out this experiment, taking into account considerations about the ecological validity of previous studies, a more closer-to-reality paradigm formed by full-length video clips and an interactive task was created.

All in all the studies carried out will provide useful data about the temporal dynamics and the neural correlates of action perception -in particular of motor, semantic and social aspects- in order to deepen our knowledge of the comprehension of human actions and possibly to clarify the roles and the interactions of the different neural systems implicated in this domain.

1

Motor aspects of action perception

Introduction

Detection of motion is of vital importance in animal and hence human life. Perceiving motion allows us to adequately interact within a dynamic environment (Kourtzi & Kanwisher, 2000), where we are surrounded by objects and people in motion. When we have to skip cars to cross a busy street or to anticipate the trajectory of walking people to not clash with them or to give the hand in response to the same gesture by a stranger, our ability to process motion is fundamental.

Of all the types of motion we perceive, a crucial role is held by the biological motion (BM), a term used to indicate motion produced by living, biological organisms (Johansson, 1973) such as walking, running, gesturing, and also including eye gaze and mouth movements (Pelphrey & Morris 2006). Visual processing of biological motion is of massive value for successful daily-life activities and, in particular, for adaptive social behavior.

Research on biological motion perception has a long tradition and traces back to Johansson (1973), the Swedish researcher who first thought and created the Point Light Displays (PLDs). PLDs are the visual stimuli most often employed in experiments aimed at investigating BM perception and its neural basis. Point Light Displays (PLDs) are visually impoverished video-clips where the individual who is in motion is represented only by means of bright dots placed on the major joints (knees, ankles etc..) and on the head against a dark background (see Fig.1.1).

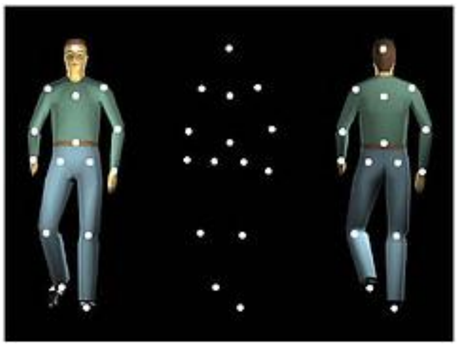
Fig. 1.1 An example of a point-light display stimulus, representing a walking man (from Brooks, Schouten, Troje, & Verfaillie, 2008)

Observers easily recognize what an actor is doing in a given PLD (Dittrich, 1993), they also can recognize without difficulty the identity (Loula et al., 2005), the gender (Kozlowski & Cutting 1977), and the emotion conveyed by the stylized body (Clarke et al., 2005).

In the last decades, research focusing on the neural underpinnings of biological motion processing greatly increased, in part due to the growing body of evidence revealing an impairment of BM perception in different clinical populations such as schizophrenia (Kim, Park, & Blake, 2011) or autism (Kaiser et al., 2010).

The most common paradigm employed to study brain areas underlying BM perception consisted of comparing brain activations evoked by observing animations of point-light-defined people with activations produced by viewing scrambled versions of the same animations. Scrambled Motion (SM) point-light displays are built with dots moving around the screen with the same velocity vector as the BM dots but with a different starting point. Hence, both kinds of sequences comprise identical individual dot trajectories and, therefore, differ only in the global, spatiotemporal coherence of the dots portraying human action.

Functional literature provided consistent evidence that the brain area that most specifically responds to the perception of biological motion (and not to other kinds of motion) is the Superior Temporal Sulcus (STS), and especially the posterior part (pSTS).

One of the first studies having found this result is a PET study conducted by Bonda, Ostry, & Evans (1996). The researchers identified regions along the posterior portions of the superior temporal sulcus more active in response to coherent point-light motion than scrambled. In a more complex fMRI study by Grossman and colleagues (2000), three difference kinds of motion were compared: biological motion, coherent motion and kinematic-boundary stimuli. The coherent-motion stimulus consisted of 100 dots moving at a constant velocity within a circular aperture. This dot speed approximated the average speed of the biological-motion sequences. Dot motions were wrapped such that dots moving out of the aperture were replaced on the other side of the window in the next frame. The kinematic-boundary motion stimuli were created by dividing the circular aperture into eight ‘‘strips’’ such that dots within adjacent strips moved in opposite directions. This display creates the impression of boundaries, or illusory contours, separating the opposing areas of motion. In comparison with coherent motion and kinematic-boundary stimuli, biological motion stimuli activated the pSTS, whereas the coherent motion response was located in an area overlapping with the homologue of the middle temporal gyrus in monkeys (human MT, hMT or MT/MST complex), an area found to be involved in general motion processing (Britten et al., 1996). Last, the kinematic-boundaries response was located in the kinetic-occipital region, an area found to be active to this kind of motion and located in the lateral-occipital sulcus.

Together with the functional studies, a line of research employing electrophysiological technique developed, aiming at exploring the neural temporal dynamics of BM motion perception.

One of the first electrophysiological studies to explore BM processing, published by Hirai and colleagues in 2003 (Hirai et al., 2003), employed PLDs representing a walking man in comparison with PLDs of Scrambled Motion. Authors distinguished two negative ERP components, of which amplitudes were greater in response to BM than SM: the former at around 200 ms (N2) and the latter at around 240 ms (N240) after stimulus onset. They were both recorded over occipito-temporal regions. In another ERP study carried out by Jokisch and colleagues (2005) PLDs showing a walking person, an inverted walking person (rotated of 180°) and scrambled motion were presented. Participants were instructed to press either the right button in response to dots patterns representing BM (both upright and inverse) or the left button in response to scrambled motion dots patterns. Even in this study, two negative ERP components were identified: an early N170 peaking at 180 ms after stimulus onset and reaching the maximum on the occipital sites, and a N300, peaking between 230 and 360 ms after stimulus onset and reaching the maximum over temporo-parietal sites. N170 peak amplitude was significantly greater for BM displays than for SM displays. Moreover, N170 amplitude was differently modulated by the two BM categories since the response to the upright walking person was greater than the one to the inverse walker. On the other hand, N300 mean amplitude was greater in response to BM than to SM displays, but no differences were found between the BM categories. Source localization analysis computed on both components revealed that generators of the early component were placed in the occipito-temporal regions, in an area matching with the human MT/MST complex. With regard to the later component, its neural sources were likely to be in the pSTS, in the fusiform gyrus and in the orbitofrontal cortex.

Functional and electrophysiological studies so far described seem to generally agree on both the neural basis of biological motion processing, namely the pSTS and to a lesser extent the MT/MST complex, and the temporal dynamics, with an earlier and a later processing stages.

A growing line of research strictly connected and partially overlapped with biological motion research regards the perception and the comprehension of human action and gesture and their brain underpinnings.

As a result of the discovery of the mirror neurons in the monkey brain in 1992 (di Pellegrino et al. 1992), it occurred a rapid and consistent increase of investigations aimed at revealing the existence of similar neurons within the human brain, their functions and the differences with the monkey’s (Rizzolatti et al. 1996; Grafton et al. 1997; Gangitano et al. 2001; Buccino et al. 2001; Iacoboni et al. 2005; Gazzola et al. 2006; Brass et al. 2007; Cheng et al., 2008; Avenanti et al. 2012).

Mirror neurons (MN) were discovered in the F5 area of the monkey premotor cortex by means of single-cell recording; they were found to discharge both during the execution of an action and the observation of the same action done by another individual (monkey or human). In humans, the brain regions considered the core of the human Mirror Neuron System (hMNS) are the inferior parietal lobule and the precentral gyrus plus the inferior frontal gyrus (IFG) (Rizzolatti & Craighero, 2004). In addition, more recent studies suggest that neurons with mirror properties are present also in the primary motor cortex, in the Supplementary Motor Area (SMA) and in the somatosensory cortex (Keysers & Gazzola 2010).

Many open questions and debates regarding what the functions of the human Mirror Neuron System (hMNS) are and what roles are held by the different hMNS brain areas, still prompt lots of studies and experiments. Notwithstanding, this blooming literature together with research on BM perception provided consistent evidence of the existence of a widespread network of brain regions that is automatically activated when perceiving other people’s actions (Turella et al., 2012). This network, the so-called Action Observation Network (AON), includes brain areas of the frontal, temporal and parietal lobes (Cross et al. 2009; Caspers et al. 2010; Turella et al. 2012).

Neural correlates of human actions requiring physical effort to be accomplished, such as running, kicking or lifting a weight object have rarely been investigated. A set of psycho-physiological studies considered the physiological reactions of the participants to the observation of highly dynamic actions. These studies demonstrated interesting correlations between the level of effort associated to the shown actions and the physiological reactions of perfectly still observers such as heart and respiration rate.

A study conducted by Paccalin and Jeannerod (2000) showed that respiration rate of seated observers watching a person running on a treadmill or lifting a weight increased as the speed of the treadmill or the load of the weight enhanced. In another study (Decety et al. 1991), subjects were instructed to mentally simulate locomotion at increasing speed: a covariation of heart rate and pulmonary ventilation with the degree of imagined effort was recorded by the authors. This result was confirmed by another study by Decety and colleagues (1993) where beyond the effects on heart rate and pulmonary ventilation, they also found an increase of respiration rate in effortful mentally simulated actions. These data suggest that the autonomic nervous system is modulated by the visual perception of human actions characterized by different effort levels. However, it is unknown how the central nervous system and particularly the brain responds to these highly dynamic actions.

Hence, the aim of the present study was to explore the temporal course of the perception of effortful actions in comparison with effortless employing the event-related potentials (ERPs) technique together with source localization analysis. Specifically we were interested in exploring the effects of this manipulation on the brain circuits involved in motion and actions perception and the activation timing.

In order to address this aim we collected 130 full-color photographs of daily social scenes representing effortful or effortless actions. We decided upon real life pictures to make the stimuli more ecological and closer to the reality. Participants were administered with a secondary perceptual task where they had to respond to target pictures not representing humans. A secondary perceptual task was preferred to an explicit task since we wished to investigate the automatic processing of the two categories of stimuli. The employment of pictures for studying motion perception is justified by research on implied motion, a term referring to dynamic information extracted from static images (Freyd 1983). Indeed functional studies demonstrated that photographs of humans, animals, and natural scenes with implied motion activated brain areas involved in action and motion perception, such as MT\MST complex, pSTS and hMNS (Kourtzi and Kanwisher 2000; Urgesi et al. 2006).

Methods

Participants

23 volunteers (12 males) participated in the study. All were right-handed, aged between 20 and 35 years (mean= 24.79, SD=3.15) and had normal or corrected-to-normal vision. Laterality preference was assessed by the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985) and a practice test for the ocular dominance. None of them had history of psychiatric or neurologic disorders. All participants had given their written informed consent. Experimental procedures were conducted in concordance with the Declaration of Helsinki (World Medical Association 2000). One subject was discarded because of the motion artifacts.

Stimuli

Stimuli consisted of 130 full-colour photographs showing people while performing an action.

Action effort was manipulated among the stimuli in order to group the stimuli into 2 categories: pictures representing low-effort actions (e.g. people who is reading or speaking) (Low-E) and pictures representing high-effort actions (e.g. running or jumping) (High-E). Age and gender of the represented person, as well as the part of the body exhibited were balanced between categories.

In order to administer an implicit task, 44 pictures (Target) representing landscapes, urban scenarios or house rooms were collected; none of them were showing people.

All the pictures were downloaded from the web.

Fig. 1.2a, 1.2b Examples of effortless actions (a) and effortful actions (b)

Procedure

Participants were comfortably seated in a dimly lit, electrically and acoustically shielded room, facing a window behind which a high resolution VGA computer screen positioned 80 cm from their eyes. At this distance photographs, 14,7 cm in height and 11 cm in width, subtended a visual angle of approximately 10°31’48” in height and 7°52’48” in width. A small bright dot (1 mm size) located at the centre of the screen served as a fixation point to minimize eye movements. Subjects were instructed to look at the fixation point and to avoid any eye or body movements during the recording session.

The task consisted of pressing a button every time a target (photo not showing people) was presented as accurately and rapidly as possible.

The experiment was built as an event-related design and consisted of four sequences. Each sequence included 34 stimuli including a number of targets ranging from 4 to 7. Only the first sequence contained 36 stimuli. Sequence order was randomized among subjects. Photographs were presented at the centre of the screen on a grey background for 1500 ms with a variable ISI (Inter Stimulus Interval) comprised between 1800 ms and 1900 ms. Each sequence lasted between 2 and 3 minutes and started with the warning words “ Steady – ready – go”. Participants were instructed to alternate across sequences the use of the left and the right hand. Hand use was counterbalanced even across subjects.

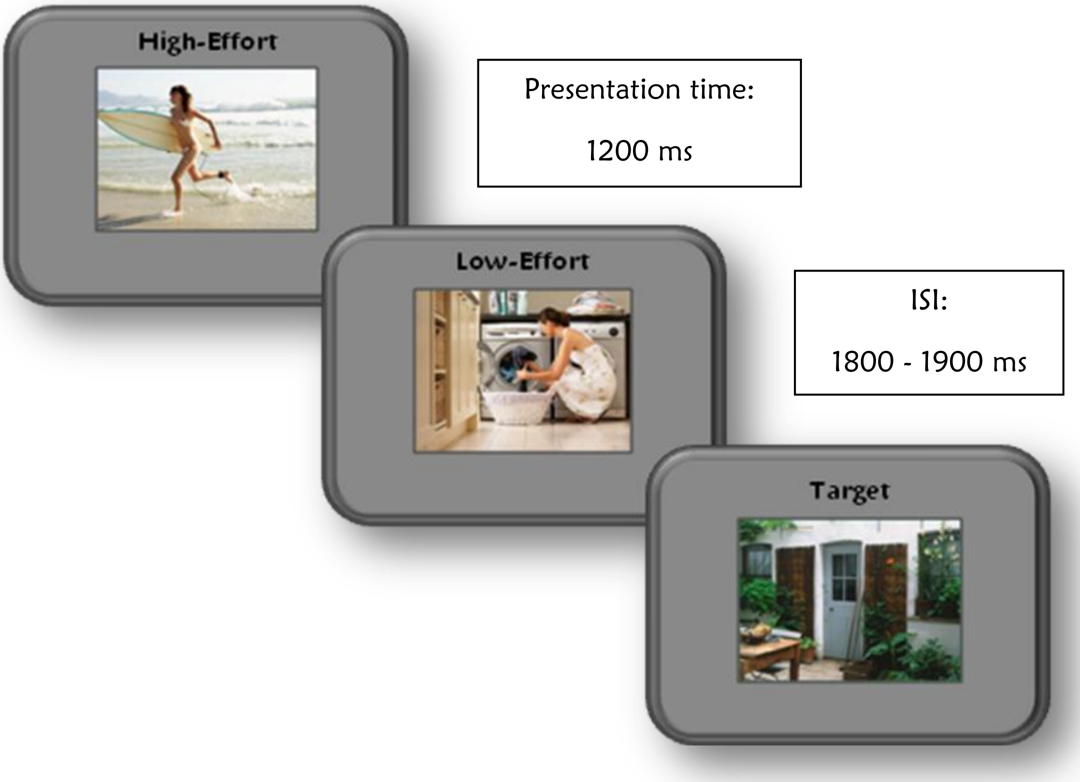

Fig. 1.3 Task: participants were instructed to watch the photographs and press a key button response to inanimate scenes (not showing people).

EEG recording

Continuous EEG was acquired through EEProbe (ANT Software, Enschede, The Netherlands) from 128 electrodes (see Fig. 2.4) mounted in an elastic cap (Electro-Cap) at a sampling rate of 512 Hz. Recording leads were placed on the scalp according to the 10.05 International System. The linked earlobes served as off-line reference leads. Horizontal and vertical eye movements were also recorded by 4 additional electrodes. Electrode impedance was kept below 5 kΩ. A notch filter of 50 Hz was applied so that possible artefacts derived from electrical interference were corrected. Also, EEG and electro-oculogram were off-line band-passed (0.016-70 Hz). In order to reject trials with large eye movements and high EMG, an artefact rejection procedure was applied. The artefact rejection criterion was a peak-to-peak amplitude exceeding 50 mV and resulted in a rejection rate of 5%. Accepted trials were averaged off-line separately for each condition from 100 ms before through 1000 ms after stimulus onset. Baseline was defined as the mean voltage over 100 ms preceding the stimulus onset (-100 to 0). Averaged trials were then filtered with a 0.016-40 Hz band-pass.

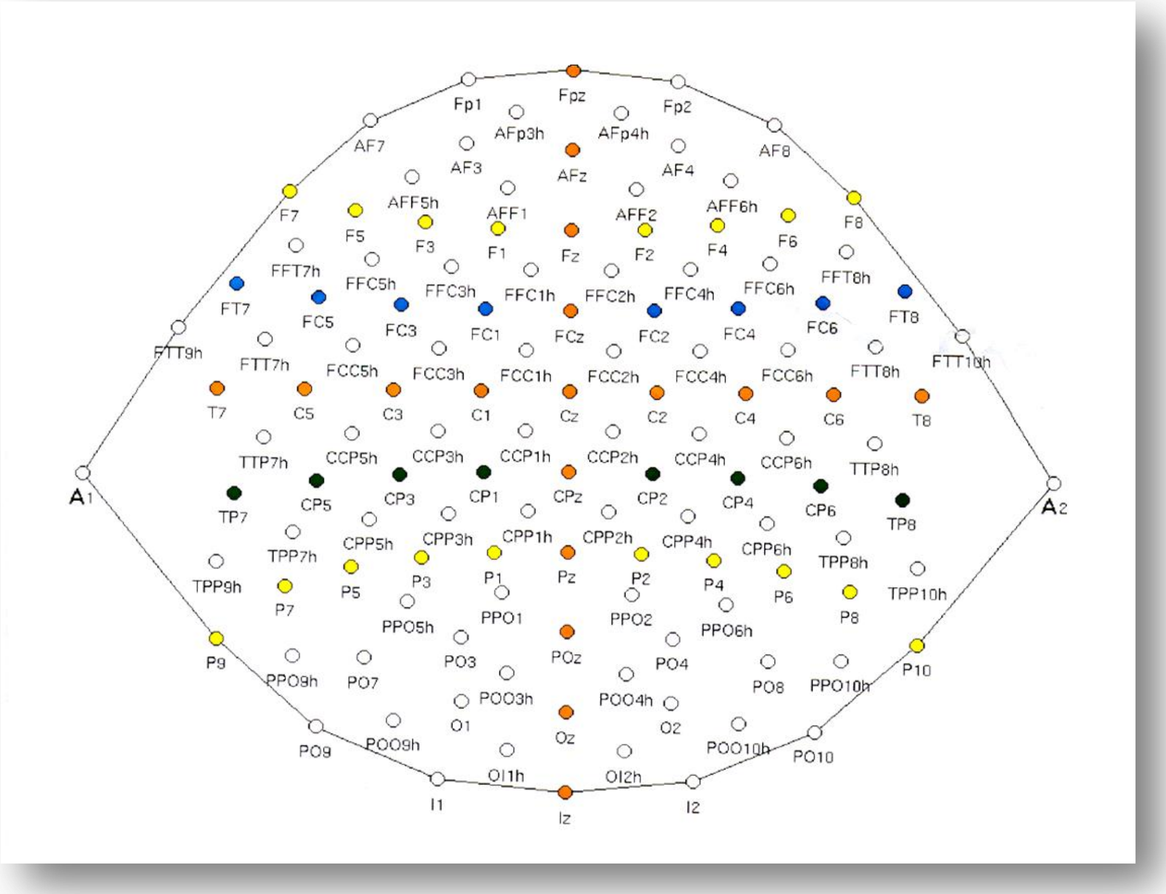

Fig. 1.4 EEG recording layout, with 128 electrodes distributed over the whole surface

Behavioural and electrophysiological analysis

Behavioural data in response to targets were collected during the EEG recording from Eevoke (vers.1.5, 2002, ANT Software, Enschedee, The Netherlands). EEG epochs corresponding to a response error were discarded.

Two ERP components of interest were identified: a temporo-occipital N2 and a centro-parietal Late Positivity Potential (LPP). Of these components mean amplitude was measured and analyzed. Temporo-occipital N2 was scored from 250 to 350 ms after stimulus onset on PO9, PO10, PPO9h, PPO10h electrode sites (see Fig.1.4). Mean amplitude of the LPP was considered in the 400-600 ms time-window and given the widespread distribution was measured on several electrodes (FFC1h, FFC2h, FCC1h, FCC2h, C1, C2, CP3, CP4).

Mean amplitude of each component was analyzed by a repeated measures ANOVA with Effort (2 levels: Low-Effort, High-Effort), Hemisphere (2 levels: Right, Left) and Electrode sites (levels depending on the components) as within-subjects factors. Greenhouse–Geisser correction was applied when appropriate.

ERP COMPONENT	TIME WINDOW	ELECTRODES
Posterior N2	250-350 ms	PO9-PO10; PPO9h-PPO10hPOO4h
LPP	400-600 ms	FFC1h-FFC2h; FCC1h-FCC2h; C1-C2; CP3-CP4

Tab. 1.1 Recorded components: Posterior N2 and LPP

Source reconstruction analysis

The anatomic sources of cognitive event-related potentials (ERPs) can be studied with methods that seek to solve the so-called ‘‘electromagnetic inverse problem’’. In this experiment source analysis was performed according to the swLORETA method (standardized and weighted Low Resolution brain Electromagnetic Tomography) with ASA software (ANT Software BV).

SwLORETA is a recent update of the standardized low-resolution brain electromagnetic tomography (sLORETA) method introduced by Pascual-Marqui in 2002. sLORETA is a useful tool for modelling spatially distinct source activities in the absence of prior knowledge of the generators' anatomical location. The sLORETA method generates statistical parametric maps that reflect the reliability of the estimated current source density distribution. It shows exact topographic properties, with a zero-localization error for single dipoles in noiseless simulated data. SwLORETA additionally incorporates a singular value decomposition-based lead field weighting that compensates for the sensors' differing sensitivity to current sources at different depths (Palmero-Soler, Dolan, Hadamschek, & Tass, 2007). This weighting enables accurate reconstruction of surface and deep current sources in simulated data - even in the presence of noise and when two dipoles are simultaneously active.

The swLORETA solution was computed using a three-dimensional grid of points (or voxels) representing the possible sources of the signal. Furthermore, the solution was restricted to the grey matter by selecting only voxels in which the grey matter probability was not equal to zero (based on the probabilistic brain tissue maps available from the Montreal Neurological Institute (Collins et al. 1994; Evans et al. 1993). Lastly, the 1056 grid points (with a 5 mm grid spacing) and the recording array (128 electrodes) were registered against the Collins 27 MRI map (with a 1 mm spatial resolution) (Evans et al. 1993). The Boundary Model was used to compute the lead field matrix. The lead field matrix models the mechanism by which the original current sources are superimposed on each other to produce the measured voltage fields at each detector. This constitutes the first step in any attempt to compute an inverse solution (Geselowitz, 1967).

The source space properties included a grid spacing (the distance between two calculation points) of 5 points and an estimated signal-to-noise ratio (SNR, which defines the regularization: a higher value indicates less regularization and therefore less blurred results) of 3. swLORETA was performed on the group data and identified statistically significant electromagnetic dipoles ($p < 0.05$) in which larger magnitudes correlated with more significant activation.

In this experiment swLORETA analysis was performed in the 250-350 ms and 450-550 ms time windows according to the component latencies separately for the High-E and the Low-E evoked response.

Results

Behavioural results

All the subjects showed high accuracy in performing the task: error rate was inferior to 1% for both categories. Since the task was implicit no additional analysis were computed.

Electrophysiological results

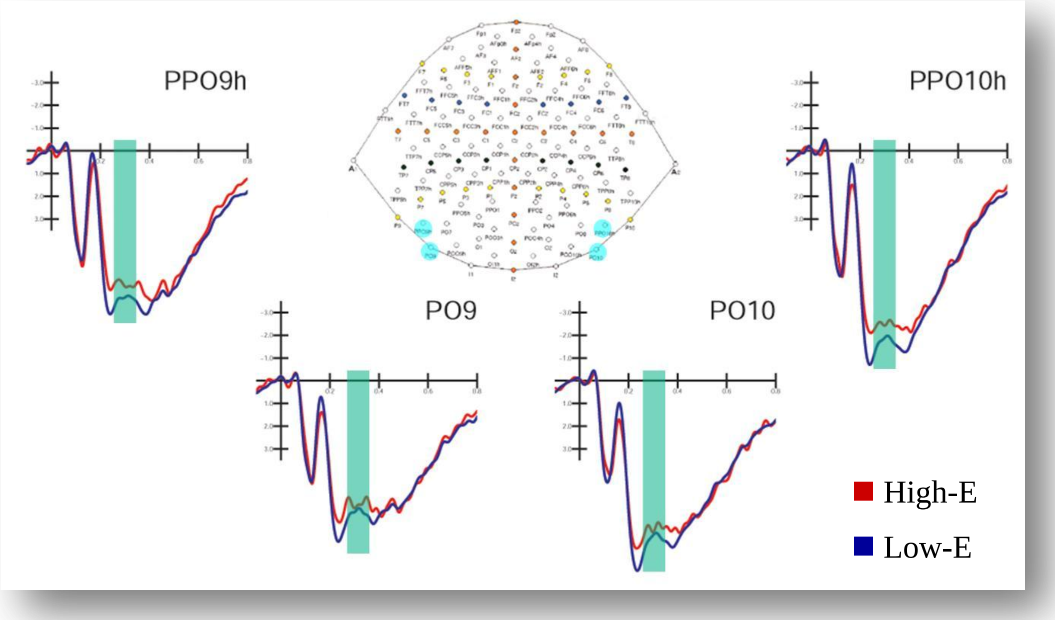

Fig. 1.5 Posterior N2 recorded on occipito-temporal electrode sites in the 250-350 ms time window

Occipito-temporal N2 (250-350 ms). This component showed a main effect of Effort ($F_{1,21}$ = 13,21, p<.05) and Electrode ($F_{1,21}$ = 16,04, p<.05). High-E category elicited a more negative neural response than Low-E category and in general the evoked response was greater on the medial temporal sites (PPO9h, PPO10h > PO9, PO10) (see Fig. 1.5).

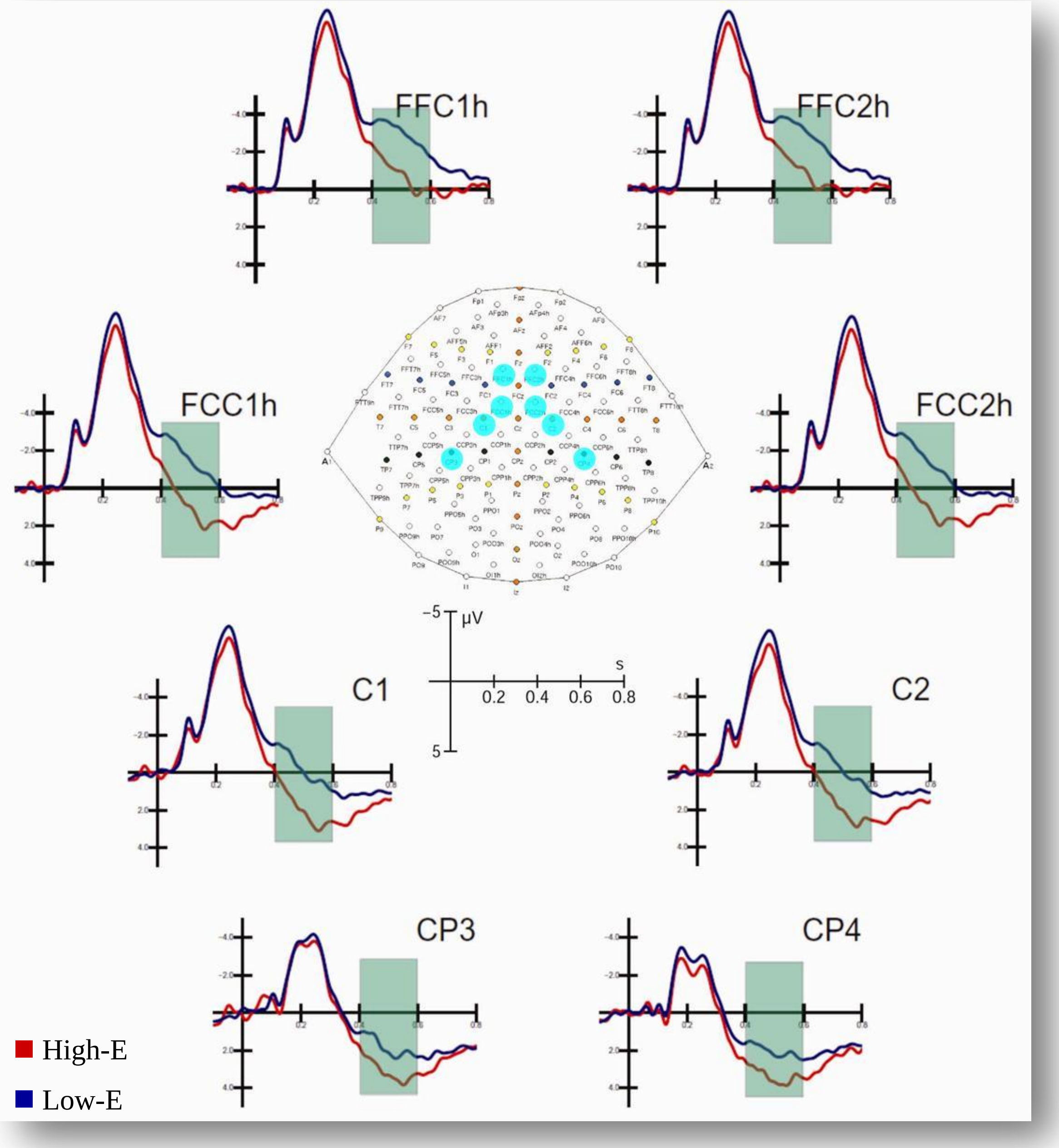

Fig. 1.6 LPP recorded on centro-parietal electrode sites in the 400-600 ms time window

Centro-parietal LPP (400-600 ms). The ANOVA computed for this long-lasting component demonstrated a significant greater amplitude in response to High-E than Low-E actions ($F_{1,21}$ = 21,21 , p<.001). Electrode site factor was also significant ($F_{1,21}$ = 36,69, p<.05). Post-hoc test revealed greater evoked potentials on the centro-parietal electrode sites than on the fronto-central sites.

Source reconstruction results

Occipito-temporal N2 (250-350 ms). swLORETA analysis computed in this time window revealed a number of cortical generators in common to both conditions placed in the higher-order visual areas (right inferior/middle occipital cortex), in the Precentral gyrus (BA 4, BA 6), in the Middle Frontal gyrus (junction of BA 9, 10 and 46) and in the Medial Frontal gyrus (BA10). Furthermore, source reconstruction analysis showed stronger foci of activation in the Superior Temporal Gyrus and bilaterally in the BA6 in response to effortful action perception (see Tab 2.1a,b). Inferior Temporal Gyrus and Fusiform gyrus are instead more active for the effortless actions.

High-Effort (250-350 ms)					
T-x	**T-y**	**T-z**	**H**	**Area**	**BA**
50,8	-57,9	5,6	R	Superior Temporal Gyrus	39
40,9	-87,3	-4,9	R	Inferior Occipital Gyrus	18
31	-79,2	12,7	R	Middle Occipital Gyrus	19
-48,5	-57,9	5,6	L	Middle/Superior Temporal Gyrus (EBA)	39/37
1,5	64,4	16,8	R	Medial Frontal Gyrus	10
-38,5	-21	35,7	L	Postcentral Gyrus/Precentral	¾
40,9	43,4	23,9	R	Middle Frontal Gyrus	10/9/46

-38,5	43,4	23,9	L	Middle Frontal Gyrus	10/9/46
50,8	45,3	6,1	R	Middle Frontal Gyrus	46
40,9	2,4	29,4	R	Precentral Gyrus	6
-38,5	2,4	29,4	L	Precentral Gyrus	6

Tab. 1.2a Tailarach coordinates corresponding to the intracranial generators for the High-E Condition computed in the time window between 250 and 350 ms. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Low-Effort (250-350 ms)					
T-x	**T-y**	**T-z**	**H**	**Area**	**BA**
50,8	-55,9	-10,2	R	Middle-Inferior Temporal gyrus/Fusiform	20/37
40,9	-87,3	-4,9	R	Middle/Inferior Occipital gyrus	18/19
-48,5	-55,9	-10,2	L	Fusiform gyrus	37
-38,5	-21	35,7	L	Postcentral gyrus/Precentral	¾
1,5	64,4	16,8	R	Medial Frontal gyrus	10
-38,5	46,3	-2,3	L	Inferior Frontal gryus	10
-38,5	43,4	23,9	L	Middle Frontal gyrus	10/9/46
-8,5	38,2	-17,9	L	Inferior Frontal gyrus/Rectal gyrus	11
40,9	43,4	23,9	R	Middle Frontal gyrus	10/9/46
40,9	2,4	29,4	R	Precentral gyrus	6

Tab. 1.2b Tailarach coordinates corresponding to the intracranial generators for the Low-E Condition computed in the time window between 250 and 350 ms. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).
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Centro-parietal LPP (400-600 ms). For this component swLORETA was computed on the wave peak in the central time window comprised between 450 and 550 ms. As for the previous component source reconstruction analysis showed dipoles active for both conditions: the fusiform gyrus, the middle – inferior temporal gyrus, the precentral gyrus (BA6 and BA4), the Prefrontal cortex. For this component there were also active sources in the Inferior Parietal Lobule and in the parahippocampal gyrus/Uncus. Effortful actions also showed activations in the bilateral precentral gyrus (BA 6).

High-Effort (450-550 ms)					
T-x	**T-y**	**T-z**	**H**	**Area**	**BA**
50,8	-55	-17,6	R	Fusiform Gyrus	37
-58,5	-44,8	-16,9	L	Middle/Inferior Temporal Gyrus	20/37
21,2	-24,5	-15,5	R	Parahippocampal Gyrus	35
31	-15,3	-29,6	R	Uncus/	20/28
-18,5	-8	-28,9	L	Uncus	36/28
50,8	-0,6	-28,2	R	Middle/Inferior Temporal Gyrus	21/20
1,5	-20,3	26,8	R	Cingulate Gyrus	23
40,9	-30,4	34,9	R	Inferior Parietal Lobule	40
-38,5	2,4	29,4	L	Precentral Gyrus	6
-28,5	-14,4	45,5	L	Precentral Gyrus	4
-28,5	53,4	24,8	L	Superior Frontal Gyrus	10/9
40,9	2,4	29,4	R	Precentral Gyrus	6
1,5	64,4	16,8	R	Medial Frontal gyrus	10

Tab 1.3a Tailarach coordinates corresponding to the intracranial generators for the High-E Condition computed in the time window between 450 and 550 ms. . In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Low- Effort (450-550 ms)					
T-x	**T-y**	**T-z**	**H**	**Area**	**BA**
50,8	-55	-17,6	R	Fusiform Gyrus	37
-58,5	-44,8	-16,9	L	Inferior Temporal Gyrus	20

21,2	-24,5	-15,5	R	Parahippocampal Gyrus	35/28
-28,5	-15,3	-29,6	L	Uncus	20/28
31	-15,3	-29,6	R	Uncus	20/36
50,8	-0,6	-28,2	R	Middle Temporal Gyrus	21
40,9	-30,4	34,9	R	Inferior Parietal Lobule	40
-28,5	-14,4	45,5	L	Precentral Gyrus	4
-38,5	2,4	29,4	L	Precentral Gyrus	6
1,5	64,4	16,8	R	Medial Frontal gyrus	10
40,9	55,3	7	R	Middle Frontal Gyrus	10

Tab 1.3b Tailarach coordinates corresponding to the intracranial generators for the Low-E Condition computed in the time window between 450 and 550 ms. . In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Discussion

This study was designed to investigate the brain responses to the perception of effortful and effortless implied actions by means of ERP technique and source localization analysis with swLORETA software, with specific interest on the temporal dynamics of the cortical activations associated with motion and action perception.

Potentials evoked by observing photographs of human agents executing effortful actions differed significantly from potentials evoked by photographs of analogue human agents executing effortless actions in two time windows: an early period lasting from 250 to 350 ms after stimulus onset, and a late period comprised between 400 and 600 ms. The early response was mostly localized on the occipito-temporal areas, while the late response was long lasting and reaching the maximum over the centro-parietal cortex even though it was widespread over most of the surface.

Results from the current study are in line with the electrophysiological studies exploring BM (Biological Motion) aforementioned, (Hirai et al. 2003; Jokisch et al. 2005), where BM perception is basically described as occurring in two consecutive steps, starting back in the occipito-temporal area to prosecuting rostrally in the fronto-parietal cortices. In the present experiment stimuli employed were *photographs* of actors in the middle of an action, so the motion was not actual, but implied. The overlapping of the present ERP responses with those elicited by using real motion confirms previous evidence (Kourtzi & Kanwisher, 2000) that human brain is able to extract dynamic information from still pictures and processing them as objects in motion.

Similar results were found in a study conducted by Lorteije (2006) who compared photographs of people in the middle of a movement with photogrpahs of the same people completely still. Bioelectrical responses were recorded from 59 scalp sites and the authors identified a positive deflection over most of the scalp surface, following a posterior/anterior gradient, peaking at approximately 290 ms and lasting for 80 ms. This positive component were found to be significantly greater in response to implied motion stimuli than no-implied motion. In a second experiment of the same paper the authors presented to the subjects actual motion stimuli compared with still images. A substantially overlying component, anticipated of about 90 ms, was identified and measured resulting in significantly greater amplitude in response to in motion than still stimuli. Source reconstruction analysis were computed for both components: neural generators were localized most in areas of occipito-temporal cortex defined as motion-sensitive, leading the authors to conclude that this positive component is an index of dynamic information processing.

The LPP recorded in the present study shares some similarities with the long-lasting positive component measured by Lorteije, providing further evidence of this component as an index of motion information processing. Moreover, in our study the effect on LPP amplitude was produced not by a marked difference in the stimuli such as by motion or implied motion vs. static stimuli, but by a subtler gap, namely by a difference in action effortfullness. Hence, LPP can be considered in all respects as an index of the detection and processing of human motion. Also, these data suggest that the same functional mechanism is responsible for detecting human motion and processing different features (in this case level of effort) of the motion perceived.

It’s worth noting that the components found in the present study are delayed compared to those recorded in BM experiments. This delay is likely to be due to the use in this experiment of implied-motion images and not actual BM stimuli. However, a delay is emerged even when comparing the LPP with the positive ERP elicited by implied motion stimuli in the Lorteije’s experiment. In this case we suggest the delay may rather be due to the thinner difference occurring between effortful vs. effortless actions than between implied motion vs. non-implied motion images. Also, the complexity of the employed stimuli, that is real world photographs, and not visually impoverished stimuli, might have concurred to delay the overall action processing.

Source localization analysis, in correspondence of the early N2, showed, among other activations, strong sources located in regions underlying motion/BM perception and belonging to the AON, namely: the MT/MST complex, the Extrastriate Body Area (EBA), and the premotor and motor areas. The EBA, located in the lateral occipitotemporal cortex, was first reported to respond selectively to visual images of human bodies or body parts (Downing et al. 2001). Subsequently it was shown that the EBA responds not only during the perception of other people’s body parts, but also during goal-directed movements of the observer’s body parts (Astafiev et al., 2004). Neural sources identified in the motor and premotor areas are in line with results from a study conducted by Urgesi and co-workers (2006). In this research the authors demonstrated, by means of Transcranial Magnetic Stimulation (TMS) and electromyography, that a response of the motor system occurred when subjects observed photographs portraying implied human motion, specifically a hand in the middle of a pincer grip movement.

In the later time window, 450-550 ms, source localization analysis provided a number of cortical generators overlapping with those detected in the previous time window, confirming the activation of the AON. In addition, active dipoles were found also in the inferior parietal lobule, an area belonging to the hMNS, in the cingulate cortex, in the parahippocampal gyrus and in the prefrontal cortex. These data suggest that while crucial areas associate with motion, BM and action perception are active during the whole process, other areas step in later. This might be due to a possible switch from a visual-motor coding of action to a more abstract cognitive/affective representation.

Sources in the STS and the left premotor area were more active for the effortful than for the effortless actions. As already said, these brain cortices are part of the AON and are commonly elicited by observing human motion. Thus, the STS and the left premotor area are likely associated with processing actions characterized by physical and muscular fatigue and hence are the best candidates for the cortical counterpart to the autonomic response described above by physiological literature showing a correlation in perfectly still observers between greater effort of observed actions and increased respiration and heart rates. The premotor cortex is part of hMNS and so contains neurons that discharge both during the execution and the observation of an action. Also the physiological reactions recorded in the above cited studies are present both during the execution and the observation of an action (in this case of an effortful action). Hence, these data suggest that the premotor cortex automatically discerns between effortless and effortful actions, matching the degree of effortfulness directly on the motor code by means of mirror mechanism. Moreover, the STS is the area most associated with BM processing, it may be sensitive to human motions features such as strength and speed of the movements. A partial support to this hypothesis comes from a number of studies on monkey brains, demonstrated that the MT/MST complex is able to detect motion speed (Pasternak & Merigan, 1994).

In conclusion, the present study shows and confirms that visual motion cues in static images are detected and processed as actual motion stimuli, eliciting ERP components similar to those found in response to real motion stimuli and evoking activations in areas belonging to the AON. Also, it provided evidence that different degrees of action effort are detected quite early and elicited a response in visual-motor areas suggesting a bottom-up processing of the stimulus, according to the studies demonstrating an activation of the autonomic system in response to effortful actions. Finally it clearly shows that the time-course of action/motion perception involves different areas in different time, the occipito-temporal cortices and premotor areas firstly and higher-order cognitive areas later.

[This study was performed in collaboration with Alice Mado Proverbio and Alberto Zani]

2

Semantic aspects of action perception

Introduction

Understanding other people's actions is crucial for our survival. Indeed, humans are beings intrinsically social who need to live in a social world and to adequately interact with other people. Providing an appropriate social response to an individual implies inferring proper desires and motivations from the observed behavior. It follows that comprehension of other's actions is a fundamental ability in our daily life, and it usually occurs automatically and effortlessly.

The aim of the present study was to investigate the neural mechanisms responsible of the comprehension of human actions.

For this purpose a well known electrophysiological paradigm coming from the neurolinguistic literature was borrowed: the N400 paradigm (Kutas & Hillyard 1980). The N400 component is a large negative deflection occurring roughly at 400 ms after stimulus onset over centro-parietal scalp areas and is associated with semantic integration and meaning attribution processes. The N400 response is usually evoked by a word (target) that provokes semantic anomalies with respect to context provided before. Two typical experimental paradigms are usually employed to modulate N400 amplitude, namely the semantic-priming

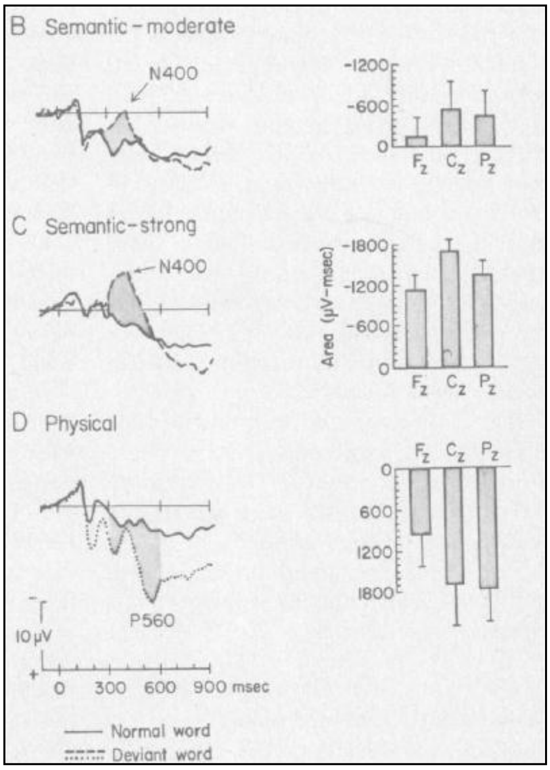

Fig. 2.1 N400 component as appeared in the first study by Kutas & Hillyard, 1980. In the B-C graphs the N400 amplitude is greater for semantic deviant words than for congruent words. In the D graph N400 was not elicited by physically deviant words.

paradigm and the semantic-anomaly paradigm (Lau et al., 2008). In the former the target word can be related or unrelated to a word previously displayed (e.g.: flower-vase, school-vase), while in the latter the target word is a conclusion to a sentence presented before and can be congruous or incongruous with it. In both cases N400 amplitude is greater for unrelated, incongruent or unfamiliar words.

Several evidence proved that the N400 amplitude is affected by different linguistic factors, such as word frequency, concreteness, cloze probability (Kutas & Hillyard 1984), semantic relatedness (Bentin et al., 1985), language proficiency (Proverbio et al. 2004), and contextual constraint (for a comprehensive review see Kutas & Federmeier, 2011).

In addition to clear semantic anomalies (e.g., ‘‘He takes his tea with sugar and socks’’), it has been demonstrated that the N400 response is sensitive to violation of real-world knowledge of what is common (e.g., ‘‘He takes his tea with sugar and ginger’’, Kutas & Hillyard, 1980) or factually true (e.g., ‘‘American school buses are blue’’, Hagoort et al. 2004).

Along with research centered on investigating the functional role of the N400 and factors affecting its latency and amplitude, a number of studies directed their effort on finding the cortical generators of this component. In a brilliant review by Lau and colleagues (2008) on this component, the authors included a set of cortical areas deemed to be responsible of the

N400 response to linguistic stimuli located in the temporal and the frontal lobe, specifically in the mid-posterior middle temporal gyrus (MTG) and the neighboring superior temporal sulcus (STS) and inferior temporal cortex (IT), in the anterior medial temporal cortex, in the inferior frontal gyrus (IFG), with substantial contribution from both hemispheres even if greater from the left one (Kutas & Federmeier, 2011).

Overall, the N400 is considered an index of semantic integration processes where the incoming stimuli are mapped into the corresponding semantic field in memory. Anomalous or incongruent stimuli are intrinsically harder to be integrated within the given context and therefore they require more effort to be processed, thus eliciting a greater neural response.

The vast majority of the N400 data comes from the neurolinguistic literature. However, in the last decade this paradigm has also been employed in some studies making use of nonlinguistic stimuli, such as static images of objects and actions or video clips depicting common stories. Just as in language comprehension, in these studies an increased N400 was identified in response to objects that are incongruous with a single picture prime (Mcpherson & Holcomb, 1999) or with a context of a surrounding scene (Ganis & Kutas, 2003). In another study (West & Holcomb, 2002) a larger N400 was found in response to visual scenes that were incongruous (vs. congruous) with sequentially presented static pictures conveying stories. Within the studies that employed nonlinguistic stimuli, of particular interest are the few experiments investigating action processing.

In a study conducted by Sitnikova and colleagues (Sitnikova et al.,2003), they showed video clips of common actions in which a person manipulated an object that was either consistent or anomalous with what the person was doing before (for example, a man standing in front of a bathroom mirror applied shaving cream to his face and reached out for something. In the congruent condition, he grabbed a razor, and in the incongruent condition, he grabbed a rolling pin). Participants were involved in an explicit task, they had to indicate whether the object manipulated are congruous or not with the context previously displayed. A centro-frontal negative deflection peaking at around 400 ms after the onset of the stimulus was identified by the authors. As expected by the previous literature, the amplitude of this component resulted to be modulated by the appropriateness of the observed objects, being greater in response to the incongruous objects.

In another study, Reid and Striano (2008) created video clips representing people executing an action with an object (inserting a spoon into the mouth), where the conclusion of the action could be anticipated (the spoon is full) or unanticipated (the spoon is empty). The authors found a negative deflection to be greater in response to the unanticipated actions vs. the anticipated actions. The researchers claimed that this ERP component likely relates to the N400 as an index of semantic processing of the information stream. Showing an action sequence made participants build a prediction with respect to the termination of the action. When this was violated, an N400 response was produced.

In their study, Bach and co-workers (Bachet al., 2009) focused on a particular kind of action, presenting to the participants static images of inserting actions (a hand that was inserting an object in another object) and asking to indicate whether the action was congruent or not. They made use of two types of violations, the violation of orientation, where the object that had to be inserted was oriented in a way that couldn’t be inserted, and the violation of function where the object was not the right object to be inserted. In response to both violations the authors found a N400-like negativity.

These studies provided evidence that the N400 component is elicited not just by linguistic semantic violations, but also by semantic violations produced by anomalous or inappropriate actions/object use. It’s worth noting that in all the studies employing visual iconic stimuli, the N400 showed a more anterior, centro-frontal distribution with respect to the linguistic component. This differentiation in the scalp topography distribution might be due to the existence of different cortical sources for the semantic network accessed by actions and words.

In general, these data seem to suggest a similarity between action and language semantic processing, where comprehension of both action and language may rely on overlapping functional mechanisms involving the same type of conceptual knowledge.

The studies conducted so far investigating action comprehension by means of the N400 paradigm, employed ecologically poor stimuli, consisted of showing just the limb executing the action or the person manipulating an object with no background context. To our knowledge ecological complex scenes representing persons engaged in purposeless or meaningless behavior, as opposed to meaningful and appropriate behavior, with respect to a given context, were not previously compared.

In this study, 230 photographs of ecological pictures representing people of different age and sex, engaged in a variety of activities were collected. Half of these photographs depicted meaningful actions, while the other half represented actions lacking any understandable goal. It was not that gestures were incomprehensible per se, but they were pragmatically implausible, with respect to the context and, especially, lacked an intelligible goal. These photographs were presented to the participants who were involved in a secondary perceptual task where they were asked to respond to the appearance of scenario pictures without humans.

On the basis of previous literature we predicted that actions would elicit a N400-like component over the frontal electrode sites, with larger amplitude in response to implausible and incongruous actions than to plausible or purposeful actions. In addition, in order to shed some light on the similarities/differences of action and language semantic processing, we computed a source reconstruction analysis aimed at identifying the neural systems involved in the comprehension of the other’s behavior.

Methods

Participants

Participants to the study were 23 Italian volunteers (12 males), all right-handed and aged between 20 and 35 years old (mean= 24.79, SD=3.15). Laterality preference was assessed by the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985) and a practice test for the ocular dominance. All of them had normal or corrected-to-normal vision and no history of psychiatric or neurologic disorders. Experiments were conducted with the understanding and the written consent of each participant. Experimental procedures were conducted in concordance with the Declaration of Helsinki (World Medical Association, 2000) and the experimental protocol was approved by the local ethical committee.

Stimuli

Stimulus set comprised 260 full-color pictures depicting males and females of various ages engaged in actions. Half of these pictures displayed appropriate, plausible, meaningful, context-congruent actions (MEANINGFUL), while the other half showed inappropriate, implausible, lacking any understandable goal, meaningless actions (MEANINGLESS).

Photographs belonging to the category of meaningful actions were those employed in the experiment described in Chapter 2.

Stimuli were selected from a wider sample of 288 photos, including 144 items for each category. Age, gender and part of the body exhibited (whole body, half bust, no face and body detail) were balanced between the categories. A questionnaire to evaluate the meaningfulness of each actions was administered to ten independent judges, that assessed each stimulus by the mean of a 3-point scale where 1 was equal to “meaningless/inappropriate”, 2 was “I don’t know” and 3 was equal to “meaningful, appropriate”. The risk of an order bias in the responses was minimized by randomly changing the order the photographs were presented with to each judge. Only pictures that were evaluated coherently by at least 80% of judges were included in the experimental set. This means that all the pictures used for this experiment received at least 8 over 10 judgments of plausibility for the appropriate actions and at least 8 over 10 judgments of no-plausibility for the inappropriate actions. Following this criterion 28 photographs were eliminated from the original set and the final set, as previously said, was composed of 260 pictures. Age, gender and part of the body exhibited were still balanced across categories (see Tab 2.1). Average luminance was also controlled among categories.

		MEANINGFUL	**MEANINGLESS**
AGE	Children	7	7
	Adults	123	123
GENDER	Women	50	45
	Men	53	55
	Both	27	30
PART OF THE BODY EXHIBITED	Whole body	58	56
	Half bust	53	47
	No face	9	19
	Body detail	10	8

Tab 2.1 The table shows matching criteria across categories

In order to have subjects performing a secondary perceptual task, 44 further photos depicting natural, urban or indoor background without visible people (including streets, offices, shops, public library, countryside, seascape, mountain landscape, etc.) were included (TARGET). They were equal to human pictures for average luminance and size.

All the pictures were downloaded from the web.

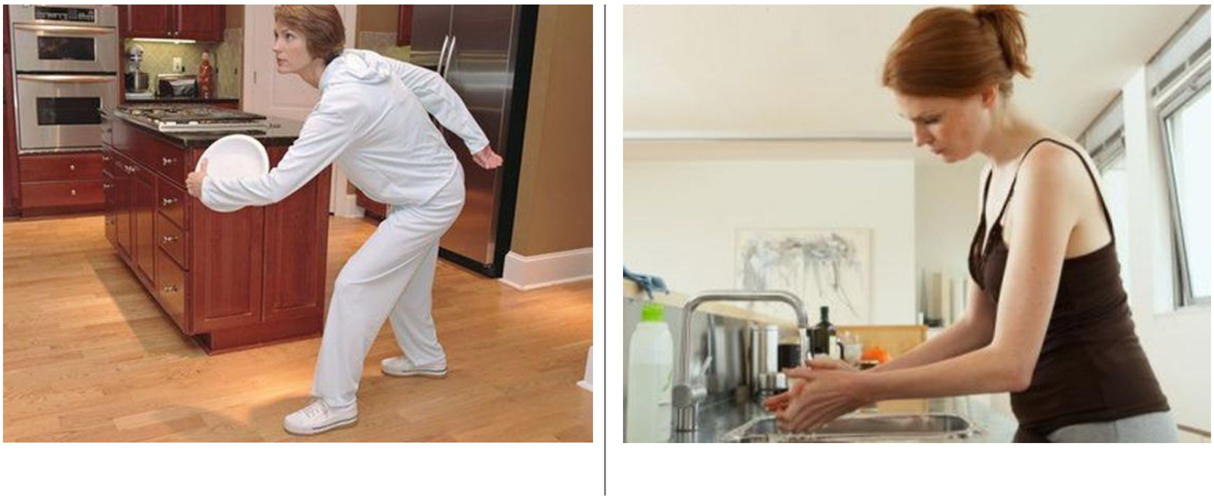

Fig.2.2a, 2.2b Examples of inappropriate (a) and appropriate actions (b)

Procedure

Participants were required to sign a consent form, performed the Italian version (Salmaso & Longoni, 1985) of the Edinburgh Handedness Inventory (Oldfield, 1971) and an ocular dominance test and were then prepared for the EEG recording. After preparation participants were comfortably seated in a dimly lit, electrically and acoustically shielded room, facing a window behind which a high resolution VGA computer screen positioned 80 cm from their eyes. At this distance, photographs, of which size was 14,7 cm in height and 11 cm in width, subtended a visual angle of approximately 10°31’48” in height and 7°52’48” in width. A small bright dot (1 mm size) located at the centre of the screen served as a fixation point to minimize eye movements. Subjects were instructed to look at the fixation point and to avoid any eye or body movements during the recording session.

The task consisted of responding as accurately and quickly as possible to the presence of photographs without people by pressing a response key with the index finger of the left or right hand. The two hands were used alternately during the recording session. The order of the hand was counterbalanced across subjects. Stimuli were presented at the centre of the screen on a grey background randomly mixed in eight different runs including 32–36 trials and a number of target varying from 4 to 7. Each sequence lasted around 2 minutes and started with the warning words “Steady – ready – go”. Time presentation was 1500 ms and ISI (Inter Stimulus Interval) varied between 1800 ms and 1900 ms**.** Sequence presentation order differed across subjects. The experiment was preceded by instructions and by a 20 trials practice block. Only if necessary, a second practice block was given.

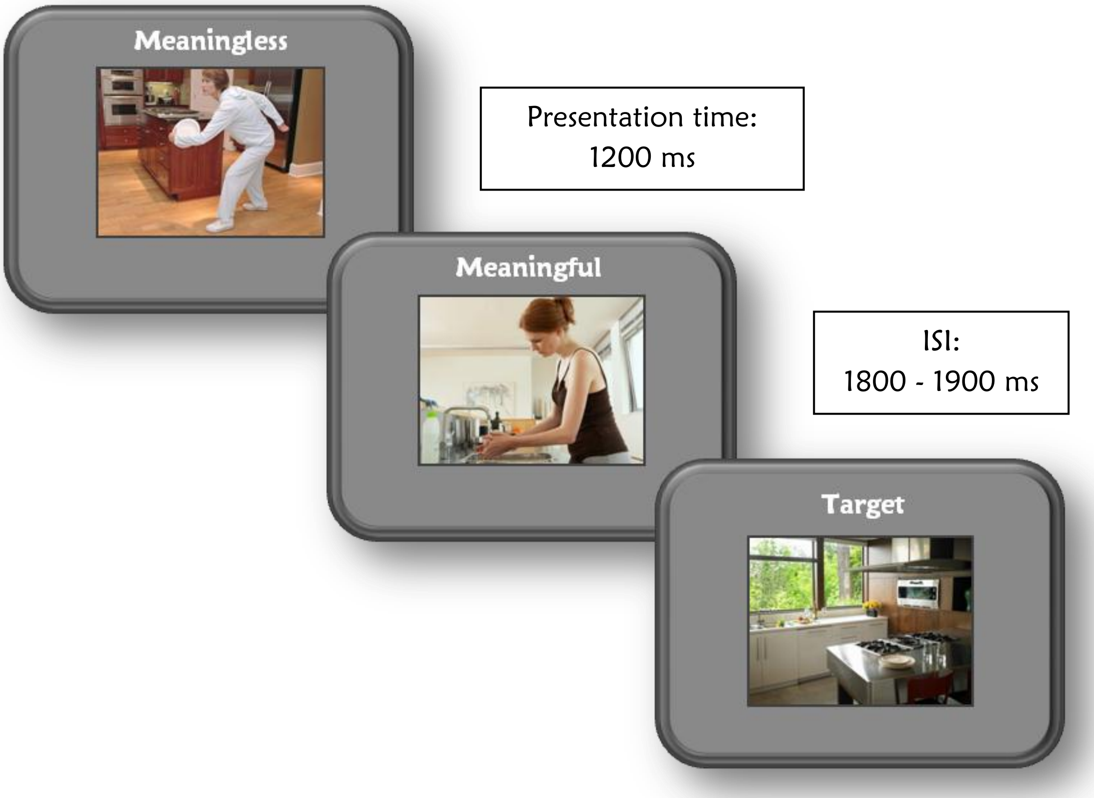

Fig. 2.3. Task: participants were instructed to watch the photographs and press a key button response to inanimate pictures (not showing people, Target.)

EEG recording and processing

Continuous EEG was acquired through EEProbe (ANT Software, Enschede, The Netherlands) from 128 electrodes (see Fig. 2.1) mounted in an elastic cap (Electro-Cap) at a sampling rate of 512 Hz. Recording leads were placed on the scalp according to the 10.05 International System. The linked earlobes served as off-line reference leads. Horizontal and vertical eye movements were also recorded by 4 additional electrodes. Electrode impedance was kept below 5 kΩ. A notch filter of 50 Hz was applied so that possible artefacts derived from electrical interference were corrected. Also, EEG and electro-oculogram were off-line band-passed (0.016-70 Hz). In order to reject trials with large eye movements and high EMG, an artefact rejection procedure was applied. The artefact rejection criterion was a peak-to-peak amplitude exceeding 50 mV and resulted in a rejection rate of 5%. Accepted trials were averaged off-line separately for each condition from 100 ms before through 1000 ms after stimulus onset. Baseline was defined as the mean voltage over 100 ms preceding the stimulus onset (-100 to 0). Averaged trials were then filtered with a 0.016-40 Hz band-pass.

Behavioural and electrophysiological analysis

Responses to targets were collected during the EEG recording from EEVoke (vers.1.5, 2002, ANT Software, Enschedee, The Netherlands). EEG epochs corresponding to a response error were discarded.

Concerning the electrophysiological responses, after visual inspection of the grand average ERPs across subjects, two ERP components were identified and measured (see Tab 3.1). The first one, N2, is a negative deflection most prominent on the occipital sites, namely OL1h, OL2h, POO3h, and POO4h, in the time window comprised between 250 ms and 350 ms after stimulus onset. The second component is a N400-like negative deflection recorded on the fronto-central surface for the electrodes F1, F2, FC1, and FC2 electrodes from 450 ms and 600 ms.

Mean amplitude values of each component were analyzed by a repeated measures ANOVA by considering Semantic Content (2 levels: Meaningful, Meaningless), Hemisphere (2 levels: Right, Left) and Electrodes (levels depending on the component) as within-group factors. Greenhouse–Geisser correction was applied when appropriate and only the corrected *p* values are reported. Post-hoc Tuckey tests were applied to all the significant interactive effects.

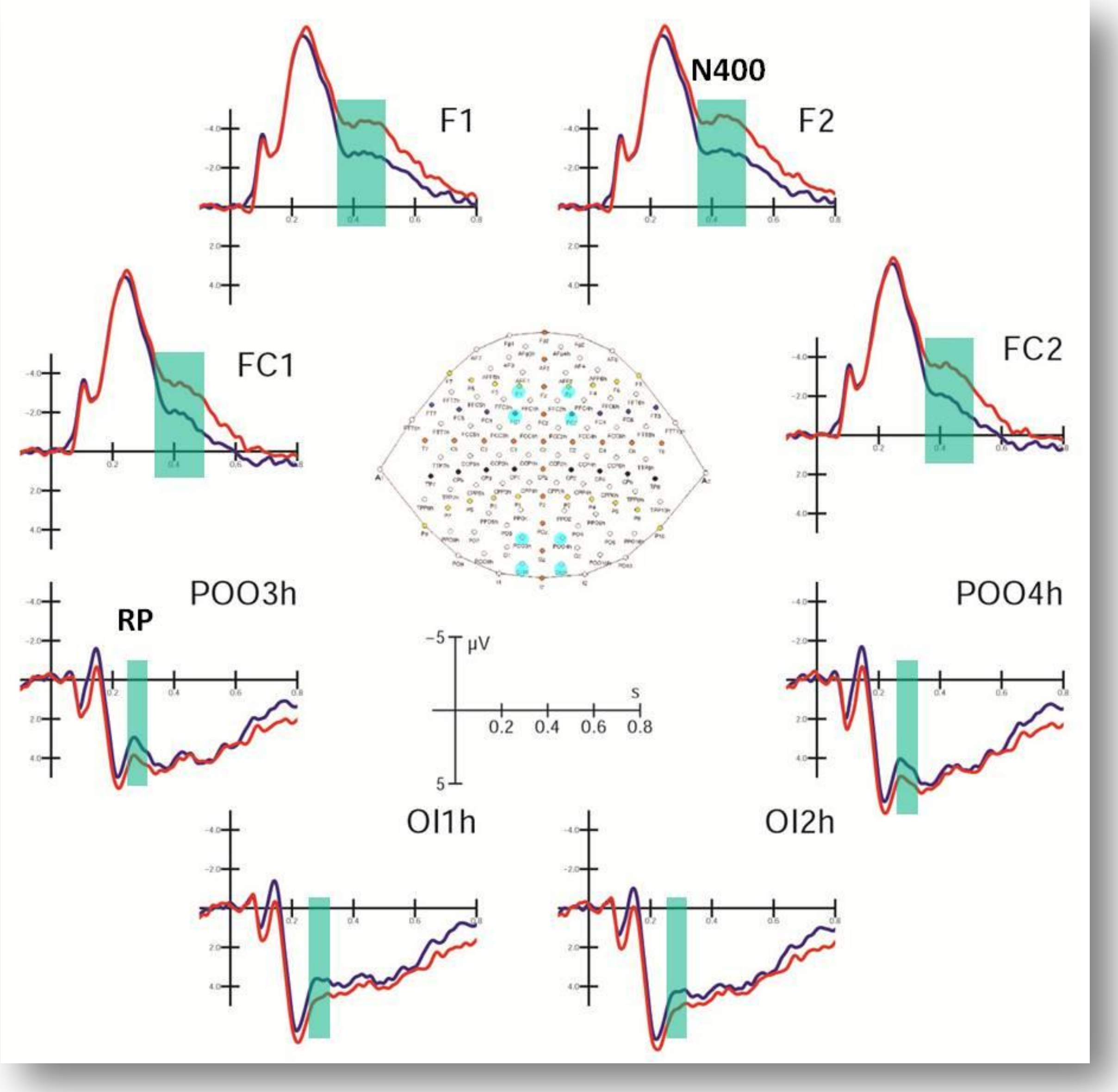

Fig 2.4. ERP components of interest: RP measured in the 250-350 ms time window and N400 in the 350-500 ms time window.

Source reconstruction analysis

In this experiment source analysis was performed according to the swLORETA method (standardized and weighted Low Resolution brain Electromagnetic Tomography) with ASA software (ANT Software BV). A detailed description of the swLORETA has been provided in the previous chapter.

In the current experiment source reconstruction analysis was computed for each component. For the N2 component, swLORETA was computed in the 250-350 ms time window, whereas for the N400 the inverse solution analysis was computed between 450 and 500 ms that corresponds to the time window with the greatest voltage difference between the two categories.

Results

Behavioural results

Subjects had a very good performance, showing an error rate inferior to 1% for both categories. EEG epochs corresponding to an error response were discarded.

Electrophysiological results

Occipital N2 (250-350 ms). ANOVA performed on the amplitude of this component recorded at the occipito/parietal electrode sites showed an effect of Semantic Content ($F_{1,22}$=12.43, p<0.005), with greater response to congruous than incongruous actions. The significance of the hemisphere ($F_{1,22}$=9.29; p<0.005) and hemisphere × electrode ($F_{1,22}$=4.24; p=.05) interaction indicated larger RP potentials over the left than the right hemisphere, especially over the parieto/occipital area, as also indicated by post hoc comparisons.

N400 (350-500 ms). N400 was strongly affected in amplitude by the Semantic Content of the stimuli ($F_{1,22}$=52.5; p<0.00001), which was much larger to incongruous than congruous actions. Overall, N400 was greater at frontal than fronto-central sites, as indicated by the significance of electrode ($F_{1,22}$=14.8; p<0.001), and relative post hoc comparisons.

ERP COMPONENT	TIME WINDOW	ELECTRODES
N2	250-350 ms	OL1h – OL2h; POO3h –
N400	350-500 ms	F1 – F2; FC1 – FC2

Tab 2.2 ERP components of interest: N2 and N400

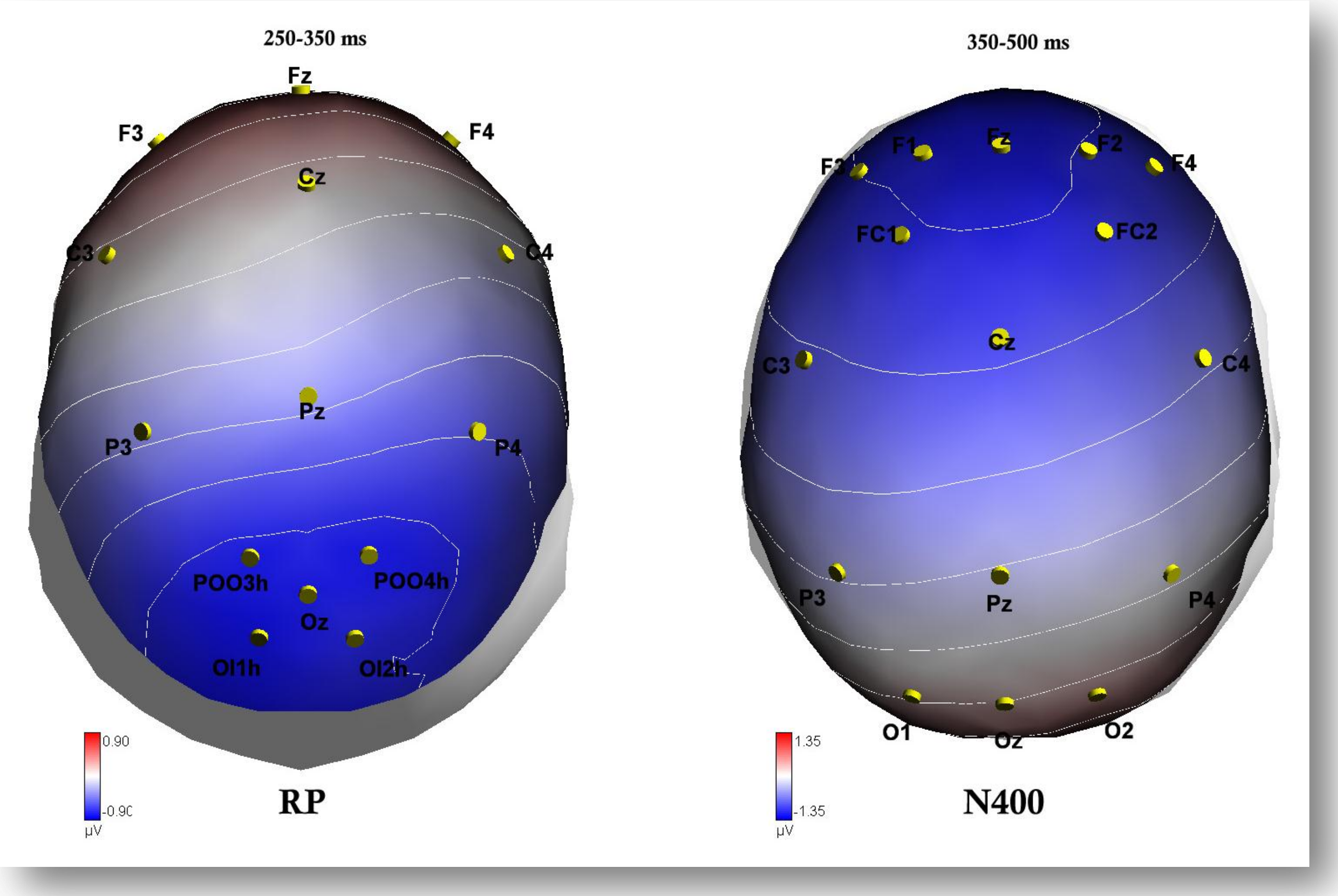

Fig. 2.5. Topographical difference maps performed by plotting difference voltages obtained by subtracting ERPs to incongruent from ERP to congruent actions in the Recognition Potential latency range, and ERPs to congruent from ERPs to incongruent actions in the N400 latency range.

Source reconstruction results

Occipital N2 (250-350 ms). The inverse solution analysis revealed that cortical sources of this component were located mainly in the middle temporal gyrus (MTG), in the superior temporal gyrus (STG), in the inferior temporal/fusiform gyrus and to a lesser extent in the left motor and right premotor cortex, and in the prefrontal cortex. Left STS was found active only for the meaningful actions.

Meaningful actions (250-350ms)

T-x	T-y	T-z	H	Area	BA
50,8	-57,9	5,6	R	Middle Temporal Gyrus/	39/37
50,8	-55,9	-10,2	R	Inferior Temporal Gyrus/	20/37
-48,5	-55,9	-10,2	L	Fusiform Gyrus	37
-48,5	-57,9	5,6	L	Middle Temporal Gyrus/	39
1,5	64,4	16,8	R	Medial Frontal Gyrus (Orbital)	10
-38,5	-21	35,7	L	Postcentral Gyrus/precentral gyrus	3/4
-38,5	46,3	-2,3	L	Inferior Frontal Gyrus	10
-38,5	43,4	23,9	L	Middle Frontal Gyrus	10/9/46
40,9	43,4	23,9	R	Middle Frontal Gyrus	10
1,5	48,2	-17,2	R	Medial Frontal Gyrus (Orbital)	11
40,9	2,4	29,4	R	Precentral Gyrus	6

Tab 2.6a Tailarach coordinates corresponding to the intracranial generators for the meaningful actions condition computed in the time window between 250 and 350 ms. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Meaningless actions (250-350ms)

T-x	T-y	T-z	H	Area	BA
50,8	-55,9	-10,2	R	Inferior temporal Gyrus/	20/37
50,8	-57,9	5,6	R	Middle Temporal Gyrus/	39/37
-48,5	-55,9	-10,2	L	Fusiform Gyrus	37
1,5	64,4	16,8	R	Medial Frontal Gyrus (Orbital)	10
-38,5	-21	35,7	L	Postcentral Gyrus/	03/4
-38,5	46,3	-2,3	L	Inferior Frontal Gyrus	10

40,9	43,4	23,9	R	Middle Frontal Gyrus	10-46-9
-8,5	38,2	-17,9	L	Inferior Frontal Gyrus(Rectal Gyrus)	11
40,9	2,4	29,4	R	Precentral Gyrus	6

Tab 2.6b Tailarach coordinates corresponding to the intracranial generators for the meaningless actions condition computed in the time window between 250 and 350 ms. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

N400 (450-500 ms). As for the previous component, the inverse solution analysis applied to the N400 revealed cortical sources in areas belonging to the ventral stream. Moreover, a consistent activation of the motor (BA4) and premotor (BA6) cortices was uncovered.

Meaningful actions (450-500ms)					
T-x	**T-y**	**T-z**	**H**	**Area**	**BA**
50.8	-55.0	-17.6	R	Fusiform gyrus	37
-48.5	-55.0	-17.6	L	Fusiform gyrus	37
1.5	-20.3	26.8	R	Cingulate gyrus/corpus callosum	23
-38.5	-21.0	35.7	L	Pre-Postcentral	4-3
40.9	2.4	29.4	R	Precentral gyrus/Inferior Frontal gyrus	6-9
-38.5	2.4	29.4	L	Precentral gyrus	6
-8.5	64.4	16.8	L	Superior Frontal Gyrus	10

Tab 2.4a Tailarach coordinates corresponding to the intracranial generators for the meaningful actions condition computed in the time window between 450 and 500 ms. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Meaningless actions (450-500 ms)					
T-x	**T-y**	**T-z**	**H**	**Area**	**BA**
50.8	-55.0	-17.6	R	Fusiform gyrus	37
-48.5	-55.0	-17.6	L	Fusiform gyrus	37

1.5	-29.4	26.0	R/L	Cingulate	23
-38.5	-21.0	35.7	L	Pre-Postcentral	4-3
40.9	2.4	29.4	R	Precentral gyrus/Inferior Frontal gyrus	6-9
-38.5	2.4	29.4	L	Precentral gyrus	6
1.5	64.4	16.8	R	Medial Frontal Gyrus	10

Tab 2.4b Tailarach coordinates corresponding to the intracranial generators for the meaningless actions condition computed in the time window between 450 and 500 ms. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Discussion

The aim of the present study was to investigate the neural correlates of the comprehension of human behavior employing the N400 paradigm to compare common human actions with actions difficult to understand/recognize, lacking a meaningful purpose and to integrate with previous world knowledge. Being the N400 a traditional linguistic component we were also interested in exploring the overlapping mechanisms between language and action coding.

The results provided by this experiment revealed two main ERP components: an earlier (250-350 ms), posterior negativity which was greater for congruous actions and a later (450-600 ms) anterior negativity that was greater for incongruous actions.

Previous studies (Martín-Loeches, 2007) demonstrated the existence of a negative component called Recognition Potential (RP) that consists of an electrical brain response to recognizable and meaningful stimuli of different nature such as words, pictures and faces. It peaks between 200 ms and 280 ms after stimulus onset and has an occipito-temporal topographical distribution.

As for the N400 component, studies on RP come from psycholinguistics. Indeed, most of the research focused on studying this component employed words or sentences. Experiments found that RP is greater for words than degraded word images (Rudell & Hua, 1995), or than letter strings and pseudo-words (Martín-Loeches 1999). Moreover, several studies found that RP is affected by semantic experimental manipulations, such as semantic priming (Rudell & Hua, 1996), semantic categories (e.g.: animal vs. non-animal) (Martín-Loeches et al., 2001) or living vs non-living entities (Marí-Beffa et al., 2005), concreteness effect (Martín-Loeches et al. 2001) and semantic expectancy (Dien et al., 2003). Beyond the linguistic literature, RP was identified even in studies employing pictures of objects. In an experiment conducted by Hinojosa and coworkers (2000), words, object pictures and Chinese characters were presented to the participants: not only words, but even pictures of common objects elicited an RP response. All these data brought researchers to interpret the RP as an electrophysiological index of semantic processing, occurring relatively early (before the N400) and reflecting part of the semantic system activity (Manuel Martín-Loeches, 2007).

Thus, considering previous literature on RP response, we suggest that the posterior N2 found in the current study in response to human actions and greater for meaningful than for meaningless actions can be thought as a Recognition Potential response elicited by observed human behavior. We hypothesize that meaningful and meaningless actions were processed as appropriate or inappropriate relative to the “semantic context” and thus elicited a RP response greater for meaningful than meaningless actions. To this regard, RP was identified even with a typical N400 paradigm where sentences ending with a semantic congruent or incongruent words were presented to the participants. RP larger amplitude was measured in response to words congruent with the previous semantic context as compared to incongruent words (Manuel Martín-Loeches et al., 2004).

Support to this interpretation comes also from the source reconstruction analysis.

Previous studies indicated part of the basal extrastriate area as the cortical sources of the RP, in particular the lingual and the fusiform gyrus, mainly left (Martín-Loeches et al. 2001). One of the cortical generator of the RP is an area located within the left mid-fusiform gyrus, identified by some authors as the Visual Word Form Area (VWFA). This area is activated by reading words vs. non-words and it is supposed to be responsible for the recognition of the visual form of the words. Moreover, some authors considered VWFA a multimodal area driven mostly by visual stimuli, but also by auditory and tactile stimuli (Price & Devlin 2003), indicating it as a higher order integrative area. It is also sensitive to many linguistic and non-linguistic factors among which semantic influences are conspicuous (Martín-Loeches, 2007).

In the present study, the most notable cortical generators of the RP detected by swLORETA included areas belonging to the ventral stream such as the inferior temporal gyrus, the fusiform gyrus and the middle-superior temporal gyrus. It's evident that there is at least a partial overlapping between the neural sources of the linguistic RP and of the action RP. These similarities reinforce the hypothesis that the posterior negative deflection found in this study to be greater in response to congruous actions than to incongruous belongs to the family of the RP components. To our knowledge this is the first time a RP has been found in response not only to words and objects, but even to complex ecological visual stimuli, such as photographs of human actions.

Given the differences in the nature of the stimuli used here and in the previous RP experiments, further specifications on the cortical sources identified are necessary. The inferior temporal gyrus is a higher-order area of the ventral stream and it's involved in processing high level visual stimuli, such as complex objects shape. Being the photographs of this study a kind of portray of daily life events, they were visually complex and included objects to which might be due the activation of this area. Also, the inferior temporal cortex is partially overlapping with the Extrastriate Body Area (EBA) that could have been active in processing the current photographs, since EBA is a cortical area found to be sensitive to the observation of the human body, of body parts (Downing et al. 2001) and of human actions

(Astafiev et al., 2004). Finally, activations in the fusiform gyrus might be associated with the presence of faces in the photographs, since the fusiform gyrus includes the Face Fusiform Area (FFA), an area found to respond selectively to human faces (Kanwisher et al., 1997).

After this early semantic response to the congruous actions, around 400 ms after stimulus onset an anterior long-lasting negativity has been found to be greater to meaningless than meaningful actions. Considering the linguistic and non-linguistic literature cited above we recognized an N400 in this negative deflection.

In a study by Balconi and Caldiroli (Balconi & Caldiroli, 2011) sequences of correct, incorrect and unusual object uses were presented to the participants. For both the unusual and the incorrect stimuli a N400 was recorded. In this study the N400 was evoked by the presence of inappropriate information of the action representation regardless of the type of violation. Thus, the N400 was associated with an increased difficulty to access to the semantic memory network containing action representations. However, the meaningless actions of our study were not just incorrect or rare, but were even incongruent with respect to the context represented and their aim was not recognizable. Thus, the N400 effect found here reflected a difficulty to both match the observed actions with those represented in the semantic memory system and integrate the action meaning with the semantic context and previous world knowledge. This result resembles what Hagoort (Hagoort et al., 2004) found in their experiment, where a N400 was recorded in response not to a semantic language violation with the sentence previous shown, but by a violation of the common world knowledge.

The presence of the same ERP component in response to action and language is a clear index that mapping the incoming visual stimulus onto the corresponding field in the semantic memory networks is functionally overlapping to mapping input words in language system (Sitnikova et al., 2008).

Conversely, confirming data from literature on the N400 for visual iconic stimuli, the N400 recorded in the current experiment had a more anterior distribution with respect to these measured in the linguistic experiments. This might be due to neuroanatomically distinct networks supporting semantic systems of action and language (Sitnikova et al., 2008)

To deepen this aspect, we computed source reconstruction analysis in the 450-500 ms time window. Bilateral fusiform gyrus, cingulate gyrus, premotor and motor cortices, and medial prefrontal cortex were identified as the cortical generators of the action N400. Comparing these with linguistic cortical sources revealed some differences. Indeed, as the surface voltage distribution, action cortical generators were more anterior than those elicited by words. Of the temporal lobe, we detected active diploes just in the bilateral fusiform gyrus, probably due to the presence of face in the pictures.

Of special interest are the sources found in the motor and premotor cortices and in the medial prefrontal cortex. It has been found that the motor and premotor cortices are part of the human Mirror Neurons System (hMNS) (Gazzola & Keysers, 2009, Avenanti et al. 2012) and they are supposed to contain representations of human actions and gestures, contributing to understand them by means of a simulation mechanism that automatically matches the observed action with the motor representations. Yet, as we already specified, in the current study actions were not showed alone, out of context, but were dipped into a daily background. So the violation of world knowledge raised from the impossibility to give sense of the human behavior in its complexity, in other words to recognize the purpose, the intentions of the actors. Several studies have associated recognition of intention to the medial prefrontal cortex (Canessa et al., 2012; Amodio & Frith, 2006; Brunet et al. 2000), a cortical source detected with swLORETA. We therefore suggest that for complex action processing the motor and premotor cortices worked together with the medial prefrontal cortex in order to attribute a meaning to the observed scene. When it becomes hard to make sense of the observed behavior, activity in these areas increase in order to solve the incongruity, the violation and to try to integrate the visual input with the previous knowledge.

In sum, with this study we aimed at study the neural mechanisms of action comprehension employing a well-known linguistic paradigm, the N400. We compared meaningful and meaningless actions and we found that the recognition of meaningful actions occurs relatively earlier, at 250 ms after stimulus onset, while at 400 ms the incongruity of the observed behavior is detected. Given the overlapping of the discovered components with those revealed by linguistic studies, similar functional mechanism that map the incoming information, words or actions, in the semantic network has been hypothesized. However, data from scalp distribution and the source localization analysis provided evidence of distinct neuroanatomically systems for action and language comprehension.

[This study was performed in collaboration with Alice Mado Proberbio]

3

From action to interaction perception

Introduction

Being bespoke for living in a social world depends on many factors, among which comprehending others' human behaviour, as it has been described in the previous chapter, is one of the most important. Understanding what other people do includes not just the comprehension of single actions or action performed by a single individual, but also the correct interpretation of people's social interactions. As a matter of fact, many of the relevant social situations occurring in our daily life involve interacting agents. Inferring the type of relationship between two agents and the goal of their interaction rest on the complex processing of bodily language and subtle social cues such as eye gazing, facial expressions, and relative body positions. Understanding human social interactions include the comprehension of actions, of the relative social signals and of the underlying intentions.

Thus, to delve deeper into the neural mechanisms responsible of comprehending human behaviour, with this experiment we aimed to investigate the neural correlates of processing human social interactions between two individuals.

Fig. 3.1 Geometrical entities employed in the pioneering study on social interactions perception by Heider and Simmel, 1944

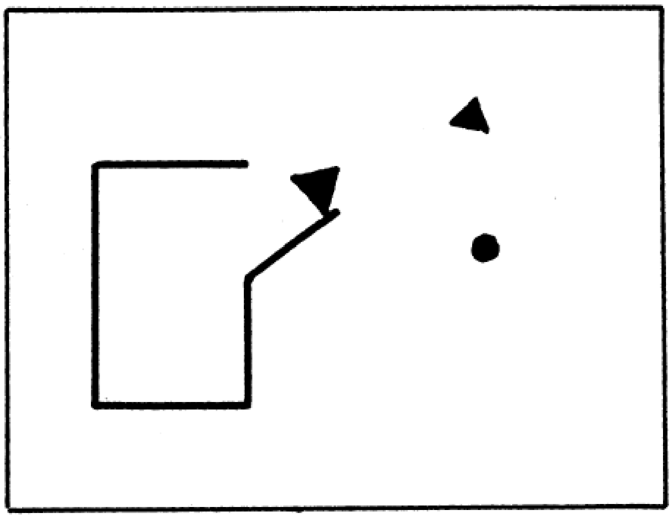

FIG. 1. EXPOSURE-OBJECTS DISPLAYED IN VARIOUS POSITIONS AND CONFIGURATIONS FROM THE MOVING FILM.
Large triangle, small triangle, disc and house.

As compared to the number of studies that employed single individuals as stimuli to investigate the neural underpinnings of action and intention understanding, the studies that focused on the processing of social interactions are quite a few.

Heider and Simmel (Heider & Simmel, 1944) were the first to present short clips in which geometrical entities moved outside and inside a rectangle following “social rules”. Investigators showed that subjects who observed them were inclined to interpret behaviour of these figures in terms of cooperative or affective intentions. In recent times, these stimuli or similar ones were employed in neuroimaging studies aiming at investigating neural basis of intention recognition.

One of the first neuroimaging study that made use of the Heider and Simmel’s stimuli was conducted by Castelli and co-workers with the PET technique (Castelli et al., 2000). Participants watched animations of a small blue triangle and a big red triangle involved in different kinds of interactions or just randomly moving. The authors found significant activations in the medial prefrontal cortex (mPFC), in the temporo-parietal junction (TPJ), in the basal temporal lobe and in the extrastriate area. Pavlova and colleagues (Pavlova et al., 2010) carried out a study analyzing the oscillatory gamma magnetoencephalographic (MEG) activity in response to the observation of revisited Heider and Simmel’s stimuli. The authors found peaks of gamma activity firstly in the right TPJ, then over the mPFC and posterior temporal cortices in the right hemisphere, and lastly over the left temporal and the right posterior temporal cortices. In another study (Centelles et al., 2011) Point Light Displays miming social interactions were presented to the participants. The authors highlighted how processing social intentions elicited significant activations in the left TPJ, in the anterior Superior Temporal Sulcus (pSTS), in the dorsomedial PFC (dmPFC). Activations foci were also located in areas of the Fronto-Parietal Mirror network such as the Intraparietal Sulcus (IaPS), the Premotor Cortex and the Inferior Frontal Gyrus (IFG). Employing different and more complex stimuli, Walter and colleagues (2004) presented several comic strips to the experimental subjects depicting private actions or social interactions, and found a greater activation of the anterior paracingulate cortex and of the mPFC in response to the latter. In an fMRI study by Iacoboni and co-workers (Iacoboni et al., 2004), video clips of two types of social interactions, communal sharing and authority rank, were shown. Significant activations were found in the dorsomedial prefrontal cortex (dmPFC) and in the medial parietal cortex (precuneus).

Taken together, these studies provided evidence that overall human social interactions processing is associated to a set of brain areas including the medial PFC, especially the dorso-medial PFC, the TPJ, the temporal pole and the aSTS, the posterior temporal sulcus. Several studies (Gallagher et al. 2000; Amodio & Frith 2006; Frith & Frith 2006) revealed that these areas are part of a brain network responsible for our ability to understand others' intentions and to make inferences about others' mental states, namely mentalizing. Above mentioned studies exhibited also some evidence, although to a lesser extent, of an involvement of areas supposed to contain Mirror Neurons, such as the premotor cortex and the Inferior Frontal Gyrus.

Thus, while data on brain areas involved in social interaction processing are quite consistent, even if the different roles have to be specified, little is known about the temporal course of the activations of these areas.

Noteworthy is also the kind of stimuli employed. Indeed, albeit insightful, these studies are based on non-lifelike agents that are quite schematic and barely resemble real individuals. These experimental stimuli might lack the complexity that a real daily scene displays and thus evoked simplified responses, not corresponding to the real, by the processing mechanisms.

Hence, the aim of the present study was to uncover the temporal dynamics, by means of ERP, of the cortical activity associated to the processing of human social interactions, employing stimuli closer to the reality. We therefore made use of photographs of everyday, realistic scene depicting humans actively engaged in a social interaction. Two types of interactions driven by distinguishable and clearly different goals were chosen: interactions characterized by pursuing a common goal requiring cooperation (such as lifting a heavy item), and interactions characterized by establishing affective contact without a further goal (not necessarily involving physical contact).

This choice was motivated by the intrinsic properties of these categories of interactions, such as being emotionally positive, involving people of both sexes and different ages, being extremely common and representable with perceptually similar pictures. These features allowed the employment of stimuli, namely daily life photographs, matched for several relevant variable (see the Method Session) and with no significant differences across the conditions except for the shared goal. Moreover, to contribute in defining the parts played by the mentalizing neural network and the hMNS in comprehending social interactions and intentions, a source reconstruction analysis by means of the swLORETA was computed. Crucially to the question, this study was conducted in collaboration with Canessa and co-workers (2012), who developed and run the fMRI version of this study. The same experimental paradigm and the same stimuli were utilized. Analysis and results of this study are reported in the Method and Results session. Data provided by this parallel study will be taken into account in the discussion.

Finally, given that previous reports brought to light gender differences in mentalizing (Krach et al., 2009), in action comprehension (Proverbio et al., 2010), in the engagement of the mirror system (Cheng et al, 2006), and in the brain response to emotional stimuli (Schulte-Rüther et al. 2008; Proverbio et al. 2009), we were also interested in determining whether gender differences occurred in processing social interactions and whether there was an interaction between observers' gender and the goal of the attended social scene.

Methods

Participants

Participants to the study were 35 (18 males and 17 females), aged between 20 and 35 (mean age=21.81; sd= 2.11), with normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. They were all right-handed as assessed by the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985). A practical test were administered to verify ocular dominance. Written consent of each participant was required and obtained. Experimental procedures were conducted in concordance with the Declaration of Helsinki (World Medical Association 2000) and with the approval from the Ethical Committee of the Italian National Research Council (CNR). Data from four men and four women were discarded due to movement artifacts.

The ovarian cycle phase of female participants was ascertained and matched across subjects (see Table 3.1).

Hormonal contraceptive		Ovarian phase	
Yes	No	I phase (1°-14° day)	II phase (15°-28° day)
8	6	7	7

Tab. 3.1. Number of female subjects that assumed hormonal contraceptives and that were in their pre-ovulatory or post-ovulatory phase of their menstrual cycle at the time of EEG recording.

Stimuli

Stimuli consisted of 260 full-color photographs depicting male and females individuals involved in goal-directed interactions belonging to the human repertoire and expressing positive emotions (see Fig.3.2a, 3.2b). The action's goal might be either cooperative, where the two agents collaborated for a common, shared aim (such as lifting a box, or helping each other climb a tree), or of purely social nature (such as to create an affective contact or just to relate to someone else, as for example shaking hands).

Stimuli were selected from a wider sample of 310 photos administering a questionnaire assessing the purpose of the interactions to 52 independent judges. Half of the examiners evaluated the pictures for their cooperative content, while the other half judged them for their affective content, in both case employing a 3-point scale [3= very cooperative (or affective); 2= vaguely cooperative (or affective) 1= not at all cooperative (or affective)]. On the basis of the judges' responses, 50 cooperative and affective pictures were discarded because of an insufficient average score. The final stimuli utilized were balanced across the two conditions in term of confounding factors such as: luminance, emotional salience, gender, age and number of depicted people, body parts (whole bodies vs. half-length bodies) and objects depicted.

The pictures were 15 X 15 cm in size, subtending a visual angle of 7' 32" 33°, and their average luminance was 15.48 Foot-lamberts.

In order to ensure and assess participants' engagement in the observation of pictures, we introduced a secondary task unrelated to the recognition of the interaction's goal. 44 further photos depicting common natural or urban landscapes without visible persons (including streets, offices, shops, a public library, the countryside, a seascape, a mountain landscape, etc.) were also included. These pictures were equal to the human pictures in terms of average luminance and size.

Fig. 3.2a,3.2b Examples of the employed stimuli: in Fig. 3.2a a cooperative interaction is depicted, while in Fig. 3.2b shows a affective interaction

Task & Procedure

Participants were seated in a comfortable chair, in a darkened, acoustically and electrically shielded room. They faced a high-resolution VGA computer screen located behind a window at 114 cm from their eyes. They were instructed to gaze at the center of the screen, where a small circle served as the fixation point, and to avoid any eye or body movements during the recording session.

Before the experimental session all participants received the same instructions for the task and a 20 trials practice block was administered. Only if necessary, a second practice block was given.

The task consisted of pressing as quickly and accurately as possible a response key with the index finger when a landscape picture appeared. Right and left hands were alternately used during the recording sessions.

Photographs were presented at the centre of the screen on a grey background for 1300 ms with a variable ISI (Inter Stimulus Interval) comprised between 1500 ms and 1700 ms. Each sequence started with the warning words " Steady – ready – go".

Stimuli were randomly mixed in 8 short sequences containing between 32 and 36 trials that lasted about 2 minutes each. For each experimental run, the target stimuli varied between 2 and 8 runs. The sequence presentation order and the hand of response were counterbalanced across subjects.

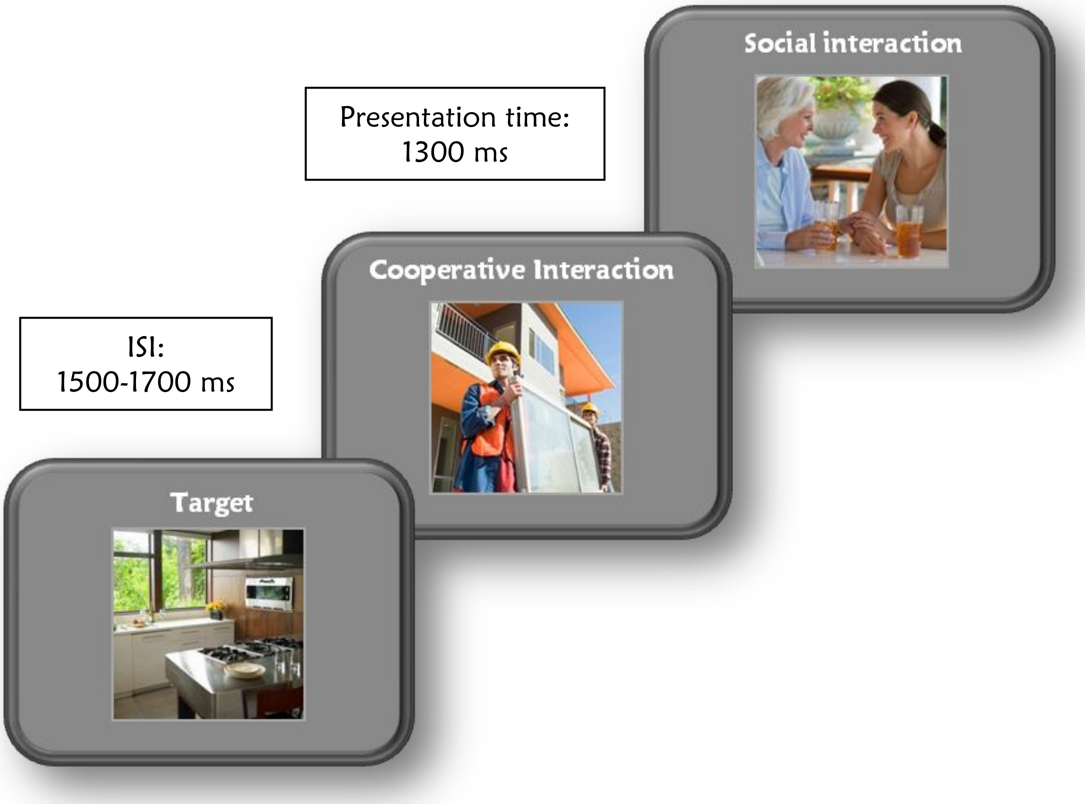

Fig. 3.3 Task: participants were instructed to watch the photographs and press a key button response to unanimated scenes

EEG recording and processing

EEG recording and processing were the same as described in the previous chapters.

Continuous EEG was acquired through EEProbe (ANT Software, Enschede, The Netherlands) from 128 electrodes mounted in an elastic cap (Electro-Cap) at a sampling rate of 512 Hz. Recording leads were placed on the scalp according to the 10.05 International System. The linked earlobes served as off-line reference leads. Horizontal and vertical eye movements were also recorded by 4 additional electrodes. Electrode impedance was kept below 5 kΩ. A notch filter of 50 Hz was applied so that possible artefacts derived from electrical interference were corrected. Also, EEG and electro-oculogram were off-line band-passed (0.016-70 Hz). In order to reject trials with large eye movements and high EMG, an artefact rejection procedure was applied. The artefact rejection criterion was a peak-to-peak amplitude exceeding 50 mV and resulted in a rejection rate of 5%. Accepted trials were averaged off-line separately for each condition from 100 ms before through 1000 ms after stimulus onset. Baseline was defined as the mean voltage over 100 ms preceding the stimulus onset (-100 to 0). Averaged trials were then filtered with a 0.016-40 Hz band-pass.

Behavioural and electrophysiological analysis

Behavioural responses to targets were collected during the EEG recording from Eevoke (vers.1.5, 2002, ANT Software, Enschedee, The Netherlands). EEG epochs corresponding to an error were discarded.

After accurate visual inspection of the grand average ERPs across subjects, four ERP components were identified and scored (see Tab. 3.2 and Fig. 3.4).

Occipito-temporal N170 was measured at the occipito-temporal electrodes (PO9, PO10, PPO9h, and PPO10h) between 150 and 190 ms.

Parietal N2 was detected at Pz, P3 and P4 electrode sites and was measured starting from 160 ms to 280 ms after stimulus onset.

Posterior P300 was measured at the same electrode sites as the N170, namely PO9, PO10, PPO9h, PPO10h in the 250-350 ms time window.

Anterior negativity was a long-lasting ERP component measured between 220 ms and 500 ms after stimulus onset on fronto-central area (F1, F2, F5, F6, C1, and C2 electrode sites).

For each component mean amplitude values were measured. Differences in amplitude between the conditions were analyzed by means of repeated measure ANOVAs where factors of variability were: Interaction goal (two levels: affective, cooperation), Electrodes (levels depending on components) and Hemisphere (two levels: left, right) as within-group factors and Gender as between-group factors. Post-hoc Tuckey test was applied to define the way of significative interactions. Greenhouse–Geisser correction was applied when appropriate and only the corrected *p* values are reported.

ERP COMPONENT	TIME WINDOW	ELECTRODES
N170	150-190 ms	PO9, PO10, PPO9h, PPO10h
N2	160-280 ms	Pz, P3, P4
P300	250-350 ms	PO9, PO10, PPO9h, PPO10h
Anterior Negativity	220-500 ms	F1, F2, F5, F6, C1, C2

Tab. 3.2 ERP components of interest for the present study

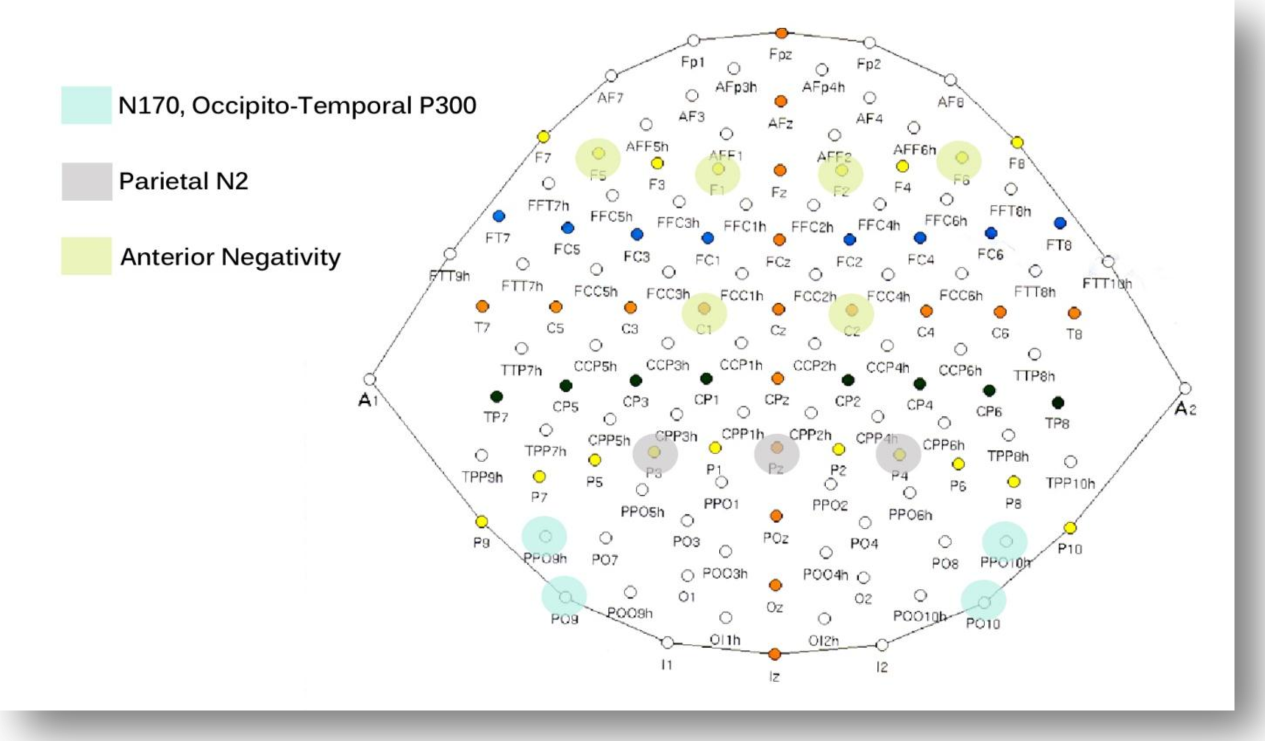

Fig. 3.4. Electrode sites corresponding to the measured ERP components.

Source reconstruction analysis

In this experiment source analysis was performed according to the swLORETA method (standardized and weighted Low Resolution brain Electromagnetic Tomography) with ASA software (ANT Software BV). A detailed description of the swLORETA has been provided in the previous chapter and will not be repeated here.

Source reconstruction analysis was computed for the occipito-temporal N170 and for the parietal N2 separately for the affective and cooperative interactions. N170 source analysis was applied between 155 and 175 ms and N2 between 200 and 250 ms, both time windows corresponded to the component peaks.

No swLORETA was computed on the P300 and the Anterior Negativity. Given that these components occurred quiet late and were long-lasting, we assumed that activations found with the fMRI experiment could be reasonably considered as their neural correlates.

Results

Electrophysiological results

Occipito-temporal N170 (150-190 ms). N170 amplitude was greater in response to affective than affective interactions pictures ($F_{1,25}$ =36.41, $p<.000$). Also, it resulted to be greater on the occipito/temporal than on the lateral occipital electrode sites ($F_{1,25}$=29.29; $p<.000$). A significant interaction of Hemisphere x Interaction content was found ($F_{1,25}$ =23.49; $p<0.000$) and relative post-hoc comparisons ($p<0.05$) demonstrated that cooperative interaction elicited a larger response over the left than the right hemisphere (see Fig. 3.5).

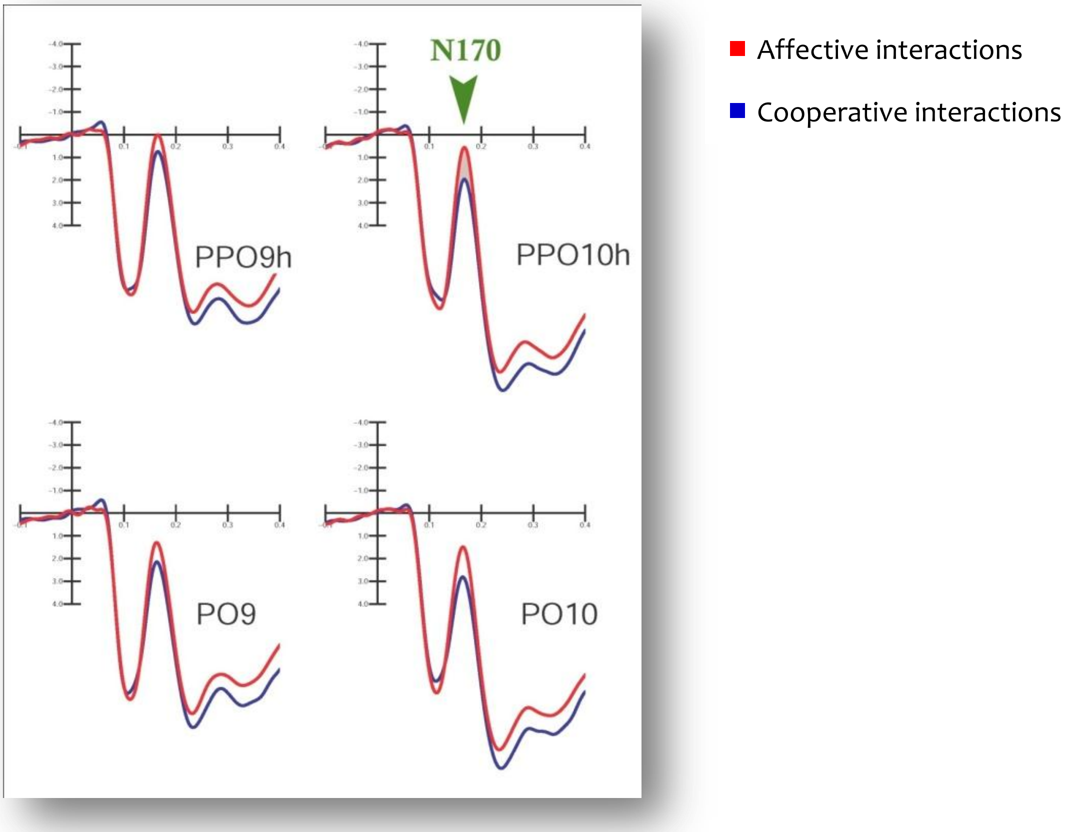

Fig. 3.5 The N170 was measured over the occipito-temporal areas and between 150 and 190 ms after stimulus onset. Its amplitude resulted to be greater in response to the affective than the cooperative interactions.

Parietal N2 (160-280 ms). Statistical analysis showed a significant effect of the Interaction content ($F_{1,25}$=5.04; $p<0.05$), with greater N2 amplitude in response to cooperative than affective actions. Significance of the factor Electrode ($F_{1,25}$=22.24; $p<0.000$) explained the greater response recorded over the central site and on the left hemisphere compared to the right, as demonstrated by the post-hoc comparisons ($p<0.05$). Interaction Content X Electrode was also significant ($F_{1,25}$=18.23; $p<0.000$), demonstrating a significant difference between the two conditions only at the left and midline electrodes but not the right side (see Fig. 3.6).

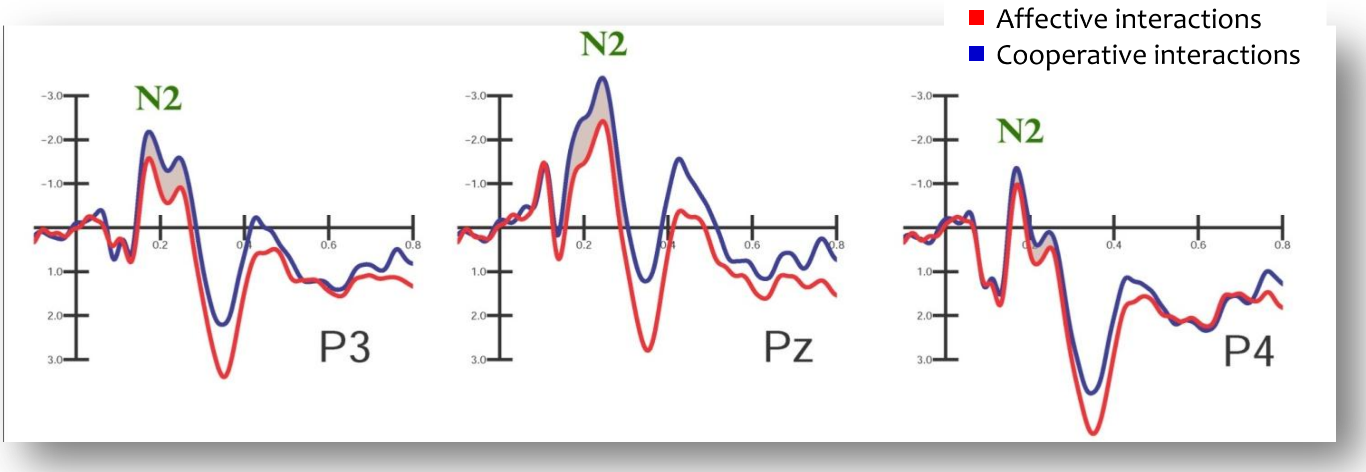

Fig. 3.6 The parietal N2 was measured between 160 and 280 ms. The parietal N2 response was greater for cooperative than affective interactions.

Posterior P300 (250-350 ms). The ANOVA computed on this positive deflection showed a significance of the main effect Interaction content ($F_{1,25}$=18.06; $p<0.000$) revealing a greater P300 amplitude in response to cooperative than affective interactions. Analysis also showed a lateralization effect ($F_{1,25}$=11.84; $p<0.005$), with a larger P300 recorded over the right than the left hemispheric sites. A visual inspection suggested a difference in the electrical responses recorded in male vs. females brain. Two repeated measures ANOVAs were run separately in the groups of females and males. Results brought to light that the Interaction content was strongly significant in women ($F_{1,13}$ =13.07; $p<0.005$; e=1) with a P300 evoked by cooperative actions exceeding 1.21 µV that evoked by affective actions, while the same effect was less significant in men ($F_{1,12}$ =5.56; $p<0.05$; e=1), with a difference between cooperative and affective of only 0.53 µV (see Fig. 3.7).

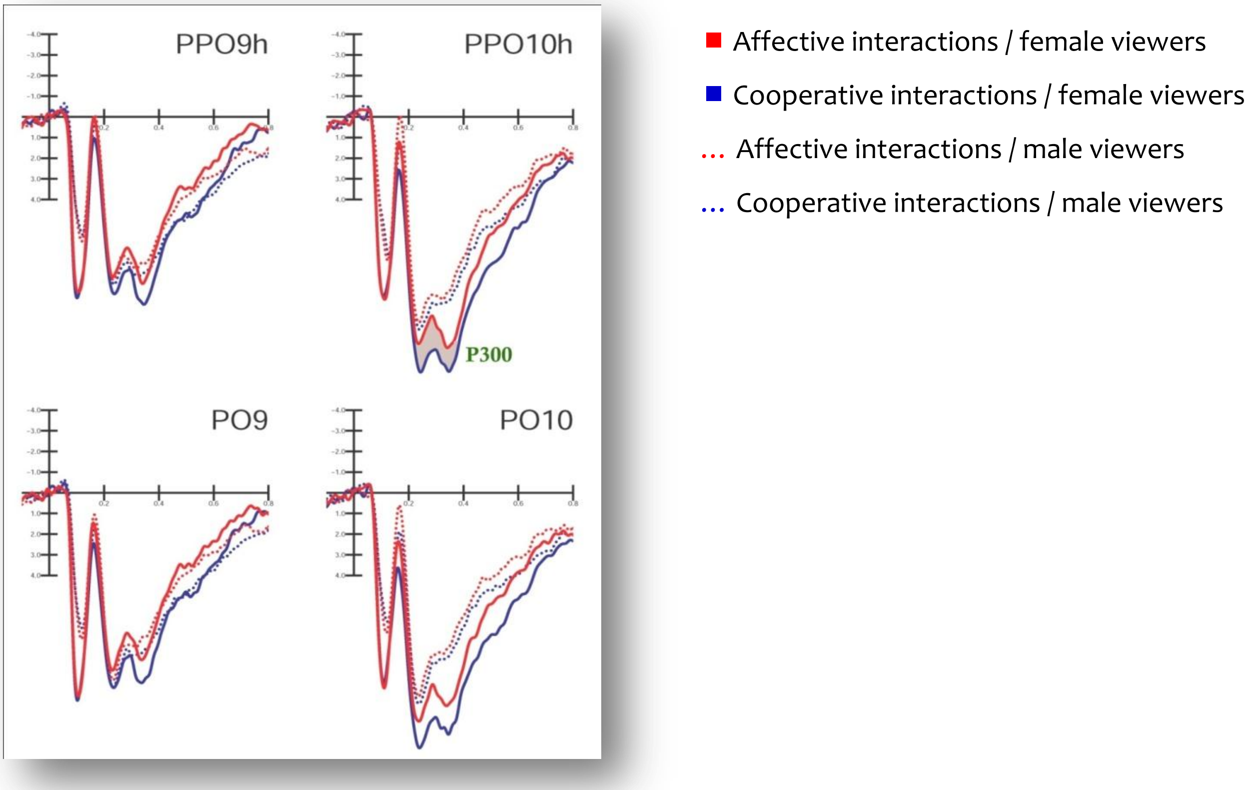

Fig. 3.7 The occipito-temporal P300 was greater for cooperative than for affective interactions. The effect was greater for female than for male subjects.

Anterior Negativity (220–500 ms). ANOVA analysis showed a significant effect of scene content ($F_{1,25}$=62.28; $p<0.000$), with a wider anterior negativity in response to cooperative compared to affective interactions. The anterior negativity was of greater amplitude on the medial frontal area than on the inferior frontal and central sites, as demonstrated by the significance of the Electrode factor ($F_{1,25}$=16.27; $p<0.000$).

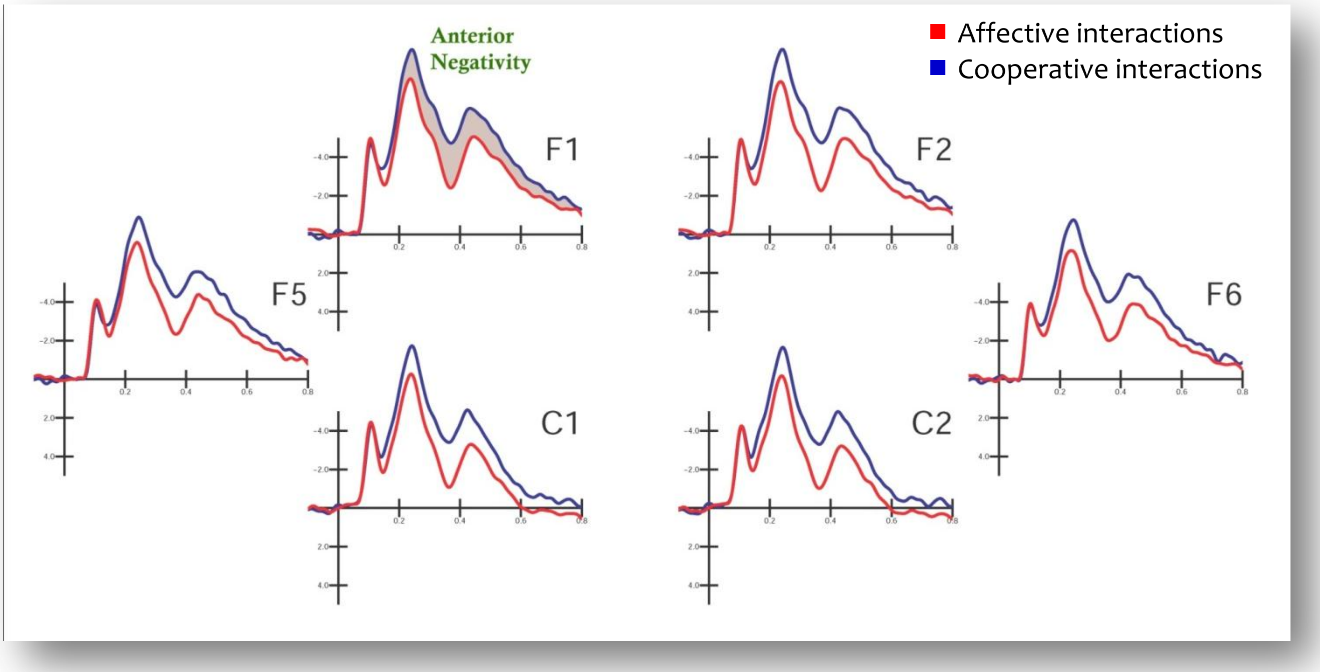

Fig. 3.8 The Anterior Negativity was recorded between 220 and 250 ms and was greater in response to cooperative than affective interactions.

Source localization results

Occipito-temporal N170. Source localization analysis computed in correspondence of the N170 peak elicited by affective actions showed significant dipoles in the right posterior cingulate cortex (BA30), in the right (BA37) and left (BA19) middle occipital gyrus and in the medial-orbitofrontal cortex (BA11). On the other hand, swLORETA analysis performed on brain activity elicited by cooperative actions was associated with the activation of the right middle temporal/ posterior STG, the right parahippocampal gyrus. For both conditions a significant neural source was found in the medial frontal cortex (see Tab. 3.3a, 3.3b, Fig. 3.9).

Affective Interactions (155-175 ms)

T-x	T-y	T-z	H	Area	BA
21,2	-57,9	5,6	R	Posterior Cingulate	30
50,8	-68	4,7	R	Middle Occipital Gyrus	37

-38,5	-78,2	3,8	L	Middle Occipital Gyrus	19
1,5	48,2	-17,2	R	Medial Frontal Gyrus/ Orbitofrontal Gyrus	11
1,5	64,4	16,8	R	Medial Frontal Gyrus	10

Tab 3.3a Tailarach coordinates corresponding to the neural sources associated with the affective interactions processing are displayed. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3). SwLORETA was computed between 155 ms and 175 ms (Grid spacing=5 mm, estimated SNR=3).

Cooperative Interactions (155-175 ms)

T-x	T-y	T-z	H	Area	BA
50,8	-57,9	5,6	R	Middle/Superior temporal Gyrus	37/39
21,2	-46,8	-2,1	R	Parahippocampal Gyrus	19/20
1,5	64,4	16,8	R	Medial Frontal Gyrus	10

Tab 3.3b Tailarach coordinates corresponding to the neural sources associated with the cooperative interactions processing are displayed. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3). SwLORETA was computed between 155 ms and 175 ms (Grid spacing=5 mm, estimated SNR=3).

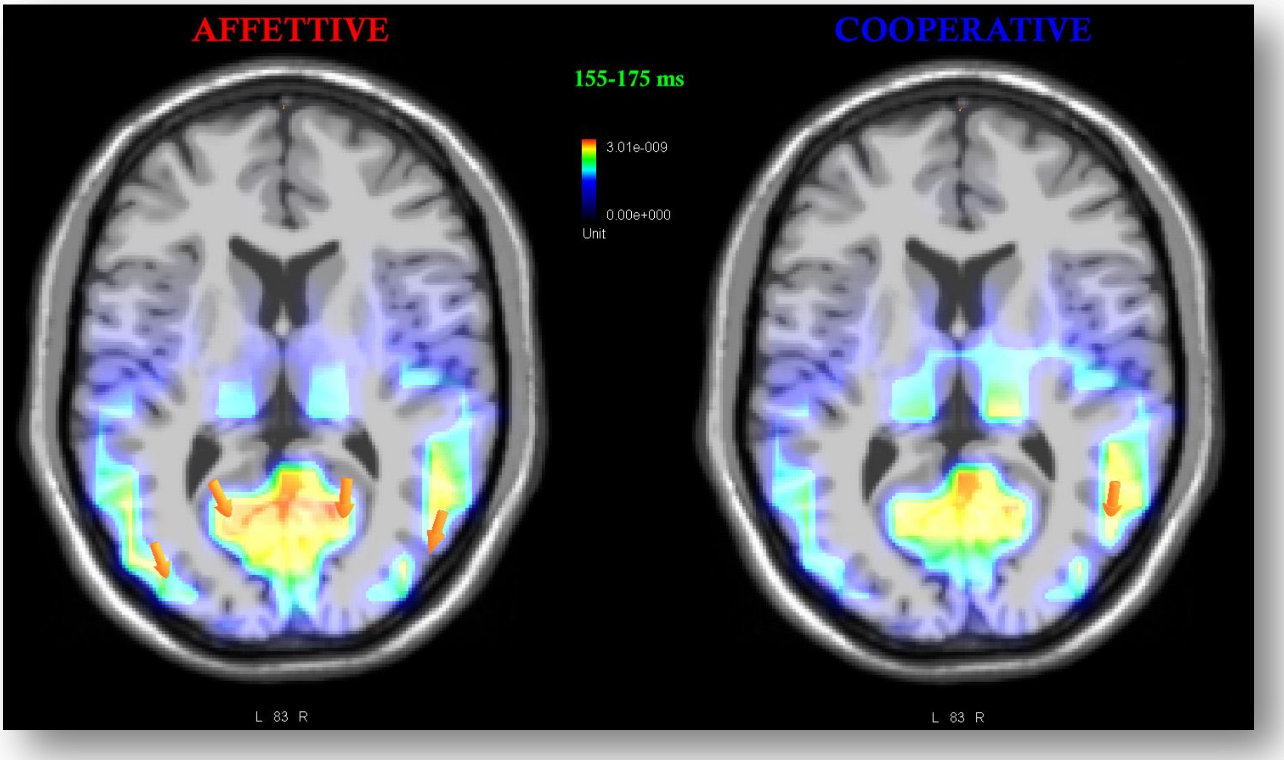

Fig. 3.9 The main cortical source for the affective interactions was found in the posterior cingulate cortex. The ventral stream was more active for the cooperative vs affective interactions.

Parietal N2. Source reconstruction analysis computed on the peak of the component elicited by affective actions revealed cortical generators in the right fusiform gyrus, in the parahippocampal gyrus, in the somatosensory area (BA3), in the premotor area (BA6), in the superior/medial frontal cortex (BA11). Processing of cooperative interactions scenes resulted in the activation of similar regions (see Tab. 3.4). A further swLORETA analysis was apllied on the difference wave obtained by subtracting the affective interactions component to the cooperative interactions component. The latter inverse solution showed an activation of the bilateral fusiform gyrus, the parahippocampal gyrus, the left motor cortex, the right premotor cortex, and the superior/medial frontal cortex (cortical generators uncovered by the source localization analysis on the difference wave are marked with an asterisk in Tab. 3.4b). Basically generators found with the difference wave overlapped to with the sources of the other swLORETA analysis computed on this component.

Affective Interactions (200-250 ms)

T-x	T-y	T-z	H	Area	BA
40,9	-55,9	-10,2	R	Fusiform Gyrus	37
-28,5	-45,8	-9,5	L	Parahippocampal Gyrus	37
-38,5	-21	35,7	L	Postcentral Gyrus	3
-8,5	57,3	-9	L	Superior/Medial Frontal Gyrus	10
-8,5	38,2	-17,9	L	Rectal Gyrus/Inferior Frontal Gyrus	11
-38,5	2,4	29,4	L	Precentral Gyrus	6
40,9	2,4	29,4	R	Precentral Gyrus	6
1,5	64,4	16,8	R	Medial Frontal Gyrus	10

Tab. 3.4a Talairach coordinates corresponding to the intracortical generators, which explain the surface voltage recorded during the 200–250 ms time window in response to affective actions. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Cooperative Interactions (200-250 ms)

T-x	T-y	T-z	H	Area	BA
-28,5	-45,8	-9,5	L	Parahippocampal Gyrus*	37
-48,5	-55,9	-10,2	L	Fusiform Gyrus*	37
40,9	-55,9	-10,2	R	Fusiform Gyrus*	37
-38,5	-21	35,7	L	Post-Central Gyrus*	3
-8,5	57,3	-9	L	Superior/ Medial Frontal Gyrus*	10
-8,5	38,2	-17,9	L	Rectal Gyrus/ Inferior Frontal Gyrus	11
40,9	2,4	29,4	R	Precentral Gyrus*	6
1,5	64,4	16,8	R	Medial Frontal Gyrus	10

Tab. 3.4b Talairach coordinates corresponding to the intracortical generators, which explain the surface voltage recorded during the 200–250 ms time window in response to cooperative actions. Asterisks indicate the brain structures that were significantly more active during perception of cooperative than affective interactions, as provided by a swLORETA inverse solution applied to the difference-waves obtained by subtracting ERPs to affective from cooperative interactions. In the H column the hemisphere is indicated (R: right; L: left), the Broadman areas are specified in the BA column. (swLORETA (ASA); grid spacing=5 mm, estimated SNR=3).

Functional analysis and results

In this paragraph a synthetic description of the analysis computed by Canessa and coworkers (Canessa et al., 2012) *in the fMRI version of the experiment is provided. To follow a report of the obtained results.*

Analysis

A two-levels procedure were employed to generate statistical maps of significant cerebral activity changes associated with interaction goal processing and observer’s gender.

At the first (single-subject) level event-related fMRI responses were modeled as delta ‘‘stick’’ functions by a design-matrix comprising the onset of cooperative, affective or landscape picture-types. Regressors modeling events were convolved with a double-gamma hemodynamic response function (HRF) and parameter estimates were computed for all regressors by maximum-likelihood estimation.

At the second level, whole brain investigations were conducted using random-effects (RFX) full factorial analyses across the 27 subjects.

Several analyses were run. First, the cerebral regions activated by the observation of either cooperative or affective interactions, compared with landscape, were assessed. Then, the regions recruited by the generic observation of interactions, regardless of their purpose, were highlighted by means of a conjunction-null analysis computed on the statistical maps previously obtained. Direct comparisons were executed to investigate the main effect of interaction goal (cooperative vs. affective) and gender (male vs. female participants). Interaction 2 X 2 of interaction content with gender was also computed. The location of the activation foci was determined in the stereotaxic space of Talairach and Tournoux.

After Whole Brain Analysis, Regions-of-Interest (ROIs) analysis was executed employing Talairach coordinates reported in a recent meta-analysis (Van Overwalle & Baetens, 2009) that examined with more than 200 studies the involvement of several brain regions in different social cognition processes. Areas associated with action understanding (including mirror system), mentalizing on action goals, and mentalizing-proper were used. The dorsal and the ventral component of the premotor cortex were assessed separately unlike the meta-analysis. Two other regions were added, the temporal pole and the right inferior frontal gyrus.

For every combination of cognitive process, anatomical region and hemispheric lateralization a combined ROI including the relevant MNI coordinates was created. The final ROIs consisted of 6 mm-radius spheres the center of which was the centre-of- mass of the combined ROIs. The final ROIs were then overlaid in a template brain to highlight possibly overlaps among different social cognitive processes. Among the final ROIs five 6 mm-radius spheres related with action and intention understanding in the right dorsal and ventral premotor portion of the mirror system, with mentalizing on action goals in the right TPJ, and with mentalizing-proper in the ventromedial and dorsomedial prefrontal cortex were selected.

Off-line statistical analyses were compute on extracted ROIs condition-specific parameter estimates. Effects of the two experimental conditions in isolation, of the direct comparison between them, and of the interactions with gender and with empathy were analyzed.

Statistical threshold was set at $p<.05$ corrected for multiple comparisons and ROIs surviving an uncorrected $p<0.05$ threshold were also reported.

Results

Results from whole brain analysis revealed a greater activations in response to cooperative compared to affective interactions of the occipito-temporal cortex (occipital-face area, fusiform face area and extrastriate body area), the occipito-parietal cortex, the inferior and superior parietal cortex, the lateral prefrontal cortex (inferior frontal, middle frontal and precentral gyri) with a right-hemispheric dominance. On the other hand, the vmPFC and the anterior cingulate cortex were more active for affective than cooperative interactions. The conjunction-analysis showed activation in two foci located in the right TPJ and in the left orbitofrontal cortex.

Results were confirmed by the ROIs analyses. Among the ROIs considered, only the right TPJ was active during observation of both cooperative and affective interactions. Furthermore, in line with whole-brain results, stronger activations evoked by cooperative, than affective interactions were activity in some detected in the regions associated with the MNS, namely the right dorsal and ventral premotor cortex including the right inferior frontal gyrus. By contrast, stronger activations in response to affective, rather than cooperative, interactions were observed the ventromedial prefrontal cortex.

Whole-brain interactions between gender and picture-type didn’t show any stronger activation in male than in female subjects in either of the two experimental conditions. At variance, female subjects displayed stronger activity than males in the left STS and ventral premotor cortex while observing cooperative interactions. For the affective scene, no regions were found to be more active in females than in males.

Discussion

This study was designed to explore the temporal course and the neural correlates of processing human social interactions and the underlying social intentions by directly comparing two types of interactions driven by different goals, namely cooperative and affective interactions.

Participants were engaged in a secondary perceptual task, that was introduced to allow an automatic and spontaneous processing and to avoid a conscious awareness of the two types of behavior. The displayed realistic human interactions were matched for several relevant variables and differed only for their shared goal. The absence of confounding discrepancies across the proposed categories of stimuli was confirmed by a post-scanning debriefing session, revealing that no subjects were aware of the two-fold nature of the observed behavior. Although the lack of explicit recognition of the affective and the cooperative goals, clear differences emerged in the resulted temporal dynamics and brain activations.

Time-locked ERP responses, the amplitude of which were significantly different between the two conditions, were detected and measured over the occipito-temporal sites along the ventral stream (N170 and P300 components), over the parietal area (N2), and at the frontal sites (late Anterior Negativity).

The first difference identified in the processing of the affective and the cooperative interactions occurred at 170 ms after stimulus onset over the occipito-temporal area. This negative deflection was recorded between 150 and 190 ms and resulted to be greater in response to affective than cooperative social interactions. The occipito-temporal N170 is an electrophysiological index historically associated to face perception (Bentin et al. 1996; Itier 2004; Proverbio et al., 2010). It has been shown that a profound N170 component is also triggered by the perception of human bodies (Thierry et al., 2006). Literature on this component provided evidence that its amplitude and latency are modulated by different factors, such as the inversion of face/body (Rossion et al., 2000; Stekelenburg et al. 2004), age of the depicted face (Proverbio et al., 2011), or emotional valence or arousal (Pizzagalli et al., 2002). The amplitude of the N170 has been found to vary also in accordance with the emotional arousal elicited by complex visual scene (Junghöfer et al., 2001). Although both types of social interactions were mildly positive, affective interactions are characterized by specific cues, such as intense smiles, caresses, hugs, kisses, or deep eye gaze, that are intrinsic to this type of interaction and are likely to have affected the emotional significance and arousal of the photographs. Thus, the effect exhibited by the N170 suggests an early coding of the affective goal underlying the interactions.

SwLORETA source localization analysis revealed a number of cortical sources for the ERP study. A strong activation of the right posterior cingulate, that is part of the limbic system, was identified in response to the affective scenes. It is known that both anterior and posterior cingulate cortices are involved in emotion processing (Adolphs, 2003), in the subjective evaluation of events, and in their emotional significance. Specifically, the coding of the emotional content of visual stimuli is associated with an activation of the ventral posterior cingulate cortex (Vogt et al. 2006), thus supporting our result of a cortical generator located in the posterior cingulate (BA30) only for affective interactions. Source reconstruction analysis also detected active dipoles in the medial occipital gyrus, medial temporal gyrus and medial frontal cortex. Sources identified in the ventral stream are likely to be elicited by the presence of humans faces and bodies in the photographs, the perception of which is associated with the activation of the Face Fusiform Area and the Extrastriate Body Area (Kanwisher et al. 1997;

Downing et al. 2001). Medial prefrontal cortex is commonly associated with mentalizing and attribution of intentions. However, given the short latency of this component, we suggest this activation might be linked to a more automatic and faster processing, such as face perception. Indeed available literature support the involvement of prefrontal neurons in the early coding of face processing. In a combined ERP/fMRI study (Henson et al., 2003) face recognition was associated with hemodynamic increases in fusiform, medial frontal and orbitofrontal cortices. Moreover, face responsive neurons have been identified in the prefrontal cortex of rhesus monkeys (Scalaidhe et al., 1999).

The subsequent ERP component was recorded slightly later, peaking 200 ms after stimulus onset, was measured between 160 and 280 ms over centro-parietal areas, particularly over the left hemisphere. The amplitude of the parietal N2 was greater in response to cooperative compared to affective interactions, suggesting that the affective content is processed earlier in the occipito-temporal cortex, while the cooperative is processed with a little delay, mainly in the parietal lobe. Source reconstruction analysis was computed on the N2 component and a set of cortical generators were detected: the right fusiform gyrus, the parahippocampal gyrus, the somatosensory cortex, the premotor area, the superior/medial frontal cortex (BA11). The cortical generator found in the right fusiform gyrus may be due to the partially temporal overlapping of the N2 with the N170 and thus being ascribed to face processing. Another temporal areas was found, the parahippocampal gyrus, where the Parahippocampal Place Area (PPA) (Epstein & Kanwisher, 1998) is located. This is a cortical region that has been associated with the visual encoding of scenarios (rather than faces or objects), such as landscapes, cityscapes, or rooms. It’s reasonable that this area has been identified since all the photographs employed in this experiment depicted common scenarios. Beyond temporal areas, parietal and frontal cortices were detected. Regarding the somatosensory cortex, it has been shown (Avikainen et al. 2002; Gazzola & Keysers 2009) that this area was active in response to the observation of human actions. Some studies (Hamilton & Grafton 2006; Riitta et al., 1998) have explicitly included the somatosensory cortex in the fronto-parietal hMNS. The premotor cortex is part of the hMNS as well (Schippers et al., 2010). Thus, finding the somatosensory and the premotor cortex as cortical sources of the N2 strongly suggest a greater involvement of the hMNS for the cooperative interactions as compared to the affective ones. Finally, the activation of more anterior brain regions (left and right superior/medial frontal gyri) might be associated with their role in perceiving social stimuli and in mentalizing.

Electrophysiological data presented so far are in general agreement with those found in the fMRI experiment that showed that observation of cooperative interactions evoked a greater response than the affective ones in the parietal and frontal components of the hMNS involved in action understanding (Iacoboni et al., 2005b). These data substantially confirmed results from the N2 source localization analysis. On the other hand, fMRI analysis also revealed a greater activation of the ventral stream (occipito-temporal and lateral temporal regions), responsible for the processing of faces, stationary bodies and biological motion (Grossman et al. 2000), in response to cooperative than affective actions. These findings are in slight contrast with N170 results above described. However, it should be taken into account that fMRI technique has a very low temporal resolution and thus, hardly detects activations due to neural processes lasting for 20-40 ms. Indeed neural sources identified with swLORETA computed on the N170 refer to the time window corresponding to the component peak, namely comprised between 155 and 175 ms. Instead, results provided by fMRI scan and analysis refer to the whole cortical process.

A better reflection of the fMRI findings might be encountered in the third measured ERP component: the occipito-temporal P300 (250-350 ms), resulted to be greater in response to cooperative than affective stimuli. Separate analyses for men and women revealed a greater discriminative effect in women than men. These data are in line with those of the fMRI experiment. Indeed, a stronger activation of the areas associated with action understanding, including portions of the STS and of the ventral premotor cortex, during the observation of cooperative (vs. affective) scenes in females (vs. males) was detected. Previous studies highlighted gender differences in social responsiveness and abilities. Indeed women seem to be more responsive to emotional stimuli (Lithari et al., 2010), to complex scenes with humans (vs. without humans) (Proverbio et al., 2009) and are more empathic (Hein & Singer, 2008); women perform better in recognizing facial expressions (Thayer & Johnsen, 2000) and in coding the action goal (Proverbio et al., 2010). Thus, higher attention to social stimuli in females than males might have evoked a greater activation of areas deeply involved in the processing of the complex social stimuli displayed.

The last identified ERP component is a long lasting and widespread anterior negative deflection measured between 220 and 500 ms, greater in response to cooperative actions. This higher order involvement of the prefrontal areas during the processing of socially-relevant information has been previously described, for example in the processing of social relations by medial prefrontal cortex (Iacoboni et al., 2004). It’s worth noting that the roles of the prefrontal medial areas in an ERP study varied during the time course. Indeed the swLORETA analysis detected the presence of the medial PFC as a cortical source at 170 ms after stimulus onset, for the N170, greater for affective (vs. cooperative) interactions. Source localization analysis revealed the medial PFC even as a neural generator of the parietal N2, greater in response to the cooperative scenes. As it has been previously described, the medial PFC is an area “sensitive” to social stimuli and especially seems to be responsible for mentalizing, mental state attribution, and theory of mind as well as face processing. This is in line with the current experiment where this area is probably activated by the automatic and spontaneous coding of social stimuli including most probably the shared goals and the underlying intentions conveyed by the human social interactions depicted in the photographs.

Additionally, besides a greater activation of the ventral stream and of the mirror system for the cooperative interactions, the fMRI parallel study revealed an greater neural response of the vmPFC and of the anterior cingulate cortex. These regions are considered to be part of the mentalizing system and of the emotional brain (Pessoa, 2008), a link between cognition and emotion, and mainly associated with attributing emotional state (Van Overwalle, 2009), with emotional judgment (Northoff et al., 2004) and emotion regulation (Quirk & Beer, 2006).

In conclusion, with this study we wished to shed some light on the temporal course and the neural correlates of processing complex human behavior employing ecological stimuli, specifically photographs of affective and cooperative interactions. Data from the current experiment were integrated with data from an fMRI parallel experiment that made use of the same stimuli and of the same task. Overall, obtained results provided evidence of an earlier (170 ms) coding of the affective content compared to the cooperative, that occurs later (200 ms). Affective interactions elicited neural responses mainly in area linked to the emotional processing such as anterior and posterior cingulate and ventro-medial prefrontal cortex; on the other hand, the cooperative interactions were associated mostly with the activation of brain areas responsible for coding the action goal, such as the pSTS and regions of the hMNS. Little gender differences were also uncovered during the processing of human social behavior, confirming previous data showing a greater responsiveness to social stimuli in females than in males.

[This study was performed with Laura Paganelli, Nicola Canessa, Federica Alemanno, Daniela Perani, Stefano Cappa, Alberto Zani and Alice Mado Proverbio]

4

Communicative actions and Interaction

Introduction

Research on human action perception and on its neural bases, as it has been described in the previous chapters, has been subjected to an impressive growth in the last decades.

Most of these studies focused their attention on perception of actions driven by private intentions and performed to satisfy a private goal, namely actions that involve just one person to be accomplished (e.g. hand grasping movement) (Ciaramidaro et al. 2007).

Within the repertoire of actions that humans can execute and observe, a crucial role for the social dynamics is held by the communicative actions. A communicative action is defined as an action intentionally performed to convey a message to another person, who recognizes the communicative intent of the first agent (Bara, 2010). It follows that a communicative act always occurs in a context of social interactions (Manera et al., 2010).

Compared to private actions, communicative actions received less attention by neuroscientific literature, resulting in poor and sparse data regarding their neural basis.

One of the first and few studies regarding communicative action perception was conducted by Montgomery and coworkers (Montgomery et al., 2007). The authors asked the participants, while they were lied down in the fMRI scanner, to watch, imitate and later

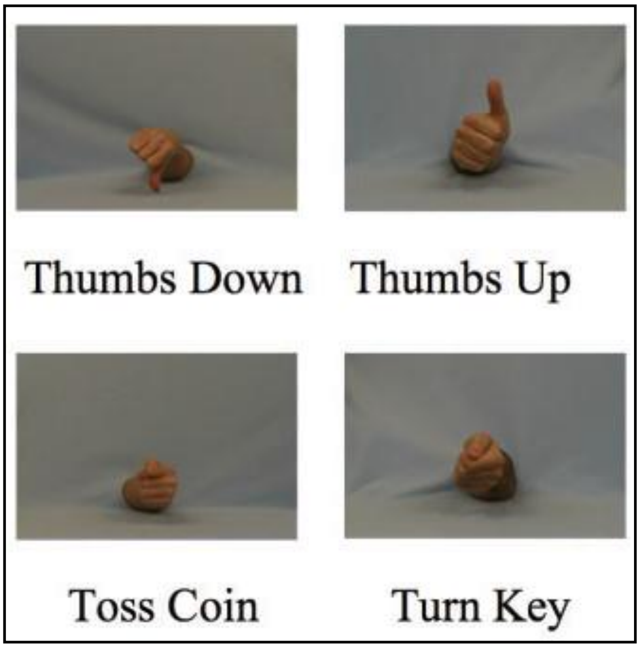

Fig. 4.1 Examples of communicative gestures employed in the study of Montgomery and colleagues (2007)

execute several hand gestures which could be object-directed (e.g. flip coin) or communicative (e.g. okay sign) (see Fig. 4.1). For the observation and imitation tasks video clips showing just the moving hand were employed. ROI (Region-Of-Interest) analysis on the Inferior Parietal Lobule (IPL), the Frontal Operculum and the posterior Superior Temporal Sulcus (pSTS) were run. No significant differences in brain activations were found in the IPL and in the Frontal Operculum due to the stimuli and the task. At variance, pSTS were more active during the execution of communicative gestures than of object-related actions. They also found greater activations of areas related to motor skills such as the cerebellum, the putamen and the premotor cortex in response to object-related actions. Communicative actions elicited a greater response in the anterior STS, temporal pole and medial prefrontal cortex, all areas associated with social cognition.

Other functional studies focused their attention on neural bases of social communicative signals, such as eye contact (Kampe et al., 2003) and approaching movements (Schilbach et al., 2006). These signals are usually executed and perceived by the addressee as indicating a communicative intent, in a certain way they proceed the communicative acts. Results from these studies showed significant activations in areas associated with mentalizing, such as the paracingulate cortex, the anterior poles and the medial prefrontal cortex (mPFC).

As it has been described, communicative actions occur in contexts of social interactions. Even in this case, neural correlates of social interactions were so far investigated to a lesser extent than the private actions. An example is the study reported in the previous chapter conducted with both ERP (Proverbio et al. 2011) and fMRI (Canessa et al., 2012), where brain underpinnings of affective and cooperative interactions were investigated. Yet, one of the most common paradigm to study social interactions consists of involving subjects in a Joint Action, namely instructing them to coordinate in order to reach a specific goal (Sebanz et al., 2006), such as building a tower with small pieces or coordinating to keep a bar in balance (Newman-Norlund et al., 2008; Newman-Norlund et al., 2007b). Comparing the same action performed in isolation vs. in coordination with another individual resulted in a significant activations of areas belonging to the human Mirror Neurons System (hMNS) and specifically of the Inferior Frontal Gyrus (IFG) and the Inferior Parietal Lobule (IPL). Paradigms including an active/interactive role of the participants in processing the observed actions have been employed to investigate neural substrates of cooperation and competition (Decety et al. 2004; Georgiou et al. 2007). To the best of our knowledge, interactive tasks haven’t been used so far to investigate the cortical response to communicative action perception. Being communicative actions intrinsically linked to interactions, with this study we wished to explore the role of an interactive task in the processing of a communicative action.

Thus, the aim of the present study was to investigate, by means of functional Magnetic Resonance, the neural response to a communicative action and how it is modulated by being part of the interaction or not. We therefore created an interactive task where video-clips showing a communicative action were presented to the subjects. The communicative action could be directed to the participants and in this case the actor was facing the camera, or be directed to another actor and in this case the first actor was facing the second actor. When the actor was facing the participant, he/she was the addressee of the action and was instructed to provide a response to the action (interactive condition), by pressing a button key. In the other case, where the actor was facing his colleague, participants were told to not respond and just observe the action (non interactive condition).

With this task we wished to create a task as closer to reality as possible. For this reason we didn’t introduce a mock response in the non interactive conditions, video-clips were shoot and used as stimuli, and actors were taken full-length (not only their executing limb).

Methods

Participants

Eleven adults (7 females) took part to the study. Participants were between 19 and 35 years old (mean=25,27; sd=4). All had normal or corrected-to-normal vision and reported no history of neurological or psychiatric disorders. All participants gave written informed consent to participate in this research. The project was approved by the Yale Human Investigations Committee.

Stimuli

Stimuli consisted of 3 seconds movie clips showing two full-body persons performing in turns either a communicative or a non communicative action. The former one consisted of a bid for a ball by folding and unfolding arms, while the second one was an up and down arm motion. The actors were filmed watching either to the camera (interactive conditions) or to each other (non-interactive conditions). In sum, stimuli comprised 4 categories: communicative action toward the subjects (COMMUNICATIVE/INTERACTIVE), non-communicative action toward the subjects (NON COMMUNICATIVE/INTERACTIVE), communicative action toward the other player (COMMUNICATIVE/NON INTERACTIVE), and non-communicative action toward the other player (NON COMMUNICATIVE/NON INTERACTIVE).

Task & Procedure

Subjects were told they were going to play a ball tossing game with two other players represented on the screen. They were asked to take turns: for half of the trials, that were the Interactive conditions, they had the ball and had to throw it to a player of their choice; for the other half, that were the non-Interactive conditions, they were instructed to just watch the players on the screen. In order to pass the ball, participants were provided with two button boxes, one in each hand, and were instructed to press the button corresponding to the side of the player they chose to toss the ball. To let the participants know when it was their turn to throw the ball, an image of the ball was shown at the bottom of the screen, whereas in the non-interactive conditions the ball was kept by the player who wasn't performing any action.

Each trial (see Fig. 4.2a and Fig. 4.2b) lasted for 7 seconds. Each trial started with a 1 sec slide showing a picture of the two players in their initial condition (i.e. where they were looking at and where the ball was) followed by a 1 s fixation slide. Subsequently, a 3 sec movie clips was shown and then a 1 sec prompt slide including a written cue was displayed: a "go!" text for the –Toward conditions and a "look!" text for the –Away conditions. Participants were instructed to respond during the presentation of this slide, in order to limit the effect of the motor response during the viewing of the video clips. The trials ended with a slide lasting 1 sec presenting the final result of the ball tosses: in the –Toward conditions the player whom the participant passed the ball to was keeping it; in the –Away conditions, if the moving player had asked for a ball, he/she received it, otherwise the ball was passed to the participant and thus shown at the bottom of the movie. A variable inter-trial fixation ranging from to 2 to 10 s (6 sec on average) was used and assigned randomly to the trials.

The experiment consisted of 3 runs including 32 trials per run following 3 distinct pseudo-random orders, for a total of 96 trials (24 trials per condition). At the beginning and at the end of every run a fixation slide of 16 sec was showed. The order of the runs was counterbalanced across individuals.

In order to avoid gender effects, two sets of videos containing either female or male actors were recorded and each participant was presented just with actors of the same sex.

This paradigm was created and presented using E-Prime 2.0 software (Psychology Software Tools, Inc., Pittsburgh, PA).

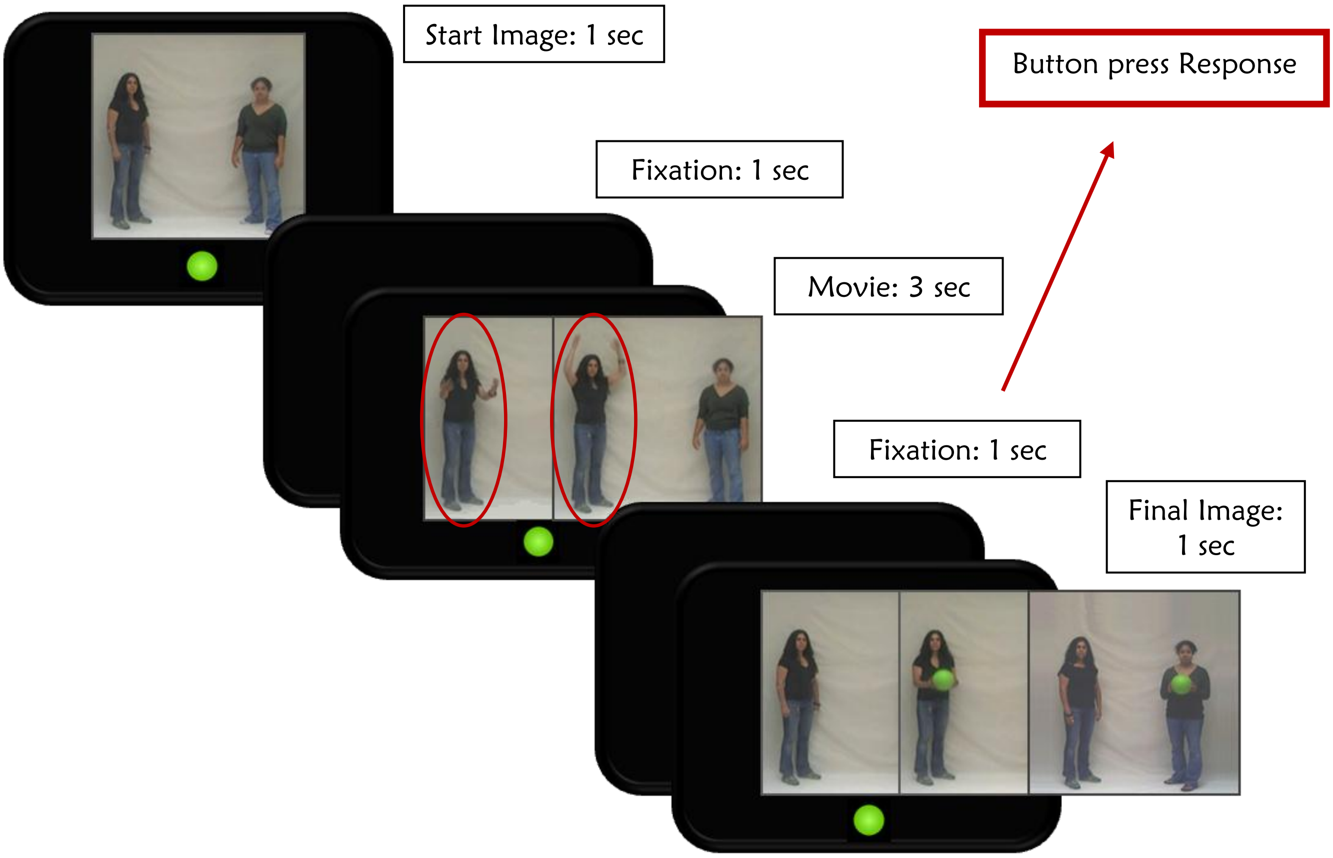

Fig 4.2a in the picture the paradigm employed for the Interactive Conditions is shown: the red circles frame the player performing the communicative and the non communicative actions. In the second fixation subjects were instructed to provide the response: they had to choose whom to pass the ball to. In the final image the possible results of the participant's ball toss.

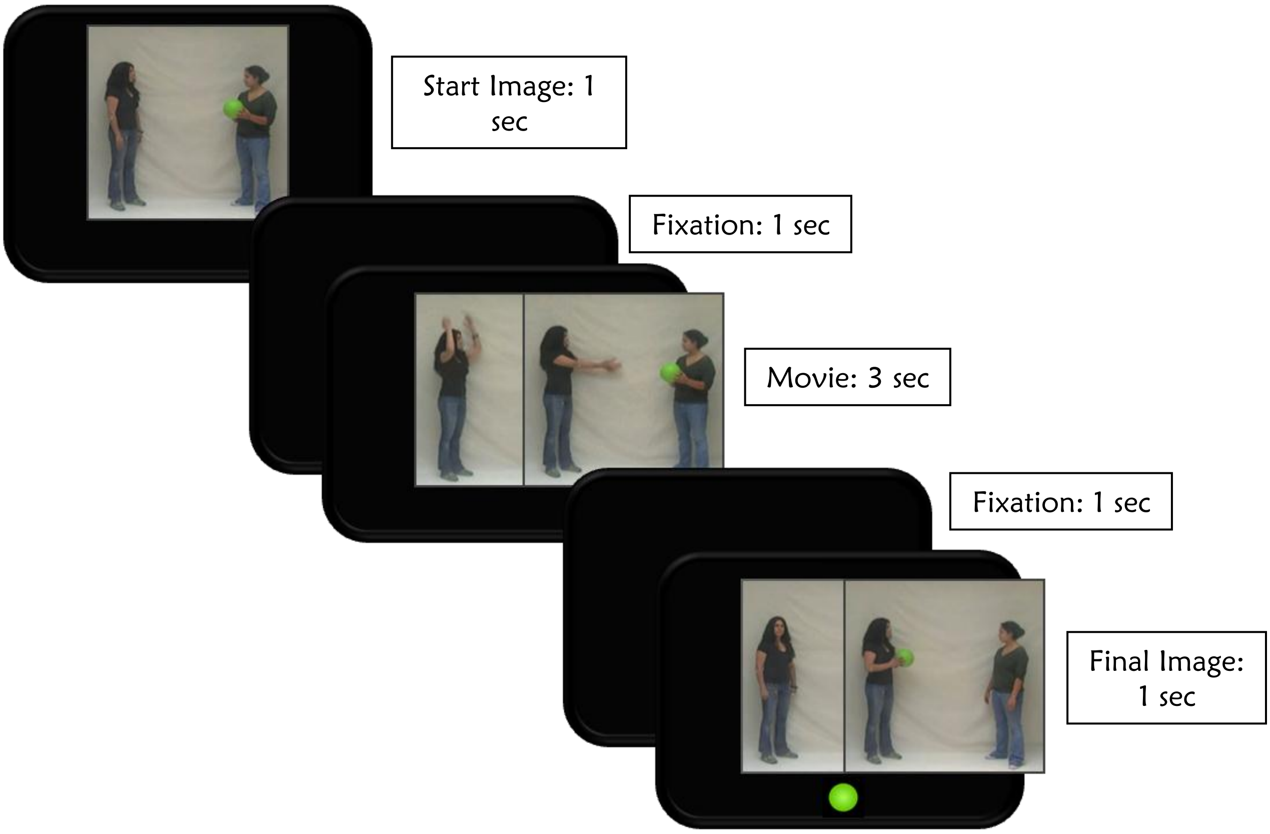

Fig 4.2b In the picture the paradigm employed for the Non Interactive Conditions is shown: in this case the players were facing each other and the actions were directed to the other player. In the final image the two possible results of the ball toss.

Imaging protocol

Images were collected on a Siemens 3T Tim Trio scanner located in the Yale Magnetic Resonance Research Center. Whole-brain T1-weighted anatomical images were acquired using an MPRAGE sequence (TR = 1900 ms; TE = 2.96 ms; flip angle = 9_; FOV = 256 mm; image matrix 256 mm$_2$; voxel size = 1 · 1 · 1 mm; 160 slices; NEX = 1). Whole-brain functional images were acquired using a single-shot, gradient-recalled echo planar pulse sequence (TR = 2000 ms; TE = 25 ms; flip angle = 60_; FOV = 220 mm; image matrix = 64 mm$_2$; voxel size = 3.4 · 3.4 · 4 mm; 34 slices) sensitive to blood oxygen level dependent (BOLD) contrast.

Functional analysis

Imaging data were preprocessed and analyzed using the BrainVoyager QX 2.4 (BrainInnovation, Maastricht, the Netherlands) software package. The first five volumes were discarded to allow for magnetic equilibrium to be reached. Preprocessing of the functional data included slice time correction using sinc interpolation, 3D rigid-body motion correction using trilinear-sinc interpolation to correct for small head movement, linear trend removal, spatial smoothing with a FWHM 7-mm Gaussian kernel, and temporal high-pass filtering (GLM with Fourier basis set, using 2 cycles ⁄ time course). Participants' estimated translational (mm) and rotational motion (◦) parameters were examined prior to analysis. The processed functional data sets were coregistered to within-session anatomical images, which were subsequently normalized to Talairach space (Talairach and Tournoux, 1988). Estimated motion plots depicting head drift from the position at first volume acquisition were generated for each participant to identify movement and eliminate runs with head drift greater than 2 mm in any direction or 2° of rotation (for which one participant was eliminated).

General linear model (GLM) based analyses were conducted for each participant to assess task-related BOLD responses. Regressors were defined as boxcar functions with values of 1 during each condition and 0 otherwise, convolved with a double-gamma hemodynamic response function (HRF). Each individual's estimated motion parameters computed during preprocessing were z-transformed and were included in the model as predictors of no-interest.

Given that button press motion responses were present only in the two Interactive categories, confounding brain activity associated with each participant's ball-throwing events was regressed out and motion responses were included in the model as predictors of no-interest. Specifically, BOLD signal was modulated starting from 50 ms before the response to 50 ms after.

Predictor beta values derived from the first-level analyses were subsequently entered into multiparticipant, random-effects analyses described below.

Whole Brain Analysis

An anatomical mask was constructed by averaging participants' Talairach normalized anatomical images, excluding voxels outside the averaged brain, white matter, and ventricles, and including subcortical structures and the cerebellum. This mask was applied to all analyses.

Whole brain investigations were conducted using random-effects (RFX) GLM-based analyses. Statistical maps from the second-level, random-effects analysis were set at a threshold of $p < .005$. Correction for multiple comparisons was done at the cluster-level. A cluster-size threshold was computed by an iterative Monte Carlo simulation to estimate an acceptable cluster-level false-positive rate determined by the Brain Voyager QX cluster-level statistical threshold estimator plug-in (Forman et al., 1995; Goebel et al., 2006). After 5,000 iterations of a Monte Carlo simulation, the relative frequency of each cluster size was evaluated, and the cluster size corresponding to a corrected threshold of $\alpha <.01$ was determined.

We first isolated the main effects, the Communicative and the Interactive Effect. For the Communicative effect we contrasted the Communicative Conditions with the Non-Communicative (Communicative/Interactive + Communicative/Non Interactive > Non Communicative/Interactive + Non Communicative/Non Interactive), whereas for the Interactive effect we compared the Interactive Conditions with the Non-Interactive (Communicative/Interactive + Non Communicative/Interactive > Communicative/Non Interactive + Non Communicative/Non Interactive). We then considered the Interactive conditions separately from the Non-Interactive in order to not contrast conditions with and without motor responses. It follows that the Non-Communicative conditions were subtracted to the Communicative both in the Interactive and in the Non-Interactive conditions. Finally, to assess the statistic interaction between the two main effect we compared the Communicative effect in the Interactive situation with the Communicative effect in the Non-interactive situation (Communicative/Interactive – Non Communicative/Interactive > Communicative/Non Interactive – Non Communicative/Non Interactive).

Results

Behavioral results

Behavioral results regard only the Interactive conditions since in the non-interactive conditions participants were asked to just observe the videos (see Fig. 4.3).

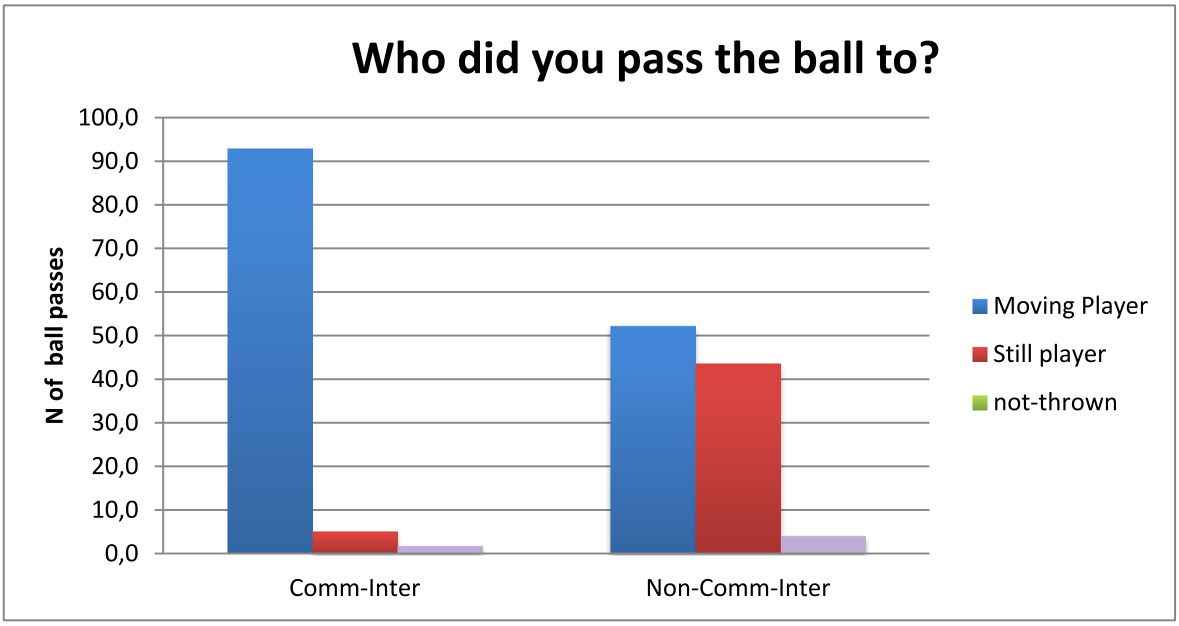

Fig. 4.3 In the graph, the number of ball tosses (%) are shown for the COMMUNICATIVE/INTERACTIVE (Comm-Inter) condition and for the NON COMMUNICATIVE/INTERACTIVE (Non-Comm-Inter) condition. The percentage of passes to the player performing the action (Moving Player) is much higher compared to the passes to the still player in the COMMUNICATIVE than in the NON COMMUNICATIVE condition.

In the Communicative/Interactive condition the ball was thrown to the moving player (the one who asked for the ball) for 93% of the times, to the still player for the 5% of the time and for the 2% it was not thrown. In the Non-Communicative/Interactive condition participants threw the ball to the moving player for the 52% of the times, to the still player for the 44% of the times and not thrown for the 4%. (see Fig. 4.3).

Functional results

No significant differences between Interactive and Non-Interactive conditions were observed. For the Communicative main effect, estimated cluster-level false positive rate was 38 and a significant activation greater for Communicative than Non-Communicative actions was found in the left dorso-medial prefrontal cortex (DMPFC).

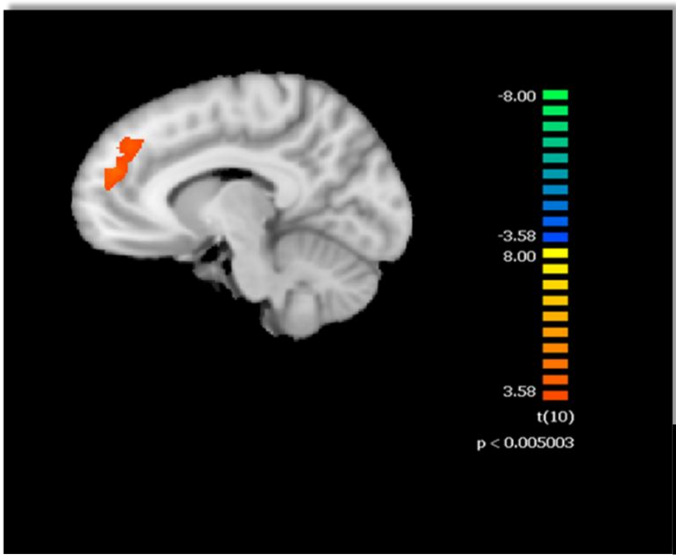

Fig. 4.4 Whole-brain comparison of Communicative with Non-communicative actions regardless of the Interaction. Regions in orange showed greater activation in response to Communicative than Non-Communicative. (p<.005, cluster threshold of 38 contiguous voxels).

Comparison of Communicative with Non-Communicative actions in the Interactive situation, with a computed cluster threshold of 29 contiguous functional voxels, revealed that right Superior Temporal Gyrus (STG), bilateral Motor Cortex, right DMPFC, Medial and Superior frontal Gyrus, left Inferior Frontal Gyrus, and left posterior Cingulate Cortex were more active for Communicative than Non-communicative conditions. No significant activations were found in response to the Non-Communicative vs. Communicative actions.

Communicative with Non-Communicative actions were contrasted even for the Non-Interactive conditions and in this case no significant activations were found. By contrast, subtracting the Communicative actions to the Non-Communicative resulted in significant activations at a cluster threshold of 54 of the right and to a lesser extent left premotor cortex, right Extrastriate Body Area (EBA), and right Occipital Cortex greater for Non-Communicative than Communicative.

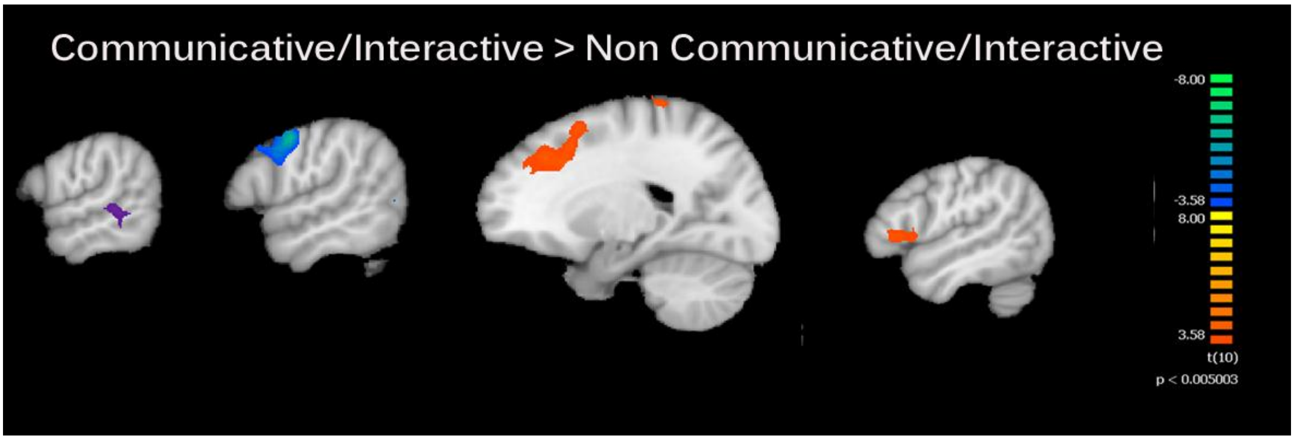

Fig. 4.5 Whole-brain comparison of Communicative with Non-communicative actions in the Interactive conditions. Colored regions showed greater activation in response to Communicative than Non-Communicative actions. (p<.005, cluster threshold of 29 contiguous voxels).

The interaction of Communicativeness by Interactivity has a cluster threshold of 31 and significant activations were found in the right mid-Superior Temporal gyrus, right premotor cortex, right Superior Temporal Sulcus, and right DMPFC.

Brain Region	T-x	T-y	T-z	t	p
Communicative/Interactive + Communicative/Non Interactive > Non Communciative/Interactive + Non Communicative/Non Interactive					
Left dmPFC	-10	49	24	5,872381	0,000157
Communicative/Interactive > Non Communicative/Interactive					
Right Mid-Superior Temporal Sulcus	47	-32	3	6,399655	0,000078
Right dmPFC	14	13	54	10,21779	0,000001
Right precentral gyrus	14	-29	73	8,578695	0,000006
Left dmPFC	5	37	36	6,633621	0,000058
Posterior cingulate cortex	-4	-38	27	6,407508	0,000078
Left precentral gyrus	-34	-26	60	9,630718	0,000002

Left Inferior Frontal Gyrus	-49	22	6	4,996588	0,00054
Non Communicative/Non Interactive > Communcative/Interactive					
Right Premotor Cortex	56	-2	43	7,510159	0,00002
Right Occipito-Temporal Cortex	38	-68	0	4,924843	0,000601
Right Occipital Cortex	17	-89	36	4,726883	0,000808
Left premotor area	-34	-14	60	4,529809	0,001092
Communicative/Interactive – Non Communicative/Interactive > Communcative/Non Interactive – Non Communicative/Non Interactive					
Right Mid-Superior Temporal Gyrus	66	-47	9	4,949177	0,000579
Right premotor cortex	56	-5	39	6,264493	0,000093
Right Superior Temporal Sulcus	47	-44	-6	4,948857	0,00058
Right dmPFC	17	10	57	6,094802	0,000116

Tab. 4.1 Activation in the Ball pass task. Regions identified in a full brain contrast. Talairach coordinates and statistics refer to the voxel with the maximum signal change in each region of interest. Abbreviations: dorsomedial prefrontal cortex (dmPFC).

Discussion

The study object of the current chapter was implemented and carried out to explore the cortical mechanisms underlying the processing of communicative actions. Specifically our interest was directed to uncover the effect on the processing of a communicative action induced by being part of the social interaction, namely being the addressee of this action.

To pursue this goal we developed a new paradigm where a communicative action (a bid for a ball) could be directed either to the participant or to a third person. In the case the action was addressed to the participant, he/she was involved in an interaction, indeed it was required to provide a response to the communicative action. On the other hand, when the action was directed to the other player, subjects were involved in a passive viewing task. Beyond the communicative action, the players could perform an up-and-down arm movement; this action was included as a control action.

Behavioral results showed that responses were modulated by the type of the observed actions, confirming the comprehension of the communicative intent by the subjects. Indeed in the Communicative/Interactive condition more than the 90% of the participants passed the ball to the player who asked for it, whereas in the Non Communicative/Interactive condition the ball tosses to the moving and to the still player were almost equally distributed, being closer to 50%. Negligible were the number of trials when participants did not throw the ball.

Regarding the functional data, obtained results have highlighted that being the addressee of a communicative action vs. being an external observer strongly affects the cortical response to this action. As a matter of fact, the comparison between the communicative and the non communicative action provided different results in terms of brain activations whether it was computed between the Interactive conditions or the Non Interactive.

Communicative vs. non-communicative actions contrast revealed significant activations in a set of cortical regions associated with the perception and understanding of human actions and in the attribution of mental states. Firstly, an activation of the right Superior Temporal Sulcus (STS) emerged. A consistent literature demonstrated that STS is a “highly social” area, being engaged in a wide range of social tasks, including eye gaze perception (Puce et al. 1998), face perception (Haxby et al. 2000), and speech perception (Vouloumanos et al. 2001). Particularly relevant to the current study, the STS region exhibits significant activations for Biological Motion perception (Pelphrey & Morris 2006) and for the recognition of the action purpose (Brass et al., 2007; Vander Wyk et al., 2012). Activation in the STS has been found to be elicited even by social stimuli presented in different modalities. In an fMRI study by Shultz and coworkers (2012), vocal sounds, divided in communicative and non-communicative, were presented to the participants. A greater activation of the STS in response to communicative vocal sounds vs. non communicative emerged. Interestingly, Redcay (2008) proposed an unitary view of the of the STS in all the social tasks, that is to interpret the communicative significance conveyed by both auditory and visual inputs. Our data are therefore in line with previous literature ascribing to the STS a primary role in the perception of human action and in the recognition of the communicative meaning exhibited by the stimuli.

Secondly, the comparison of communicative with non-communicative actions in the interactive conditions revealed a significant activation of the bilateral motor cortex and of the left inferior frontal gyrus (IFG). In the interactive conditions, participants had to toss the ball by pressing a button key, thus moving their finger. It could be argued that activations in these areas were found as a result of the finger movements. However, this hypothesis should be excluded since on one hand the comparison at issue is between two interactive conditions (Communicative/Interactive vs. Non Communicative/interactive), thus the button presses were balanced; on the other hand, in computing the analyses, the button press responses were included as confounding variables in the model and hence the resulting BOLD signal was corrected for this factor. Left out this hypothesis, motor cortex and the IFG are part of the human Mirror Neuron System (Gazzola & Keysers 2009; Iacoboni et al. 2005a) and have been found to be active not only during planning and execution of an action, but during action observation as well. The STS, the motor cortex and the IFG are part of the so-called Action Observation Network (Cross et al., 2009; Schippers et al., 2010), a complex network of brain areas that are supposed to be responsible of action processing and of the action’s goal recognition.

A strong activation of the medial Prefrontal Cortex (mPFC) was also detected when Communicative action was compared to the control action. MPFC is an area associated with Theory of Mind, an umbrella term to indicate the ability of humans to infer intentions, beliefs, mental states and desires of other people (Gallagher et al., 2000). Specifically, data from this study revealed an activation of the dorsomedial Prefrontal Cortex (dmPFC). Literature suggests a differentiation between the ventromedial PFC (vmPFC) and the dmPFC, claiming that the former is associated with emotional perspective taking and the latter with cognitive perspective taking (Amodio & Frith 2006). For example in an experiment by Hynes et al. (2006), participants were required to make inference about what other people were thinking vs. were feeling; results provided a differentiation in the neural response of the mPFC, with a dmPFC activation associated with inferring others' thoughts and a vmPFC activation associated with inferring others' feelings. Thus, our results are in agreement with previous literature as the stimuli here employed weren't emotionally characterized and so elicited an activation in the dmPFC.

Lastly, an activation in the posterior cingulate cortex (PCC) emerged from the Communicative/Non Communicative comparison in the Interactive conditions. This area has been found to be associated with self-monitoring tasks and emotional face perception (Schulte-Rüther et al. 2007; Vogt et al. 2006), processes not really implicated in the current study. However, a set of papers included the PCC in the neural network responsible for mentalizing (Gobbini et al. 2007; Spunt et al. 2011; de Lange et al. 2008) and thus the activation we found is likely to be associated with intention recognition..

Overall, observing a communicative action recruits a set of cortical areas belonging to the AON associated with action understanding and a set of areas supporting the mentalizing system. Although these results might seem in contrast with the previous literature (Van Overwalle & Baetens, 2009), it should be said that communicative actions are special actions that involve both the recognition of the action's goal and the comprehension of the communicative intent prompting the action. Indeed, the comparison of communicative with non communicative actions regardless of the Interaction conditions revealed an activation in the dmPFC that is involved, as previously described, in the attribution of intention. Thus, the obtained results from the Communicative vs. Non Communicative condition in the Interactive situations are perfectly compatible with an activation of both the AON and the mentalizing system.

Unlike for the interactive conditions, the contrast between communicative and non communicative actions in the Non Interactive conditions didn’t reveal any significant activations.

Taken together, these results provide evidence of the importance of the observer’s role in the perception of communicative actions. Being a protagonist in the social interaction is dramatically different from being just an external observer. These results are further confirmed by the significant activations emerged in the STS, in the premotor cortex and in the dmPFC when the Communicative effect (Communicative minus Non Communicative) computed in the Interactive conditions was “cleaned up” by the Communicative effect emerged from the Non Interactive conditions. In the case there were no differences between the two effects and so being part of the interaction didn’t modulate the action perception, significant activations wouldn’t be found.

Finally, an unexpected result emerged in this study. Subtracting the Non Communicative conditions to the Communicative conditions in the Non Interactive conditions didn’t result in any activation. By contrast, comparing non communicative actions with communicative in conditions with no interactions revealed significant activations in the premotor cortex, in the right Extrastriate Body Area (EBA), and in the right Occipital Cortex. The premotor cortex is part of the hMNS and it responds not just to goal-directed actions but also to intransitive movements (Buccino et al. 2001b). Activation in EBA is elicited by observing both human bodies and actions (Downing et al. 2006; Astafiev et al. 2004). Lastly the right Occipital Cortex is involved in the perception of biological and non-biological motion (Grossman & Blake 2002). Given these activations, out hypothesis is that in the Non Interactive conditions have prevailed a general processing of the human motion, with no or few attention to the scope of the actions. Actually these results confirmed data above described on the part played by the state of the observer in the perception of human actions.

Overall, with this study it has been demonstrated that the observer's role is of crucial importance in the processing of communicative actions. This result should be taken into account in the study of action processing and most of all in the investigations of action perception and its impairments in disabling pathologies as autism (Cattaneo et al., 2007) and schizophrenia (Takahashi et al., 2010).

[This study was performed in collaboration with Brent Vander Wyk, Alice Mado Proverbio and Kevin Pelphrey]

General Conclusions

Comprehension of other people’s behavior is a simple as much as a complex process.

We daily meet people and interact with them in an automatic way, easily understanding their actions and inferring their intentions and thoughts. Humans naturally live in a social environment and human brain shows a high specialization to process social stimuli and to drive appropriate responses.

Notwithstanding the apparent simplicity of these processes, they are indeed very complex.

To understand what a conspecific is doing requires the analysis of his/her movements, to observe whether he/she is interacting with an individual or grasping an object, to detect where his/her gaze is directed, to perceive subtle signs of the body language and lastly to integrate what we see with the information we already have about this person and with our general previous knowledge on the world facts.

How our brain compute all these processes is a matter of study of the social neuroscience, and specifically of that branch interested in elucidating the neural mechanisms underlying the comprehension of human actions. As it has already been described, much progress has recently been made in this field with the combination of distinct approaches and the employment of different and sophisticated techniques.

While significant advancements have been made in the identification of cortical regions underlying action processing thanks to neuroimaging and brain stimulation experiments, weaknesses emerge when considering the temporal dynamics of the neural bases of human action understanding.

The present doctoral project is dedicated to partially narrow this gap in the research about the timing of human action processing.

In particular, with the experiments described in the first three chapters we wished to investigate, employing the ERP technique, the temporal course of brain activations evoked by manipulating three specific aspects of human actions. In the first experiment a variation of the action motor content was introduced; in the second, meaningful and meaningless actions were presented, and lastly differences in the social goals beyond human interactions were the focus of the third experiment. The experiment presented in the fourth chapter encountered the need to supply to another lack detectable in the literature, that is the research about the neural mechanisms underlying communicative action perception. Thus, the fourth chapter aimed to explore, with the fMRI technique, the brain bases of communicative action perception manipulating the role of the perceiver on a fundamental dimension for communication, namely being or not the addressee of the action.

Furthermore, in this project we paid special attention to the type of stimuli employed. Indeed, we wished to investigate human action perception with visual inputs as much as possible closer to reality. Pictures from everyday life were utilized in the first three chapters and video-clips depicting full-length people were presented in the last.

In the first experiment, the brain response to the action motor content was modulated by presenting to participants effortful and sporty actions in comparison with effortless actions. Results clearly uncovered the central counterpart of the well-known autonomic response to the observation of physical fatigue revealing a two steps process of the action motor content: the first, at 250 ms after stimulus onset, at the level of the higher-order visual areas as the medial-superior temporal cortex, and the second, at 400 ms after stimulus onset, at the level of the fronto-parietal network and especially of the premotor cortex. These results therefore suggest that, in the processing of motor aspects of actions, a transition from a visual to a motor code occurs, involving the temporal cortex and mostly the human Mirror Neuron System (hMNS).

The attribution of meaning to human actions, investigated in the second experiment comparing meaningful and meaningless actions, appears to follow a temporal course surprisingly similar to that found for the motor content. An early effect was detected on the occipital sites at 250 ms after stimulus onset and lately an effect emerged at 400 ms after stimulus onset on the fronto-central sites. The involvement of the fusiform gryus and the superior temporal sulcus in the early processing of the actions and of the motor and premotor cortex at the time of the second component indicates, even in this case, a transition from a visual to a motor-“mirror” processing. In addition, the activation of the medial Prefrontal Cortex (mPFC) in correspondence of the second component, suggests an involvement of the mentalizing system in processing action meaning, probably elicited by the need to integrate the observed actions with the context and previous knowledge. As indicated by the striking likeness of the recorded ERP components - “action RP” and “action N400” - with the linguistic Recognition Potential and N400, the process of integrating the observed actions with the semantic memory is likely to be functionally similar to the way humans integrate language with meaning,

The temporal course of the brain activations due to the observations of social actions was investigated in the third experiment. The comparison of affective with cooperative interactions modulated the brain response as early as 170 ms after stimulus onset when the affective content elicited a greater activations in the temporal and limbic areas. A comparison of the latency of this component with those found in the previous chapters clearly highlights how the affective content of a social scene is the first one to be recognized.

At a later stage, at the same latency of the early components identified in the first and in the second experiments, between 200 and 300 ms after stimulus onset, the difference in the interaction goal evoked different brain responses, once again in the temporal cortex and in fronto-parietal network. A later component recorded on the frontal sites, as well as in the case of the motor and the semantic content, suggests an involvement of the prefrontal areas and likely of the mPFC, in coding the action social content. The results of this experiment were also accompanied by those obtained with the fMRI, that suggested a greater involvement of the fronto-parietal network for the cooperative interactions and of the emotional-mentalizing system (ventromedial Prefrontal Cortex and cingulate cortex) for the affective interactions. Moreover, converging results from the ERP and the fMRI experiments revealed a deeper processing by female participants of the stimuli presented, indicating, as it has been suggested by previous literature, a more developed social sensibility in women.

Taken together the results from these three experiments, it clearly emerges what has been anticipated at the beginning of this essay, namely that although the ease with which we understand other people’s behavior, comprehending human actions is a composite process that requires the simultaneous participation of distinct brain networks. As supported by previous literature, neural networks associated with human action perception involve the Action Observation Network including the superior temporal sulcus with the fronto-parietal mirror circuit and the mentalizing system mostly including the medial Prefrontal cortex and the cingulate and paracingulate cortex.

The investigation of the temporal dynamics of the brain activations involved in processing different aspects of human actions provides striking evidence that our brain detects at first its affective content. This finding is more than plausible given that humans are a social species that hardly would survive alone. Recognizing the affective content of an action is fundamental when considering the importance of maternal cure for an adequate social and cognitive development (Makinodan et al., 2012) and of the affiliation need that drives the search of stable affective relationships in order to guarantee the survival of the species.

After the very early recognition of the affective content, closely similar temporal courses characterized by a synchronous transition from visual to motor code depict the processing of the motor, semantic and broadly social aspects. At a later stage, an intervention of the mPFC indicate a further, more cognitive, step.

Overall, these data strongly suggest that the processing of distinct aspects of human action doesn't follow a serial elaboration, but occur in parallel in order to build in very little time a meaningful representation of the action. Moreover, it's evident a first activation of the AON to provide an immediate sense of the action goal, followed by the activation of the mentalizing system, likely to integrate the recognized action goal with inferences on the mental states and intentions of the action performer.

The perception of others' behavior, however, is not only modulated by the characteristics of the observed actions (e.g., levels of effort or meaning of the action). In the fourth experiment the role held by the observer with respect to a communicative and interactional context was manipulated. Being the addressee of the communicative act or, at variance, just an external observer completely changes the way we perceive the action. Activations of the AON and of the mentalizing system differentiated between a communicative action and a simple arm gesture only when the participants was involved in the social interaction, not with participants required to just observe the actions. These findings strongly point out the importance of the observer's role, highlighting the significance of social involvement in processing communicative actions. Future studies interested in the neural bases of social action perception should take into account the crucial difference emerged in this study.

All in all, this project represents a contribute to the research of the spatiotemporal dynamics of the cortical networks associated with human action perception, demonstrating a simultaneous and rapid processing of distinct important aspects defining an action. This effective elaboration allows humans to rapidly and efficiently comprehend the surrounding social environment. The successful processing of human behavior is further specialized in the elaboration of its affective/social content highlighting once again the social nature of the human brain.

References

Adolphs, R. (1999). Social cognition and the human brain. *Trends in cognitive sciences*, *3*(12), 469–479.

Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nature reviews. Neuroscience*, *4*(3), 165–78.

Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, *11*(9), 1109–1116.

Allison, T., Puce, a, & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in cognitive sciences*, *4*(7), 267–278.

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature reviews. Neuroscience*, *7*(4), 268–77.

Astafiev, S. V, Stanley, C. M., Shulman, G. L., & Corbetta, M. (2004). Extrastriate body area in human occipital cortex responds to the performance of motor actions. *Nature neuroscience*, *7*(5), 542–8.

Avenanti, A., Annella, L., Candidi, M., Urgesi, C., & Aglioti, S. M. (2012). Compensatory Plasticity in the Action Observation Network: Virtual Lesions of STS Enhance Anticipatory Simulation of Seen Actions. *Cerebral cortex (New York, N.Y. : 1991),*

Avikainen, S., Forss, N., & Hari, R. (2002). Modulated Activation of the Human SI and SII Cortices during Observation of Hand Actions, *646*, 640–646.

Bach, P., Gunter, T. C., Knoblich, G., Prinz, W., & Friederici, A. D. (2009). N400-like negativities in action perception reflect the activation of two components of an action representation. *Social neuroscience, 4*(3), 212–32.

Balconi, M., & Caldiroli, C. (2011). Semantic violation effect on object-related action comprehension. N400-like event-related potentials for unusual and incorrect use. *Neuroscience*, *197*, 191–9.

Bara, B. G. (2010). *Cognitive Pragmatics*. MIT Press.

Baron-Cohen, S. (1989). The Autistic Child's Theory of Mind: A Case of Specific Developmental Delay. *Journal of Child Psychology and Psychiatry, 30*, 285–297.

Baron-cohen, S., Leslie, A. M., & Frith, U. T. A. (1985). the autistic child have a "theory of mind"? *Cognition*, *21*, 37–46.

Bassili, J. N. (1978). Facial motion in the perception of faces and of emotional expression. *Journal of Experimental Psychology: Human Perception and Performance*, *4*(3), 373–379.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies of Face Perception in Humans. *Journal of cognitive neuroscience*, *8*(6), 551–565.

Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual review of psychology*, *58*, 47–73.

Bonda, E., Ostry, D., & Evans, A. (1996). Specific Involvement of Human Parietal Systems in the Perception of Biological Motion and the Amygdala, *76*(11), 3737–3744.

Brass, M., Schmitt, R. M., Spengler, S., & Gergely, G. (2007). Investigating action understanding: inferential processes versus action simulation. *Current biology : CB*, *17*(24), 2117–21.

Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S., & Movshon, J. A. (1996). A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Visual Neuroscience*, *13*, 87–100.

Brunet, E., Sarfati, Y., Hardy-Baylé, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *NeuroImage*, *11*(2), 157–66.

Buccino, G, Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., et al. (2001b). Action observation activates premotor and parietal areas in a somatotopic manner : an fMRI study. *European Journal of Neuroscience*, *13*, 400–404.

Buccino, Giovanni, Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H., Rizzolatti, G., et al. (2004). Neural circuits underlying imitation of Hand Actions : An Event-Related fMRI Study. *Neuron*, *42*, 323–334.

Canessa, N., Alemanno, F., Riva, F., Zani, A., Proverbio, A. M., Mannara, N., Perani, D., et al. (2012). The Neural Bases of Social Intention Understanding: The Role of Interaction Goals. (N. Wenderoth, Ed.)*PLoS ONE*, *7*(7), e42347.

Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, *50*(3), 1148–67.

Castelli, F., Happé, F., Frith, U., & Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage*, *12*(3), 314–25.

Cattaneo, L., Fabbri-Destro, M., Boria, S., Pieraccini, C., Monti, A., Cossu, G., & Rizzolatti, G. (2007). Impairment of actions chains in autism and its possible role in intention understanding. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(45), 17825–30.

Centelles, L., Assaiante, C., Nazarian, B., Anton, J.-L., & Schmitz, C. (2011). Recruitment of both the mirror and the mentalizing networks when observing social interactions depicted by point-lights: a neuroimaging study. *PloS one*, *6*(1), e15749.

Charvet, C. J., & Finlay, B. L. (2012). Embracing covariation in brain evolution: Large brains, extended development, and flexible primate social systems. *Program Brain Research*, (607), 71–87.

Cheng, Y., Lee, P.-L., Yang, C.-Y., Lin, C.-P., Hung, D., & Decety, J. (2008). Gender differences in the mu rhythm of the human mirror-neuron system. *PloS one*, *3*(5), e2113.

Cheng, Y.-W., Tzeng, O. J. L., Decety, J., Imada, T., & Hsieh, J.-C. (2006). Gender differences in the human mirror system: a magnetoencephalography study. *Neuroreport*, *17*(11), 1115–9.

Ciaramidaro, a, Adenzato, M., Enrici, I., Erk, S., Pia, L., Bara, B. G., & Walter, H. (2007). The intentional network: how the brain reads varieties of intentions. *Neuropsychologia*, *45*(13), 3105–13.

Clarke, T. J., Bradshaw, M. F., Field, D. T., Hampson, S. E., & Rose, D. (2005). The perception of emotion from body movement in point-light displays of interpersonal dialogue. *Perception*, *34*(10), 1171–1180. doi:10.1068/p5203

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). SHORT COMMUNICATION Observation and execution of movement : similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*, *11*, 1839–1842.

Colle, L., Baron-Cohen, S., & Hill, J. (2007). Do children with autism have a theory of mind? A non-verbal test of autism vs. specific language impairment. *Journal of autism and developmental disorders*, *37*(4), 716–23.

Collins, D., Neelin, P., Peters, T., & Evans, A. (1994). Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. *Journal of Computer Assisted Tomography*, *18*(2), 192–205.

Cross, E. S., Kraemer, D. J. M., Hamilton, A. F. D. C., Kelley, W. M., & Grafton, S. T. (2009). Sensitivity of the action observation network to physical and observational learning. *Cerebral cortex (New York, N.Y. : 1991)*, *19*(2), 315–26.

De Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current biology : CB*, *18*(6), 454–7.

Decety, J, Gre, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., et al. (1997). Brain activity during observation of actions Influence of action content and subject ' s strategy, 1763–1777.

Decety, Jean, Jackson, P. L., Sommerville, J. a, Chaminade, T., & Meltzoff, A. N. (2004). The neural bases of cooperation and competition: an fMRI investigation. *NeuroImage*, *23*(2), 744–51.

Decety, Jean, Jeannerod, M., Germain, M., & Pastene, J. (1991). Vegetative response during imagined movement is proportional to mental effort. *Behavioural brain research*, *42*(1), 1–5.

Decety, Jean;, Jeannerod, M., Durozard, D., & Baverel, G. (1993). Central activation of autonomic effectors during mental simulation of motor actions in man. *Jounral of Physiology*, *461*, 549–563.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental brain research*, *91*, 176–180.

Dien, J., Frishkoff, G. a, Cerbone, A., & Tucker, D. M. (2003). Parametric analysis of event-related potentials in semantic comprehension: evidence for parallel brain mechanisms. *Brain research. Cognitive brain research*, *15*(2), 137–53.

Dittrich, W. H. (1993). Action categories and the perception of biological motion. *Perception*, *22*(1), 15–22.

Downing, P. E., Peelen, M. V, Wiggett, A. J., & Tew, B. D. (2006). The role of the extrastriate body area in action perception. *Social neuroscience*, *1*(1), 52–62.

Downing, P., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science (New York, N.Y.)*, *293*(5539), 2470–3.

Dunbar, R I M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*(6), 469–493.

Dunbar, Robin I.M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190.

Enticott, P. G., Kennedy, H. a, Bradshaw, J. L., Rinehart, N. J., & Fitzgerald, P. B. (2010). Understanding mirror neurons: evidence for enhanced corticospinal excitability during the observation of transitive but not intransitive hand gestures. *Neuropsychologia*, *48*(9), 2675–80.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*(6676), 598–601.

Evans, A., Collins, D., Mills, S., Brown, E., Kelly, R., & Peters, T. (1993). 3D statistical neuroanatomical models from 305 MRI volumes (pp. 1813–7).

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation : a magnetic stimulation study Motor Facilitation During Action Observation : A Magnetic Stimulation Study. *Journal of Neurophysiology*, *73*, 2608–2611.

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, *50*(4), 531–4.

Gallagher, H. L., Happé, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: an fMRI study of "theory of mind" in verbal and nonverbal tasks. *Neuropsychologia*, *38*(1), 11–21.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain : a journal of neurology*, *119 (Pt 2*, 593–609.

Gangitano, M, Mottaghy, F. M., & Pascual-Leone, a. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, *12*(7), 1489–92.

Gangitano, Massimo, Mottaghy, F. M., & Pascual-Leone, A. (2004). Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *The European journal of neuroscience*, *20*(8), 2193–202.

Ganis, G., & Kutas, M. (2003). An electrophysiological study of scene effects on object identification. *Cognitive Brain Research*, *16*(2), 123–144.

Gazzola, V, Rizzolatti, G., Wicker, B., & Keysers, C. (2007). The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *NeuroImage*, *35*(4), 1674–84.

Gazzola, Valeria, Aziz-Zadeh, L., & Keysers, C. (2006). Empathy and the somatotopic auditory mirror system in humans. *Current biology : CB*, *16*(18), 1824–9.

Gazzola, Valeria, & Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cerebral cortex (New York, N.Y. : 1991)*, *19*(6), 1239–55.

Gazzola, Valeria, Van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., & Keysers, C. (2007). Aplasics born without hands mirror the goal of hand actions with their feet. *Current biology : CB*, *17*(14), 1235–40.

Georgiou, I., Becchio, C., Glover, S., & Castiello, U. (2007). Different action patterns for cooperative and competitive behaviour. *Cognition*, *102*(3), 415–33.

Geselowitz, D. B. (1967). On bioelectric potentials in an inhomogeneous volume conductor. *Biophysical journal*, *7*(1), 1–11.

Gobbini, M. I., Koralek, A. C., Bryan, R. E., Montgomery, K. J., & Haxby, J. V. (2007). Two takes on the social brain: a comparison of theory of mind tasks. *Journal of cognitive neuroscience*, *19*(11), 1803–14.

Grafton, S T, Fadiga, L., Arbib, M. a, & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *NeuroImage*, *6*(4), 231–6.

Grafton, Scott T. (2009). Embodied cognition and the simulation of action to understand others. *Annals of the New York Academy of Sciences*, *1156*, 97–117.

Grafton, Scott T, Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography. *Experimental brain research*, *112*, 103–111.

Grezes, J. (1998). Top Down Effect Of Strategy On The Perception Of Human Biological Motion : A Pet Investigation T Op-Down E Ffect Of S Trategy On The P Erception Of H U Man B Iological M Otion : A Pet I Nvestigation. *Cognitive Neuropsychology*, *15*(December 2012), 553–582.

Grossman, E. D., & Blake, R. (2002). Brain Areas Active during Visual Perception of Biological Motion. *Neuron*, *35*(6), 1167–75.

Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of cognitive neuroscience*, *12*(5), 711–20.

Grèzes, J., Armony, J. ., Rowe, J., & Passingham, R. . (2003). Activations related to “mirror” and “canonical” neurones in the human brain: an fMRI study. *NeuroImage*, *18*(4), 928–937.

Hagoort, P., Hald, L., Bastiaansen, M., & Petersson, K. M. (2004). Integration of word meaning and world knowledge in language comprehension. *Science (New York, N.Y.)*, *304*(5669), 438–41.

Hamilton, A. F. D. C., & Grafton, S. T. (2006). Goal representation in human anterior intraparietal sulcus. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *26*(4), 1133–7.

Hari, R, Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(25), 15061–5.

Hari, Riitta, & Ha, R. (1998). Three hands : fragmentation of human bodily awareness. *Neuroscience Letters*, *240*, 131–134.

Haxby, J., Hoffman, E., & Gobbini, M. (2000). The distributed human neural system for face perception. *Trends in cognitive sciences*, *4*(6), 223–233.

Heider, F., & Simmel, M. (1944). An experimental Study of Apparent Behavior. *The American journal of Psychology*, *57*(2), 243–259.

Hein, G., & Singer, T. (2008). I feel how you feel but not always: the empathic brain and its modulation. *Current opinion in neurobiology*, *18*(2), 153–8.

Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, a, & Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebral cortex (New York, N.Y. : 1991)*, *13*(7), 793–805.

Hinojosa, J. a, Martín-Loeches, M., Gómez-jarabo, G., & Rubia, F. J. (2000). Common basal extrastriate areas for the semantic processing of words and pictures. *Clinical neurophysiology : official journal of the International Federation of Clinical Neurophysiology*, *111*(3), 552–60.

Hirai, M., Fukushima, H., & Hiraki, K. (2003). An event-related potentials study of biological motion perception in humans. *Neuroscience Letters*, *344*(1), 41–44.

Hynes, C. a, Baird, A. a, & Grafton, S. T. (2006). Differential role of the orbital frontal lobe in emotional versus cognitive perspective-taking. *Neuropsychologia*, *44*(3), 374–83.

Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., & Fiske, A. P. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *NeuroImage*, *21*(3), 1167–73.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005a). Grasping the intentions of others with one's own mirror neuron system. *PLoS biology*, *3*(3), e79.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C., & Rizzolatti, G. (2005b). Grasping the intentions of others with one's own mirror neuron system. *PLoS biology*, *3*(3), e79.

Ikeda, H., Blake, R., & Watanabe, K. (2005). Eccentric perception of biological motion is unscalably poor. *Vision research*, *45*(15), 1935–43.

Itier, R. J. (2004). N170 or N1? Spatiotemporal Differences between Object and Face Processing Using ERPs. *Cerebral Cortex*, *14*(2), 132–142.

Jellema, T., Baker, C. I., Wicker, B., & Perrett, D. I. (2000). Neural representation for the perception of the intentionality of actions. *Brain and cognition*, *44*(2), 280–302.

Johansson, G. (1973). Visual perception of biological motion and a model for its visual analysis. *Perception Psychophysics*. 14 (2), 201-211.

Jokisch, D., Daum, I., Suchan, B., & Troje, N. F. (2005). Structural encoding and recognition of biological motion: evidence from event-related potentials and source analysis. *Behavioural brain research*, *157*(2), 195–204. doi:10.1016/j.bbr.2004.06.025

Junghöfer, M., Bradley, M. M., Elbert, T. R., & Lang, P. J. (2001). Fleeting images: a new look at early emotion discrimination. *Psychophysiology*, *38*(2), 175–8.

Kaiser, M. D., Hudac, C. M., Shultz, S., Lee, S. M., Cheung, C., Berken, A. M., Deen, B., et al. (2010). Neural signatures of autism. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(49), 21223–8.

Kampe, K. K. W., Frith, C. D., & Frith, U. (2003). “Hey John”: signals conveying communicative intention toward the self activate brain regions associated with “mentalizing,” regardless of modality. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *23*(12), 5258–63.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *17*(11), 4302–11.

Kessler, K., Biermann-Ruben, K., Jonas, M., Siebner, H. R., Bäumer, T., Münchau, A., & Schnitzler, A. (2006). Investigating the human mirror neuron system by means of cortical synchronization during the imitation of biological movements. *NeuroImage*, *33*(1), 227–38.

Keysers, C., & Gazzola, V. (2010). Social neuroscience: mirror neurons recorded in humans. *Current biology : CB*, *20*(8), R353–4.

Kim, J., Park, S., & Blake, R. (2011). Perception of biological motion in schizophrenia and healthy individuals: a behavioral and FMRI study. *PloS one*, *6*(5), e19971.

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of cognitive neuroscience*, *12*(1), 48–55.

Krach, S., Blümel, I., Marjoram, D., Lataster, T., Krabbendam, L., Weber, J., Van Os, J., et al. (2009). Are women better mindreaders? Sex differences in neural correlates of mentalizing detected with functional MRI. *BMC neuroscience*, *10*, 9.

Krakowski, A. I., Ross, L. a, Snyder, A. C., Sehatpour, P., Kelly, S. P., & Foxe, J. J. (2011). The neurophysiology of human biological motion processing: a high-density electrical mapping study. *NeuroImage*, *56*(1), 373–83.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual review of psychology*, *62*, 621–47.

Kutas, M., & Hillyard, S. (1984). Brain Potentials during reading reflect word expectancy and semantic association. *Nature*, *307*.

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: brain potentials reflect semantic incongruity. *Science*, *207*(4427), 203–205.

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature reviews. Neuroscience*, *9*(12), 920–33.

Lieberman, M. D. (2005). Principles, processes, and puzzles of social cognition: an introduction for the special issue on social cognitive neuroscience. *NeuroImage*, *28*(4), 745–56.

Lithari, C., Frantzidis, C. a, Papadelis, C., Vivas, A. B., Klados, M. a, Kourtidou-Papadeli, C., Pappas, C., et al. (2010). Are females more responsive to emotional stimuli? A neurophysiological study across arousal and valence dimensions. *Brain topography*, *23*(1), 27–40.

Lorteije, J. a M., Kenemans, J. L., Jellema, T., Van der Lubbe, R. H. J., De Heer, F., & Van Wezel, R. J. a. (2006). Delayed response to animate implied motion in human motion processing areas. *Journal of cognitive neuroscience*, *18*(2), 158–68.

Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of experimental psychology. Human perception and performance*, *31*(1), 210–20.

Lui, F., Buccino, G., Duzzi, D., Benuzzi, F., Crisi, G., Baraldi, P., Nichelli, P., et al. (2008). Neural substrates for observing and imagining non-object-directed actions. *Social neuroscience*, *3*(3-4), 261–75.

Makinodan, M., Rosen, K. M., Ito, S., & Corfas, G. (2012). A critical period for social experience-dependent oligodendrocyte maturation and myelination. *Science (New York, N.Y.)*, *337*(6100), 1357–60.

Manera, V., Schouten, B., Becchio, C., Bara, B. G., & Verfaillie, K. (2010). Inferring intentions from biological motion: a stimulus set of point-light communicative interactions. *Behavior research methods, 42*(1), 168–78.

Martín-Loeches, M, Hinojosa, J. a, Fernández-Frías, C., & Rubia, F. J. (2001). Functional differences in the semantic processing of concrete and abstract words. *Neuropsychologia*, *39*(10), 1086–96.

Martín-Loeches, M, Hinojosa, J. a, Gómez-Jarabo, G., & Rubia, F. J. (1999). The recognition potential: An ERP index of lexical access. *Brain and language*, *70*(3), 364–84.

Martín-Loeches, M, Hinojosa, J. a, Gómez-Jarabo, G., & Rubia, F. J. (2001). An early electrophysiological sign of semantic processing in basal extrastriate areas. *Psychophysiology*, *38*(1), 114–24

Martín-Loeches, Manuel. (2007). The gate for reading: reflections on the recognition potential. *Brain research reviews*, *53*(1), 89–97.

Martín-Loeches, Manuel, Hinojosa, J. A., Casado, P., Munoz, F., & Fernandez-Frias, C. (2004). Electrophysiological evidence of an early effect of sentence context in reading. *Biological Psychology*, *65*(3), 265–280.

Marí-Beffa, P., Valdés, B., Cullen, D. J. D., Catena, A., & Houghton, G. (2005). ERP analyses of task effects on semantic processing from words. *Brain research. Cognitive brain research*, *23*(2-3), 293–305.

Mcpherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, 36, 53–65.

Montgomery, K. J., Isenberg, N., & Haxby, J. V. (2007). Communicative hand gestures and object-directed hand movements activated the mirror neuron system. *Social cognitive and affective neuroscience*, *2*(2), 114–22.

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. a. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Brain research. Cognitive brain research*, *19*(2), 195–201.

Newman-Norlund, R. D., Bosga, J., Meulenbroek, R. G. J., & Bekkering, H. (2008). Anatomical substrates of cooperative joint-action in a continuous motor task: virtual lifting and balancing. *NeuroImage*, *41*(1), 169–77.

Newman-Norlund, R. D., Van Schie, H. T., Van Zuijlen, A. M. J., & Bekkering, H. (2007a). The mirror neuron system is more active during complementary compared with imitative action. *Nature neuroscience*, *10*(7), 817–8.

Newman-Norlund, R. D., Van Schie, H. T., Van Zuijlen, A. M. J., & Bekkering, H. (2007b). The mirror neuron system is more active during complementary compared with imitative action. *Nature neuroscience*, *10*(7), 817–8.

Norman, J. F., Payton, S. M., Long, J. R., & Hawkes, L. M. (2004). Aging and the perception of biological motion. *Psychology and aging*, *19*(1), 219–225.

Northoff, G., Heinzel, A., Bermpohl, F., Niese, R., Pfennig, A., Pascual-Leone, A., & Schlaug, G. (2004). Reciprocal modulation and attenuation in the prefrontal cortex: an fMRI study on emotional-cognitive interaction. *Human brain mapping*, *21*(3), 202–12.

Paccalin, C., & Jeannerod, M. (2000). Changes in breathing during observation of effortful actions. *Brain research*, *862*(1-2), 194–200.

Palmero-Soler, E., Dolan, K., Hadamschek, V., & Tass, P. a. (2007). swLORETA: a novel approach to robust source localization and synchronization tomography. *Physics in medicine and biology*, *52*(7), 1783–800.

Pasternak, T., & Merigan, W. H. (1994). Motion perception following lesions of the superior temporal sulcus in the monkey. *Cerebral cortex (New York, N.Y. : 1991)*, *4*(3), 247–59.

Pavlova, M., Birbaumer, N., & Sokolov, A. (2006). Attentional modulation of cortical neuromagnetic gamma response to biological movement. *Cerebral cortex (New York, N.Y. : 1991)*, *16*(3), 321–7.

Pavlova, M., Guerreschi, M., Lutzenberger, W., & Krägeloh-Mann, I. (2010). Social interaction revealed by motion: dynamics of neuromagnetic gamma activity. *Cerebral cortex (New York, N.Y. : 1991)*, *20*(10), 2361–7.

Pelphrey, K. a, Mitchell, T. V, McKeown, M. J., Goldstein, J., Allison, T., & McCarthy, G. (2003). Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *23*(17), 6819–25.

Pelphrey, K. a, & Morris, J. P. (2006). Brain Mechanisms for Interpreting the Actions of Others From Biological-Motion Cues. *Current directions in psychological science*, *15*(3), 136–140.

Pelphrey, K. a, Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: the perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of cognitive neuroscience*, *16*(10), 1706–16.

Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: a comparison between EEG desynchronization in the mu-range and previous fMRI results. *Brain research*, *1282*, 126–32.

Pessoa, L. (2008). On the relationship between emotion and cognition. *Nature reviews. Neuroscience*, *9*(2), 148–58.

Piefke, M., Kramer, K., Korte, M., Schulte-Rüther, M., Korte, J. M., Wohlschläger, A. M., Weber, J., et al. (2009). Neurofunctional modulation of brain regions by distinct forms of motor cognition and movement features. *Human brain mapping*, *30*(2), 432–51.

Pizzagalli, D. a, Lehmann, D., Hendrick, A. M., Regard, M., Pascual-Marqui, R. D., & Davidson, R. J. (2002). Affective Judgments of Faces Modulate Early Activity (∼160 ms) within the Fusiform Gyri. *NeuroImage*, *16*(3), 663–677.

Pollick, F. E., Paterson, H. M., Bruderlin, a, & Sanford, a J. (2001). Perceiving affect from arm movement. *Cognition*, *82*(2), B51–61.

Price, C. J., & Devlin, J. T. (2003). The myth of the visual word form area. *NeuroImage*, *19*(3), 473–481.

Proverbio, A. M., Adorni, R., Zani, A., & Trestianu, L. (2009). Sex differences in the brain response to affective scenes with or without humans. *Neuropsychologia*, *47*(12), 2374–2388.

Proverbio, A. M., Leoni, G., & Zani, A. (2004). Language switching mechanisms in simultaneous interpreters: an ERP study. *Neuropsychologia*, *42*(12), 1636–56.

Proverbio, A. M., Riva, F., Martin, E., & Zani, A. (2010). Face coding is bilateral in the female brain. *PloS one*, *5*(6), e11242.

Proverbio, A. M., Riva, F., Paganelli, L., Cappa, S. F., Canessa, N., Perani, D., & Zani, A. (2011). Neural coding of cooperative vs. affective human interactions: 150 ms to code the action's purpose. *PloS one*, *6*(7), e22026.

Proverbio, A. M., Riva, F., & Zani, A. (2009). Observation of static pictures of dynamic actions enhances the activity of movement-related brain areas. *PloS one*, *4*(5), e5389.

Proverbio, A. M., Riva, F., & Zani, A. (2010). When neurons do not mirror the agent's intentions: sex differences in neural coding of goal-directed actions. *Neuropsychologia*, *48*(5), 1454–63.

Proverbio, A. M., Riva, F., Zani, A., & Martin, E. (2011). Is it a baby? Perceived age affects brain processing of faces differently in women and men. *Journal of cognitive neuroscience*, *23*(11), 3197–208.

Puce, a, Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, *18*(6), 2188–99.

Quirk, G. J., & Beer, J. S. (2006). Prefrontal involvement in the regulation of emotion: convergence of rat and human studies. *Current opinion in neurobiology*, *16*(6), 723–7.

Redcay, E. (2008). The superior temporal sulcus performs a common function for social and speech perception: implications for the emergence of autism. *Neuroscience and biobehavioral reviews*, *32*(1), 123–42.

Reid, V. M., & Striano, T. (2008). N400 involvement in the processing of action sequences. *Neuroscience letters*, *433*(2), 93–7.

Richerson, P. J., & Boyd, R. (2001). Institutional Evolution In The Holocene : The Rise Of Complex Societies. *The Origin of Human Social Institutions. Proceedings of the British Academy* (Vol. 110, pp. 197–204).

Rilling, J. K., Sanfey, A. G., Aronson, J. a, Nystrom, L. E., & Cohen, J. D. (2004). The neural correlates of theory of mind within interpersonal interactions. *NeuroImage*, *22*(4), 1694–703.

Rizzolatti, Giacomo, & Craighero, L. (2004). THE MIRROR-NEURON SYSTEM. *Annual Review of Neuroscience*, *27*, 169–192.

Rizzolatti, Giacomo, & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature reviews. Neuroscience*, *11*(4), 264–74.

Rizzolatti, Giacomo;, Luciano;, F., Matelli, M., Bettinardi, Paulesu, E., Perani, D., & Fazio, F. (1996). Localization of grasp representations in humans by PET : *Experimental brain research. Experimentelle Hirnforschung. Expérimentation cérébrale*, 246–252.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport*, *11*(1), 69–74.

Rudell, A. P., & Hua, J. (1995). Recognition Potential Latency and Word Image Degradation. *Brain and Language*, 51, 229-241.

Rudell, A. P., & Hua, J. (1996). The Recognition Potential and Word Priming. *Internationa Journal Of Neuroscience*, *87*(3-4), 225–240.

Sartori, L., Becchio, C., Bara, B. G., & Castiello, U. (2009). Does the intention to communicate affect action kinematics? *Consciousness and cognition*, *18*(3), 766–72.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking peopleThe role of the temporo-parietal junction in “theory of mind”. *NeuroImage*, *19*(4), 1835–1842.

Scalaidhe, S. P., Wilson, F. a, & Goldman-Rakic, P. S. (1999). Face-selective neurons during passive viewing and working memory performance of rhesus monkeys: evidence for intrinsic specialization of neuronal coding. *Cerebral cortex (New York, N.Y. : 1991)*, *9*(5), 459–75.

Schenk, T., & Zihl, J. (1997). Visual motion perception after brain damage: II. Deficits in form-from-motion perception. *Neuropsychologia*, *35*(9), 1299–310.

Schilbach, L., Wohlschlaeger, A. M., Kraemer, N. C., Newen, A., Shah, N. J., Fink, G. R., & Vogeley, K. (2006). Being with virtual others: Neural correlates of social interaction. *Neuropsychologia*, *44*(5), 718–30.

Schippers, M. B., Roebroeck, A., Renken, R., Nanetti, L., & Keysers, C. (2010). Mapping the information flow from one brain to another during gestural communication. *Procedeengs of National Academy of Science*. 107(20), 9388-9393

Schulte-Rüther, M., Markowitsch, H. J., Fink, G. R., & Piefke, M. (2007). Mirror neuron and theory of mind mechanisms involved in face-to-face interactions: a functional magnetic resonance imaging approach to empathy. *Journal of cognitive neuroscience*, *19*(8), 1354–72.

Schulte-Rüther, M., Markowitsch, H. J., Shah, N. J., Fink, G. R., & Piefke, M. (2008). Gender differences in brain networks supporting empathy. *NeuroImage*, *42*(1), 393–403.

Sebanz, N., Bekkering, H., & Knoblich, G. (2006). Joint action: bodies and minds moving together. *Trends in cognitive sciences*, *10*(2), 70–6.

Shultz, S., Vouloumanos, A., & Pelphrey, K. (2012). The superior temporal sulcus differentiates communicative and noncommunicative auditory signals. *Journal of cognitive neuroscience*, *24*(5), 1224–32.

Sitnikova, T., Holcomb, P. J., Kiyonaga, K. a, & Kuperberg, G. R. (2008). Two neurocognitive mechanisms of semantic integration during the comprehension of visual real-world events. *Journal of cognitive neuroscience*, *20*(11), 2037–57.

Sitnikova, T., Kuperberg, G., & Holcomb, P. J. (2003). Semantic integration in videos of real-world events: an electrophysiological investigation. *Psychophysiology*, *40*(1), 160–4.

Spunt, R. P., Satpute, A. B., & Lieberman, M. D. (2011). Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. *Journal of cognitive neuroscience*, *23*(1), 63–74.

Stekelenburg, J. J., & Ca, B. D. G. (2004). The neural correlates of perceiving human bodies : an ERP study on the body-inversion effect, *15*(5), 9–12.

Takahashi, H., Kato, M., Sassa, T., Shibuya, T., Koeda, M., Yahata, N., Matsuura, M., et al. (2010). Functional deficits in the extrastriate body area during observation of sports-related actions in schizophrenia. *Schizophrenia bulletin*, *36*(3), 642–7.

Thayer, J. F., & Johnsen, B. H. (2000). Sex differences in judgement of facial affect : A multivariate analysis of recognition errors, 243–246.

Thierry, G., Pegna, A. J., Dodds, C., Roberts, M., Basan, S., & Downing, P. (2006). An event-related potential component sensitive to images of the human body. *NeuroImage*, *32*(2), 871–9.

Troje, N. F. (2002). Decomposing biological motion: a framework for analysis and synthesis of human gait patterns. *Journal of vision*, *2*(5), 371–87.

Turella, L., Tubaldi, F., Erb, M., Grodd, W., & Castiello, U. (2012). Object presence modulates activity within the somatosensory component of the action observation network. *Cerebral cortex (New York, N.Y. : 1991)*, *22*(3), 668–79.

Urgesi, C., Moro, V., Candidi, M., Aglioti, S. M., Neurologiche, S., Umana, F., Verona, I.-, et al. (2006). Mapping Implied Body Actions in the Human Motor System, *26*(30), 7942–7949.

Vaina, L. M., Lemay, M., Bienfang, D. C., Choi, A. Y., & Nakayama, K. (1990). Intact “biological motion” and “structure from motion” perception in a patient with impaired motion mechanisms: a case study. *Visual neuroscience*, *5*(4), 353–369.

Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Human brain mapping*, *30*(3), 829–58.

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *NeuroImage*, *48*(3), 564–84.

Vander Wyk, B. C., Voos, A., & Pelphrey, K. a. (2012). Action representation in the superior temporal sulcus in children and adults: an fMRI study. *Developmental cognitive neuroscience*, *2*(4), 409–16.

Vogt, B. a, Vogt, L., & Laureys, S. (2006). Cytology and functionally correlated circuits of human posterior cingulate areas. *NeuroImage*, *29*(2), 452–66.

Vouloumanos, a, Kiehl, K. a, Werker, J. F., & Liddle, P. F. (2001). Detection of sounds in the auditory stream: event-related fMRI evidence for differential activation to speech and nonspeech. *Journal of cognitive neuroscience*, *13*(7), 994–1005.

Walter, H., Adenzato, M., Ciaramidaro, A., Enrici, I., Pia, L., & Bara, B. G. (2004). Understanding intentions in social interaction: the role of the anterior paracingulate cortex. *Journal of cognitive neuroscience*, *16*(10), 1854–63.

West, W. C., & Holcomb, P. J. (2002). Event-related potentials during discourse-level semantic integration of complex pictures. *Cognitive Brain Research*, *13*, 363–375.

Whiten, A., & Byrne, R. W. (1988). Tactical deception in primates. *Behavioral and Brain Sciences*, *11*(02).