Dealing with others: investigations on automatic and controlled processes in Social Cognitive Neuroscience.

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Abstract

Human beings are social animals. By living in society with other individuals, the number of social stimuli is due to be higher than when living alone. Thus, correctly and efficiently processing, and adapting to, those stimuli means increased fitness to the environment, and, as such, increased survivability and gene propagation. Ultimately, evolutionary success.

Social cognitive neuroscience addresses the processes that let individuals interpret their own behavior and others': how and what individual think about conspecifics. Both processes that aim at making sense of the social environment and those that aim at adapting the behavior to the social environment are aimed at obtaining the best possible fitness to the environment. However, some processes occur automatically under certain conditions, out of the individual awareness, while others are generated and carried on intentionally. In this work, I explore automatic and controlled processes in action perception and emotion regulation, two cognitive functions that aim at making sense of the social environment and adapting the behaviour to it. I heavily draw from the methods of neuroscience by using tools such as transcranial magnetic stimulation, electromyography and electrocardiography that have only recently been introduced in social cognition studies. Finally, I discuss theoretically these results in light of possible implementations in educational videogames as the new medium that may be able to create the optimal learning environment.

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Social Cognitive Neuroscience

1.1 Neuroscience and the social domain

It is known that the size of the neocortex, the part of the mammalian brain with the most recent phylogenetic evolution, correlates with the size of the social group in primates (Dunbar, 1992). Theories for the link between brain size and social group size currently favour social factors as the trigger of evolutionary development, such as pairbonding (Dunbar & Shultz, 2007). An increase in social group determines an increase in the ratio between the number of social and non-social stimuli. As such, the social brain needs to correctly and efficiently process these stimuli and increase the organism fitness to the environment, gaining survivability and better chance for gene propagation. Ultimately, evolutionary success.

Historically, philosophy has determined whether social stimuli were anything different from non-social stimuli, but recent neuroscientific discoveries seem to draw the line and clearly suggest that the social domain is, indeed, special.

1.2 Social is special

A long lasting belief about brain functions is that, in the social domain, it processes stimuli with more depth. This belief arose while interpreting the results of experiments that contrasted social *vs.* non-social tasks. In a classical behavioural paradigm used in social psychology that seemed to initially support this interpretation, the subjects read some utterances in two conditions: in one, they had the explicit goal of remembering the passages for a subsequent test, while, in the other, they had to form an impression of the protagonist, with no later test planned. However, experimenters had different plans: they tested subject’s memory of the utterances after both conditions. The results were surprising: even tough in the second condition subjects weren’t informed about the test, they performed better than subjects in the first condition (Hamilton, Katz, & Leirer, 1980). The general consensus upon the interpretation of this result was that the encoding of social information was deeper than the encoding of non-social information. However, more recent development in neuroscientific methods of inquiry led to a huge contributes in reversing this argument: indeed, when the same paradigm was used while inside a functional magnetic resonance imaging (fMRI) scanner, it was found that remembering the utterances and trying to form a social impression of the protagonist were two tasks that lit up different regions in the brain (Mitchell, Macrae, & Banaji, 2004). This result means that those tasks, being underpinned by different neural substrates, are qualitatively different (i.e., they are different in their nature) rather than quantitatively (i.e., different in the magnitude of a shared dimension).

The contributes of cognitive neuroscience to social psychology in the last few decades allowed scientists to disentangle previous constructs by looking at dissociated brain underpinning of processes’ components. Scholars have found that there are distinct areas of the brain in which neurons fire exclusively or preferentially for social stimuli or events, such as faces (e.g., Kanwisher, McDermott, & Chun, 1997), bodies (e.g., Downing, Jiang, Shuman, & Kanwisher, 2001), beliefs about other’s mental states (e.g., Hynes, Baird, & Grafton, 2006), other’s actions (e.g., Cattaneo & Rizzolatti, 2009), other’s trustworthiness (e.g., Adolphs, Tranel, & Damasio, 1998), sense of agency (e.g., Lau, Rogers, Haggard, & Passingham, 2004), fairness in interaction (e.g., de Quervain et al., 2004), implicit attitudes (e.g., Phelps et al., 2000) and so on. Moreover, it has been found that a resting brain is set by default on the social areas. All these results suggest that indeed the social is special for the human beings.

1.3 Defining Social Cognitive Neuroscience

Social cognitive neuroscience refers to the study of the processes that subserve perceiving, processing, understanding, storing and adapting to the information about conspecifics by means of using tools from cognitive psychology and neuroscience. The term was first used in a conference in 2001 at University of California, Los Angeles, in which talks about stereotyping, self-control, emotion, imitation, social interaction and theory of mind were held (Lieberman, 2007). Of course, studies that led to understanding neurocognitive mechanism in the social domain have already been done in the decade before, but it was at that point that the discipline was granted its own identity. A Google search with the terms “social cognitive neuroscience” returned 6 hits in 2001, while, at the moment of this writing, Google returns more than one million hits. What sets apart social cognitive neuroscience from social psychology is the methods of inquiry. Indeed, while social psychology already transformed itself on the cognitive revolution, social cognitive neuroscience already uses cognitive tools, but, additionally, borrows neuroscientific tools as well.

1.4 Methods in Social Cognitive Neuroscience

Primarily, the neuroscientific methods used in Social Cognitive Neuroscience are functional magnetic resonance imaging (fMRI), positron emission tomography (PET) , event-related potentials (ERP), lesion studies and transcranial magnetic stimulation (TMS). In PET, subjects inhale or are injected with a radioactive tracer, the emissions of which can be detected by the scanner. Depending on the distribution of the radioactive tracer in the brain, a different functioning state of the brain can be inferred. PET temporal/spatial resolution is about one minute/one cubic centimeter. Its most important feature is that more than one kind of molecule can be targeted, and as such more than just blood diffusion in the brain can be studied. fMRI largely supplanted PET for scientific studies because it has better temporal/spatial resolution of 1 to 2 seconds/3 mm^3 and for the fact that it is noninvasive: indeed, the scanner traces oxygen in the blood by taking advantage of magnetic proprieties of the oxygenated blood, on the premise that blood in active brain areas is more oxygenated than in inactive areas. ERP studies use electroencephalography electrodes placed over the scalp to detect brain electrical activity. ERP has excellent temporal resolution (milliseconds), but poor spatial resolution, and thus is used to study the time course of brain activity when following a stimulus or a response. In lesion studies, individuals with brain damage to different areas are examined and the contribute to each region to psychological functions is inferred. Differently from neuroimaging techniques (PET and fMRI), in lesion studies causal relationships can be inferred, whereas in neuroimaging studies only localization can be performed. TMS is a technique with which electromagnetic pulses are delivered on the scalp, making neurons of specific areas of the neocortex fire to different goals: by making neurons of a specific area fire repeatedly until they stop operating efficiently, the functioning of that area is interefered with for several minutes; by targeting specific areas such as the motor cortex, an event-related potential is produced and its outcome in a different region can be measured, such as muscular activity in the corresponding muscle; by stimulating an area at different times after the presentation of a stimulus and measuring the functional outcome of that area, the time course of the stimulus processing can studied; and so on.

1.5 Domains of Social Cognitive Neuroscience

Social Cognitive Neuroscience operates on three levels of analysis: i) social, encompassing social and emotional stimuli, experiences, behaviors ii) cognitive, encompassing the information processes mechanisms, and iii) neural, encompassing the brain and neural basis. In contrast, social psychology operates mainly on social and cognitive levels, while cognitive neuroscience operates mainly on cognitive and neural. Social cognitive neuroscience draws heavily on social psychology for theories, but the last decade and half proved that new theories can emerge in this field even with no precursor in social psychology. Indeed, a longstanding distinction between automatic and controlled processes hypothesized in social psychology was confirmed by social cognitive neuroscience; however, in a review of the social cognitive neuroscience contributes, Lieberman (2007) suggested that data-driven evidence for a novel neurocognitive core-processing distinction with no precursor in social psychology has been found. As such, social cognitive neuroscience can be applied in different domains that are cut across by some core-processing distinctions. Indeed, the domains of social cognitive neuroscience are (Lieberman, 2007):

- Understanding others
- Understanding oneself
- Self-regulation
- Processes that occur between self and others (social environment)

and some core-processing distinction that cuts across them are:

- Automatic *vs.* controlled processes
- Internally-focused *vs.* externally-focused processes

Lieberman describes each domain as follows.

Understanding others

Understanding other people means understanding that others aren’t just physical objects in the world, but have minds and internal mental states. Representing in one’s mind the psychological state of others, or their psychological traits (theories of mind) and the phenomenon of empathy are ways of knowing others’ internal states.

Understanding oneself

The nature of the self is elusive. We don’t know if our self is developed by internalizing others’ opinions on us or if it is a secluded entity. Social cognitive neuroscience may shed light on (and already contributed to the knowledge of) the nature of the self and its development. Visual self-recognition, perceiving agency, reflecting on one’s current or past experience or self-concept are processes that bring one to make sense of its own self.

Self-regulation

Self-regulation allows one to act in accordance to social contexts, needs, short- and long-term goals instead of responding in a reflex-like impulse-driven emotional way. Impulse control and reappraisal of emotional events are ways to regulate the behaviour and act more in accordance to the social environment, adapting to its pressures and features.

Processes that occur between self and others (social environment)

The last domain encompasses all the processes that can't be clearly divided into understanding *vs.* regulating or self *vs.* others. As such, attitudes and prejudice can't be studied without referring to both the concepts that one retains and the perception of the other, as attitude change and prejudice regulation can't be studied without referring to both understanding of the other and self-regulation. Similarly, but in a more complex way that will be addressed in the second chapter, the study of how we understand other's actions needs to both address the self and the other and the understanding and regulation. Finally, a third subdomain is the social cooperation, in which morality, trustiness, fairness are studied and in which no understanding *vs.* regulating or self *vs.* others distinction can be clearly made.

Across all these domains, patterns of neural activations emerge. The following are the proposed distinctions between patterns (Lieberman, 2007).

Internally-focused *vs.* externally focused processes

The first core-processing data-driven distinction across domains hypothesizes two different neurocognitive systems for internally-focused and externally-focused processes. Internally-focused refers to mental processes focused on one's or other's internal states (feelings, experience, etc.), while externally-focused refers to processes focused on one' or other's external states (visible, physical, etc.). Internally-focused processes are associated with a medial frontoparietal network, while externally-focused processes are associated with a lateral frontotemporoparietal network. The networks don't overlap, suggesting that the nature of the processes is distinct.

Automatic *vs.* controlled processes

Dual-process theories are ubiquitous in every field of psychology. Controlled processes are associated with awareness, intention, effort and the possibility of being interrupt, while automatic processes lack one or more of these features (Wegner & Bargh, 1998). Along with the long-lasting notion that these processes are supported by different systems, different neurocognitive systems have been found: automatic processes have been associated with neural activity in amygdala, basal ganglia, ventromedial prefrontal cortex, lateral temporal cortex and dorsal anterior cingulate cortex; in contrast, controlled processes have been associated with neural activity in lateral prefrontal cortex, medial prefrontal cortex, lateral parietal cortex, medial parietal cortex, medial temporal lobe and rostral anterior cingulate cortex. The neural areas correlating with controlled and automatic processes don't overlap, again suggesting that the nature of the processes is distinct.

1.6 The perception-behavior relationship, automated *vs.* controlled processes and the purpose of this thesis

Perception appears superficially to be aimed at understanding the world. However, evolutionary studies highlights many mechanisms in various animal species that directly connect perception and action. Interestingly, in the same species, different direct perception-action mechanisms can be disrupted independently, suggesting that the understanding of the environment is not important inasmuch the behavior remains functional (Dijksterhuis & Bargh, 2001). It is generally accepted now that perception leads to action. The link, however, seems to be more complex than the traditional thesis, such as behaviorists' (Watson, 1913) or Gibson's (1977), that stimuli directly suggest the appropriate response through a direct link or through specific perceivable features. On the contrary, in humans perception does lead to not obligatory actions, leading to great flexibility. Indeed, it is possible that our brain is built in such a way that perception leads to action tendencies but not to overt responses by itself. Motivation could be a factor in translating tendency to overt action, acting as a facilitator. Or it can be that perception is sufficient by itself to create overt responses, but these are inhibited, preventing them to occur. This second possibility is more evolutionary plausible, since inhibitory or modulating brain parts can be added without modules being thrown away, while the first needs to account for modules ceasing to exist (see Dijksterhuis & Bargh, 2001 for further details on this discussion).

Within current notions of perception-behavior relations, it seems particularly interesting the above-mentioned across-domains distinction between automatic and controlled processes. Indeed, by exploring both automatic processes and controlled processes both unintentional and intentional components are dealt with. As such, the interaction between automatic unintentional responses to the environment and intentional actions can be assessed.

In this thesis I contrast automatic and controlled processes in social perception and adaptation within a social cognitive neuroscientific framework. In particular, in the social perception chapter, I'll focus on motor resonance *vs.* mentalized action perception as, respectively, automatic *vs.* controlled processes; in the social adaptation chapter, I'll focus on affective reaction *vs.* emotion regulation as, respectively, automatic *vs.* controlled processes. As such, I hope to shed some light on the interaction between unintentional and intentional domains in dealing with others.

In the second chapter, my research questions targets a specific problem in how we understand the action performed by others, while, in the third chapter, other my purpose is to address the problem of how we regulate our emotional response to the social environment. Both are research questions that address how we deal with others, by understanding them and regulating our behavior to act better with them. In both cases, I intentionally keep a basic research profile in order to be as much independent from putative applications as possible, as to avoid being influenced by them in the analysis and in the interpretation of the results. However, the results of both studies can be used to understand social dynamics that seem to me to have a possible immediate impact in multimedia learning and in education. In particular, I'll focus, in the fourth chapter, on how educational videogames can benefit from my results.

2

Automatic and controlled mechanisms of action understanding in social perception

2.1 Introduction to current action perception theory

Gestures understanding has traditionally been considered the results of the integration of the visual elements and the interaction of this outcome with the conceptual system (Gallese, Keysers, & Rizzolatti, 2004). However, the relatively recent discovery of the so called “mirror neurons” (G Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) has revolutionized the theories and approaches to conspecific’s action perception and understanding. This set of neurons, originally found in the F5 area of the monkey premotor cortex, have both motor and sensory proprieties: indeed, they discharge when the monkey perform a goal-oriented action as well as when he or she looks at another monkey performing the same (G Rizzolatti et al., 1996). This finding suggests that these neurons directly link observation with execution: indeed, the observer understands the action because it knows the outcome when he or she performs it (Gallese et al., 2004). As such, a new approach to the understanding of actions made by others involving motor processes has been introduced and adopted.

2.1.1 Proprieties of the mirror neurons in the monkey

In the monkey, mirror neurons have been found to discharge also in absence of the visual information: indeed, more than half of the recorded neurons responded when the monkey knew what action was happening behind an occluding screen (Umiltà et al., 2001). Moreover, a fraction of neurons also responds to the sounds associated with an action when no visual information is available (Kohler et al., 2002). Each mirror neuron doesn’t discriminate between differently performed actions of the same category (e.g., grasping acts), but discriminates very well between categories, and as such they serve a role of action recognition, in which both the processing of the agent and the goal is needed. These results corroborate the theory that sensory features of the perceived action allow for understanding by activating a motor representation.

2.1.2 Mirror neurons system in humans

In humans, the mirror neuron system (MNS) is composed by the rostral part of the inferior parietal lobule, the *pars opercularis* of the inferior frontal gyrus (IFG) and the nearby region of the premotor cortex (G Rizzolatti, Fogassi, & Gallese, 2001). In comparison with the monkey MNS, the human MNS responds to a wider variety of stimuli. While the presence of the object that is the target of the action is needed for activating mirror neurons in the monkey, human mirror neurons discharge also in the its absence, meaning that mimed, intransitive and meaningless actions all trigger motor representations in human MNS (see for example Buccino et al., 2001). Together with another class of neurons that fire in the presence of the physical object of the action without any action performed, called the canonical neurons and also present in the monkey (see for example Gallese & Goldman, 1998), MNS accounts for a direct understanding of the action and its goals in terms of motor representation.

2.1.3 Simulation theory and the mind-reading concept

By triggering motor representations of specific actions in the premotor cortex, mirror neurons perform a sort of covert simulation of the observed action, thus mimicking the brain activations of the observed individual. As such, a simulation theory was developed (Gallese & Goldman, 1998). According to this theory, by mimicking the brain state of the observed conspecific, one can predict the outcomes of the ongoing actions as well as “retrodict” the intentions for those same actions, performing a sort of “mind-reading”: a direct, non mentalized, understanding of the mental state of another person (Gallese & Goldman, 1998). However, a more parsimonious theory was later introduced, in which a more complex role of the MNS was recognized, ranging from motor act recognition to intention attribution (Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005). Both these versions of the theory were criticized, as intention is a concept on which there is little agreement: indeed, an intentional act might be considered one produced by an intentional agent, or one produced as part of a plan, and so on (Borg, 2007). However, it is crucial that MNS motor coding includes not only the description of the motor act, but also its goal-relatedness, however the level of intentionality involved is (Sinigaglia, 2008).

2.1.4 Common coding hypothesis, visuo-perceptual and visuo-motor priming

Common coding hypotheses is the hypothesis that claim that perceived and executed actions are represented in a common code (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997; Schütz-Bosbach & Prinz, 2007), suggesting a bidirectional, causal link between perceptual and motor processing (Avenanti, Candidi, & Urgesi, 2013; Avenanti & Urgesi, 2011). In keeping with these hypotheses, several studies have shown that action execution induces short-term (Casile & Giese, 2006; Cattaneo & Barchiesi, 2011; Hamilton, Wolpert, Frith, & Grafton, 2006) and long-lasting (Abernethy, Zawi, & Jackson, 2008; Aglioti, Cesari, Romani, & Urgesi, 2008; Urgesi, Savonitto, Fabbro, & Aglioti, 2012) effects on the way others’ actions are perceived. On the other hand, there is also evidence that action perception influences the execution of one’s own motor actions. Indeed, observing a moving body parts facilitates not only the subsequent perception of similar actions (visuo-perceptual priming; Costantini, Committeri & Galati, 2008; Güldenpenning, Koester, Kunde, Matthias, & Schack, 2011), but also the execution of congruent as compared with incongruent body movements (visuo-motor priming or automatic imitation; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Heyes, 2011; Kilner, Paulignan, & Blakemore, 2003; Stürmer, Aschersleben, & Prinz, 2000). The visuo-motor action priming effect is found when viewing either dynamic action sequences (Brass et al., 2000; Brass, Bekkering, & Prinz, 2001; Kilner et al., 2003; Stürmer et al., 2000) or single frames that imply actions (Brass et al., 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Craighero, Fadiga, & Rizzolatti, 1999; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Vogt, Taylor, & Hopkins, 2003). Furthermore, the effect is considered automatic because it is independent from the observer's intent to imitate or even to process the action stimulus (Heyes, 2011) and it is not modulated by the predictability of the prime-cue association (e.g., manipulating the proportion of congruent and incongruent trials; Hogeveen & Obhi, 2013).

2.1.5 Direct evidence in favor of the common-coding hypothesis

Direct evidence of shared neural representations of observed and executed actions comes from recent neuroimaging studies that have documented the adaptation of the neural activity in the inferior parietal cortex (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008) and in the inferior frontal gyrus (Kilner, Neal, Weiskopf, Friston, & Frith, 2009) after repeated observations as well as consecutive observation and execution (or vice versa) of the same action. Thus, previously seen actions affect not only the perceptual representation of observed actions, but also the motor representation of executed actions. The overlap between the neural populations involved in unimodal visuo-perceptual and cross-modal visuo-motor adaptation effects is in keeping with the predictions of common-coding hypotheses, which point to a common mechanism underlying visuo-perceptual (perceptual) and visuo-motor (i.e., automatic imitation) action priming.

Moreover, visuo-motor priming can be investigated by applying single-pulse transcranial magnetic stimulation (TMS) over the primary motor cortex in order to evoke a neuron discharge that produces a motor response measurable by electromyography (EMG). Indeed, it is assumed that the output of the motor cortex is a measure of the parieto-premotor mirror circuit, as suggested by studies adopting mixed tecniques like single pulse TMS over motor cortex with rTMS over premotor cortex (Avenanti, Bolognini, Maravita, & Aglioti, 2007) or in studies using dual-coil TMS (Catmur & Heyes, 2011). As such, action observation triggers a strictly congruent, muscle-specific facilitation of corticospinal excitability that can be tested by using single-pulse TMS over motor-cortex (see for a review Naish, Houston-Price, Bremner, & Holmes, 2014).

2.1.6 Automaticity of visuo-motor priming

A typical behavioral paradigm to test automatic imitation requires participants to provide finger responses that are congruent or not with the observed finger movements (e.g., Brass et al., 2000). The responses to congruent movements are faster than those to incongruent movements, suggesting the observer is automatically engaged in the simulation of the observed movement, although processing the action stimulus is not explicitly required by the task and is even detrimental for task performance (Brass et al., 2000). Further studies (Bertenthal, Longo, & Kosobud, 2006; Brass et al., 2001; Catmur & Heyes, 2011; Jiménez et al., 2012; Wiggett, Downing, & Tipper, 2012) demonstrated that automatic imitation is not related to mapping the spatial compatibility between the side of observed and executed movements (Simon, Hinrichs, & Craft, 1970) , but reflects genuine processing of the action depicted in task-relevant or task-irrelevant visual stimuli; such perceptual action representation converges onto the motor representation of the executed response (Catmur and Heyes, 2011). It is worth noting that there is evidence that both motor facilitation, at the neurophysiological level, and visuomotor interference effects, at the behavioral level, are modulated by attention. For example, the electrophysiological indices of motor activation during action observation (i.e., suppression of beta band recorded from central sites) are amplified by the increasing task demands of active imitation or counting task with respect to passive observation, but they are present in all conditions (Muthukumaraswamy & Singh, 2008). In a similar vein, visuomotor interference effects are attenuated by the activation of self-related processing by mirror self-observation or judgment of evaluative personal statements, but are still present in all conditions (Spengler, von Cramon, & Brass, 2010).

In keeping with studies that manipulate the conditions under which automatic imitation effects occur (Heyes, 2011), the facilitation of corticospinal excitability in response to observed actions takes place automatically, i.e. in every instance in which a biological movement is perceived independently from the presence or absence of executive control, cognitive effort, intentionality, strategies or focus of attention of the observer (Bargh, Schwader, Hailey, Dyer, & Boothby, 2012). Although these top-down processes are not necessary for motor resonance to occur, they can modulate its intensity, increasing or attenuating its manifestations. Moreover, it occurs also during passive viewing of static images that imply body actions (Avenanti et al., 2013; Urgesi et al., 2010; Urgesi, Moro, Candidi, & Aglioti, 2006) and independently of the spatial compatibility between the observed and the executed movements (Alaerts, Aggelpoel, Swinnen, & Wenderoth, 2009; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006).

2.1.7 Conscious perception

Although mirror-like motor facilitation during action observation was initially thought to imply covert imitation, it has been demonstrated that it takes place independently of explicit instruction to rehearse the actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) and to be modulated by subtle kinematic differences in the movement kinematics even when these differences cannot be recognized by the observers (Sartori, Bucchioni, & Castiello, 2012). The visuo-motor interference effects have been demonstrated to occur even if the observer ignores the observed action stimulus while performing a different task-relevant action (Vainio, Tucker, & Ellis, 2007). Furthermore, they are not suppressed by attentional modulation of the predictability of the prime-cue association obtained by varying the proportion of congruent and incongruent trials (Hogeveen & Obhi, 2013).

It is widely known that a stimulus can influence (prime) subsequent perception and motor response even when it is not consciously perceived (Sumner, 2007). Varying the visibility of a stimulus has been widely used to manipulate perceptual awareness, as indexed by the observer’s ability to report the perception when he/she is prompted to do so (Van den Bussche, Van den Noortgate, & Reynvoet, 2009). For example, in the masked priming paradigm a prime stimulus is shortly presented and its visibility is further reduced by presenting a mask (typically a scrambled version of the same stimulus) before and/or after its presentation (respectively, forward and backward masking). After a very short interval from this “sandwich” masked prime presentation, the target stimulus is presented; results reveal better processing of the target when it is related to the prime with respect to a neutral condition in which the prime and the target are not related (Sumner, 2007). Such facilitation reflects memory processes that keep track of past perceptual experiences facilitating the perception of familiar attributes (Tulving & Schacter, 1990). The priming effect occurs at many different levels of information processing, depending on the features of stimuli and tasks (see Kristjánsson & Campana, 2010 for a review), and may regard both the perceptual similarity between the prime and the target or their association with the same motor response. The effects related to the perceptual attributes of the stimuli depend on the perceptual representation system and seem to be driven in a bottom-up manner (Campana, Cowey, & Walsh, 2002; Silvanto & Soto, 2012; Tulving & Schacter, 1990). On the other hand, the effects related to the association of the prime and target to the same motor response seem to depend on motor response selection processes (Eimer & Schlaghecken, 1998; 2003).

It has been argued that phenomenal experience is not a direct reflection of perceptual processes, and that the effect of consciously perceived stimuli may be different than that of unconsciously perceived stimuli (see for example Merikle, 1998 for a review).

For instance, masked visual presentations of prime stimuli that are associated with a lateralized motor response, including hand postures (Vainio & Mustonen, 2011), may affect the execution of incongruent versus congruent responses and modulate motor cortex activity (Dehaene, Naccache, Le Clec'H, Koechlin, & Mueller, 1998; Théoret, Halligan, Kobayashi, Merabet, & Pascual-Leone, 2004; D'Ostilio & Garraux, 2012). However, these masked visuomotor prime effects strictly depend on the selection of the motor response concurrently required by the explicit task (Eimer & Schlaghecken, 1998, 2003) and may reflect the influence of the masked primes on action execution processes rather than motor resonance representations.

On the other hand, automatic motor responses during passive observation of emotional face and body expressions have been reported even when stimuli are presented to the blind hemifield of hemianopic patients (Tamietto, Castelli, Vighetti, Perozzo, Geminiani, & Weiskrantz, 2009; Van den Stock, Tamietto, Sorger, Pichon, Grézes, & De Gelder, 2011) or to healthy individuals with masking procedures (Dimberg, Thunberg, & Elmehed, 2000). However, such automatic motor responses may be specific for stimuli with emotional valence and may not be involved in non-emotional action perception (Tamietto & De Gelder, 2010). In fact, mirror-like, muscle-specific facilitation of corticospinal excitability during observation of grasping actions was attenuated by presentation of the moving finger in partially shadowed illumination conditions (Sartori & Castiello, 2012); the grasping act, however, was still visible in the shadowed illumination condition and mirror-like motor facilitation was attenuated but not extinguished, thus leaving unquestioned whether motor resonance requires perceptual awareness.

2.2 Research questions

According to the mentioned findings and in light of the uncertainties regarding the need for awareness of the percept, my interest focused on whether mirror-like facilitation as a system for direct understanding of social intention required mentalization of the observed actions. Indeed, in everyday life, we simultaneously deal with the actions of numerous agents that we must flexibly imitate, complement or react to (Sartori, Bucchioni, & Castiello, 2013). Optimal interactions in such a crowded social world require fast, accurate and dynamic representations of others' actions, but due to the raw amount of stimuli it seems unattainable to mentalize every single action we attend to. As such, in the first part of this chapter I will deal with behavioral investigations on how we perceive non-mentalized actions by means of subliminal presentation of stimuli. This part consists in five experiments in which my colleagues and I varied the visibility of still implied actions stimuli in a masked priming paradigm. The second part of this chapter I will deal with a neurocognitive investigation of the same topic.

2.3 Unconscious processing of body actions primes subsequent action perception but not motor execution

In this study, published on Journal of experimental psychology: Human perception and performance (Mele, Mattiassi, & Urgesi, 2014), we used a masked priming paradigm to investigate how the perceptual and motor representations of actions are affected by reducing the prime visibility and by reversing the spatial and action compatibility between the prime and the probe. We presented masked prime stimuli depicting a still hand or a finger-abduction implied action in conditions of low or high visibility; the prime was followed by the presentation of a still or implied-action probe hand. We first tested the effects of low and high visibility action primes on the detection of implied actions (Experiment 1) and on the discrimination of specific finger movements (Experiment 2) in the probe hand. Thus, we tested whether visuo-perceptual action priming effects occur independently of perceptual awareness. As the perception of visual attributes, such as color and shape, facilitates the processing of target stimuli that share the same attributes (Campana et al., 2002; Silvanto & Soto, 2012; Tulving & Schacter, 1990), we expected that also implied-action primes should affect the processing of implied–action probes in conditions of low visibility. Furthermore, the action priming effects should be independent of the spatial compatibility between the side of the space occupied by the prime and probe finger movements. Therefore, in Experiment 2 we tested the effects of spatial compatibility on visuo-perceptual action priming by presenting the prime and probe hands with the fingers pointing upward or downward. This way, we opposed the correspondence between the moving finger and the space occupied by the movements in the prime and probe hand stimuli, disentangling the role of action congruence and spatial compatibility in both low and high prime visibility conditions.

The main hypothesis of this study was derived from common-coding views of action observation and action execution (Hommel et al. 2001; Prinz, 1997). According to this hypothesis, a common representation is involved in the influence of action stimuli on subsequent action perception and execution. Thus, if an implied action hand presented in conditions of low-visibility influences subsequent action perception (visuo-perceptual priming), it should have the same effect on action execution (visuo-motor priming). In Experiment 3, we used a forward and backward dynamic masking procedure and successfully prevented the conscious perception of prime stimuli depicting a still hand or index or little finger abductions. The masked prime presentation was followed by the presentation of a still or implied-action probe hand, to which participants responded performing congruent or incongruent finger movements to indicate whether the probe hand implied or not a finger movement. We tested whether the reduction of prime visibility affected in the same way its effects on the perception of the probe hand (visuo-perceptual priming) and on the preparation of manual responses that were congruent or incongruent with the observed finger movements (visuo-motor priming). Finally, in Experiment 4 and 5 we tested the masked visuo-motor action priming effects while participants executed index or little finger movements in response to neutral probes (colored squares) preceded by a prime hand implying a congruent or incongruent movement. Therefore, this paradigm allowed us to test the modulation of reducing the visibility of the prime on standard automatic imitation effects.

Overall, the results of the five experiments provided evidence that action primes affected subsequent action perception also when they are not consciously perceived by the observer. This visuo-perceptual action priming effect was independent of the spatial compatibility between the moving finger in the two perceptual stimuli and it rather reflected genuine action-specific coding. Conversely, action primes presented in conditions of low visibility did not affect motor preparation and execution processes, since congruent or incongruent movements were executed the same way. A clear visuo-motor effect was obtained only when the priming actions were presented in conditions of high visibility, thus suggesting that visuo-motor action priming requires perceptual awareness.

2.3.1 Experiment 1

In Experiment 1, we tested whether the masked presentation of a static frame implying hand action influences the processing of the action implied by a consciously perceived probe hand. We also tested whether such perceptual influence is dependent on the specific processing participants are engaged with during probe observation. We thus compared the visuo-perceptual priming effects when participants were required to process the action implied by the probe hand (action task) or its morphology (form task). The prime and probe stimuli could depict a static hand or an implied-action hand. Furthermore, the prime was presented in conditions of low (17 ms duration) and high (50 ms duration) visibility. This way, we aimed to provide evidence of modulation of unconscious action processing on the visual representation of subsequently presented actions. We expected faster response for congruent than incongruent probe-prime pairs, independently of the visibility of the prime; the effect of action congruence, however, should be specific for the processing of body actions but not of body forms.

2.3.1.1 Methods

Participants. Twenty-three right-handed students (10 men) of the University of Udine (mean age=23.47, standard deviation=2.93) participated in the experiment and gave their written informed consent. All were native Italian speakers of Caucasian ethnicity (as the models depicted in the stimuli) and reported having normal or corrected-to-normal visual acuity. All participants were right-handed according to a standard handedness interview (Briggs & Nebes, 1975). Participants were unaware of the purposes of the study and were debriefed at the end of the experimental session. The procedures were approved by the Ethics Committee of the Scientific Institute (IRCCS) Eugenio Medea (Bosisio Parini, Como, Italy) and were in accordance with the guidelines of the Declaration of Helsinki.

Stimuli. Stimuli were color pictures of the right hand of 8 models (4 men) taken at rest or during maximal abduction of the index finger. The pictures were taken with a digital camera Sony® with a resolution of 10.1 megapixels at a distance of 30 cm in front of the hand. Lighting conditions were kept stable during picture taking. The pictures were acquired in rapid sequence (multi-shot mode) in order to capture different phases of real index finger abduction movements. The pictures were presented on a 60Hz LCD screen (resolution 1024×768 pixels) and subtended a 9.5°×12.7° region.

Procedure. Participants were administered two tasks, namely an action task and a form task. In both tasks the following masked priming paradigm was used (Fig. 1A): a picture of a still hand (sample) appeared on the screen for 250 ms and was followed by a scrambled version of the prime (forward mask) for 83 ms. Then, the prime hand appeared for 17 ms or 50 ms and was subsequently masked (backward mask); the duration of the backward mask could be 100 ms or 67 ms and depended on the duration of the prime, so that the sum of prime and backward mask duration was always 117 ms. Lastly, a third hand (probe) was presented for 250 ms and was followed by a blank screen. The prime and the probe stimuli could depict a still hand (still) or an abduction of the index finger (implied-action). In the action task, the sample, the prime and the probe depicted always the same model hand that could or could not imply index finger abduction. In the form task, the probe could depict the hand of the same individual or of two different individuals of the same gender; the implied-action was manipulated orthogonally to the identity of the model. Four 64-item blocks were presented, with alternating administration of the action and form tasks. In blocks 1 and 2, the prime was presented for 17 ms, thus below the threshold of conscious perception; in blocks 3 and 4, the prime was presented for 50 ms, thus above the threshold of conscious perception (Sandberg, Martin, Timmermans, Cleeremans, & Overgaard, 2011). Subjectively, the presentation of the sequence of forward mask, prime, and backward mask was experienced by the participants as a flickering of the mask. Participants were instructed to ignore the flickering of the mask and to focus on the sample and probe hands. They had to report as fast and accurately as possible whether they perceived or not a change in the visual appearance of the probe hand with respect to the sample hand and, specifically: 1) an index finger movement in the probe hand during the action task; 2) a change in the morphology of the hand in the form task. The two tasks were administered to compare visuo-perceptual action priming effects when the participants were explicitly asked to focus on action or form cues (Urgesi, Candidi, Ionta, & Aglioti, 2007). Participants provided their responses by pressing on a two-key response box with the right index and middle fingers (Fig. 1B), thus performing flexion movements different from those shown by the pictures. The order of the tasks and the assignment of response types to the two keys were counterbalanced across participants, thus also controlling for the correspondence between the finger abducted in the pictures and the finger used to report the presence of implied-action probes. The whole procedure lasted about 30 minutes. At the end of the experimental session participants were requested to retrospectively report on the subjective perception of the prime for each block, thus allowing us to establish whether the participants noticed the presentation of the prime. All participants reported that they did not see the prime in the 17 ms prime duration blocks and saw it in the 50 ms ones.

Data analysis. We calculated the individual Error Rates (ERs) and mean Reaction Times (RTs) for the correct responses of each experimental condition (16 trials per cell). Three participants had poor performance levels (ERs >than 40%) in the action task, pointing to lack of task compliance, and were excluded from the analysis; other two participants were excluded because they had more than 5% of anticipations (RTs < 120 ms). The final sample entered in the analysis consisted, thus, of 18 participants (half with the association of "moving" responses to index finger presses and "still" responses to middle finger presses and half with the opposite association). ERs and RTs data were entered into two four-way mixed Analyses of Variance (ANOVAs). The study used a 2×2×2 design with Key assignment as between-subject factor and with three repeated-measures variables: Task (action *vs.* form), Prime duration (low *vs.* high visibility), and Congruency (congruent *vs.* incongruent prime-probe pairs). All pair-wise comparisons were performed using the Newman-Keuls post-hoc sequential test, which reduces the size of the critical difference depending on the number of steps separating the ordered means; this procedure is optimal for testing in the same design effects that may have different sizes (Duncan, 1955; Dunnett, 1970; McHugh, 2011), as it was expected in our cases for low-visibility *vs.* high visibility conditions. A significance threshold of $P < 0.05$ was set for all statistical analyses. Effect sizes were estimated using the partial eta squared measure (ηp2). The data are reported as mean ± standard error of the mean (SEM).

2.3.1.2 Results

RTs. The ANOVA on RTs (Fig. 1C) revealed significant main effect of Congruency ($F_{1,16}=30.785$, $p < 0.001$, $\eta p2=0.658$): in general RTs for congruent trials (518.59 ±16.30 ms) were faster than RTs for incongruent trials (545.81 ± 17.60 ms). The main effect of the between-subjects factor Key ($F_{1,16} < 1$) and its two-way (all $F_{1,16} < 3.3$, $P >0.089$, $\eta p2 < 0.4$) and higher-order (all $F_{1,16} < 1.7$, P

>0.214, ηp2 < 0.1) interactions with the other variables were not significant. The 2-way interactions Prime duration × Congruency (F1,16=17.651, P=0.006, ηp2=0.524) and Task × Congruency (F1,16=9.493, P=0.007, ηp2=0.372) were significant and were further qualified by a significant 3-way interaction Prime duration × Task × Congruency (F1,16=6.072, P=0.025, ηp2=0.275). To explore the significant three-way interaction we ran two follow-up Prime duration × Congruency ANOVAs, one for each task. The ANOVA for the action task showed non-significant main effect of Prime duration (F1,17=3.288, P=0.087, ηp2=0.162), but significant main effect of Congruency (F1,17=63.895, P < 0.001, ηp2=0.79) and interaction Prime duration × Congruency (F1,17=52.478 P < 0.001, ηp2=0.755). Post-hoc comparisons indicated that RTs for congruent trials were faster than RTs for incongruent trials in both low- (P=0.01) and high-visibility (P < 0.001) conditions. Thus, in both visibility conditions the presentation of congruent prime-probe pairs facilitated the responses as compared with incongruent pairs. However, the RTs for the congruent trials of the high-visibility condition were faster than those for the congruent trials of the low-visibility condition (P < 0.001), while RTs for incongruent trials did not differ between the two visibility conditions (P=0.269). This result points to a stronger facilitation effect for the high- than low-visibility primes. The ANOVA on RTs in the form task revealed no main effects or interactions (all F1,17 < 2.25, P >0.152; ηp2 < 0.117), suggesting that the congruency between the prime and probe actions did not affect the performance of participants when they had to focus on the morphology of the hand.

ERs. Although ERs, in particular in the action task, were relatively low (Table 1), we tested whether the same pattern obtained for RTs was found for ERs. A two-way Prime duration × Congruency ANOVA was, thus, run on the ERs for each task. The ANOVA on ERs in the action task revealed a significant main effect of Congruency (F1,17=24.501, P < 0.001, ηp2=0.59), further qualified by a significant 2-way interaction (F1,17=11.713, P=0.003, ηp2=0.408). Post-hoc analyses indicated that, in the low-visibility condition, participants committed a comparable proportion of errors for congruent (7.66 ± 2.05%) and incongruent trials (12.44 ± 2.41%, P < 0.001); in contrast, in the high-visibility condition, they committed fewer errors in the congruent (3.61 ± 0.93%) than incongruent trials (12.44 ± 2.41%, P < 0.001). Thus, the analysis of ERs revealed that subliminal action primes did not affect the accuracy of participants in responding to congruent *vs.* incongruent prime-probe pairs. In contrast, the performance accuracy was affected when the prime was presented in conditions of high-visibility. The ANOVA on ERs in the form task revealed only a significant main effect of Prime duration (F1,17=22.75, P < 0.001, ηp2=0.572), with better performance for the high than low visibility condition.

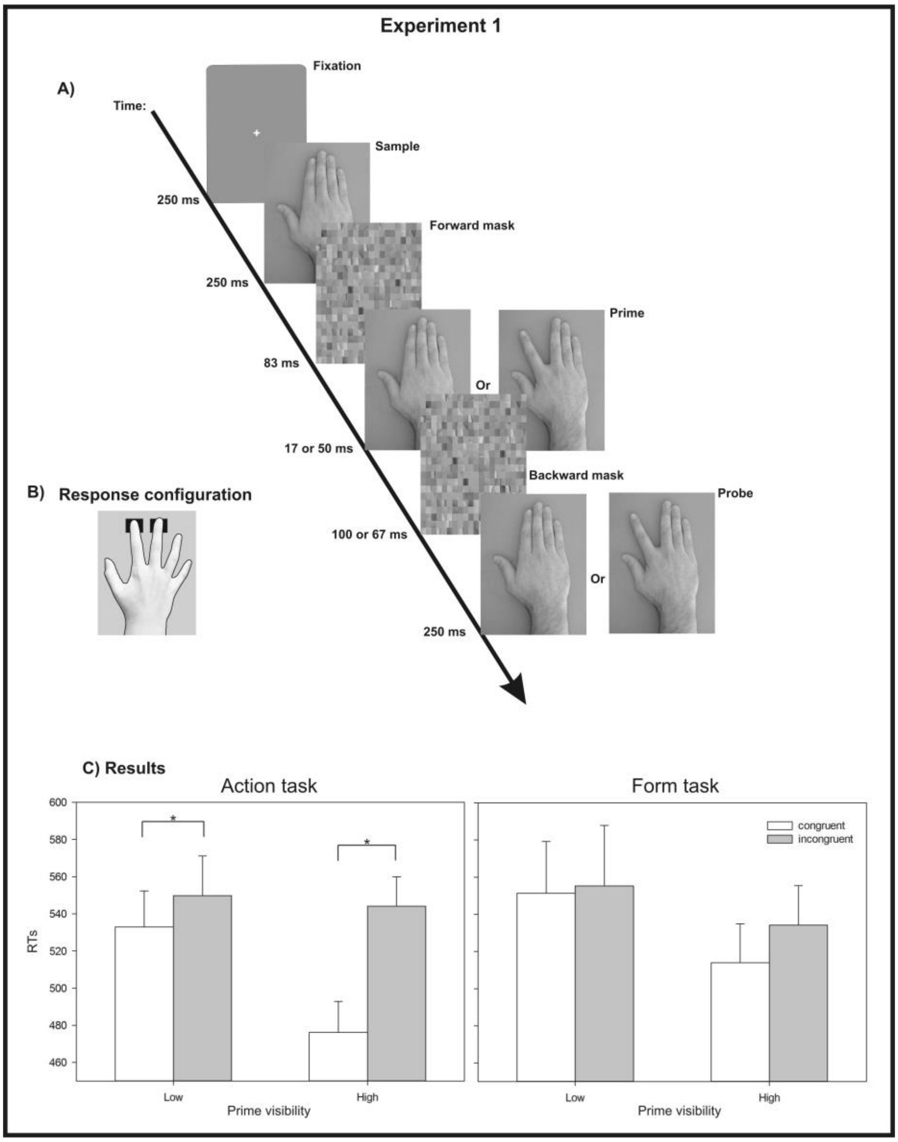


Figure 1. Trial structure (a), response configuration (b) and results (c) of experiment 1.

2.3.1.3 Discussion

The results of Experiment 1 showed that action primes can affect action perception not only when they are consciously perceived (high-visibility condition) but also when their presentation is completely unnoticed (low-visibility condition). This result can be interpreted at the perceptual level, since the action prime facilitated the perceptual processing of same stimulus probes (both static hands and both implied action hands) and is in line with the perceptual priming literature (Sumner, 2007; Tulving & Schacter, 1990). Importantly, however, the action priming effects were only obtained, independently of prime visibility, on the processing of body actions but not on the processing of body forms. The dissociation between the two tasks corroborates the action-specificity of the effects and is in keeping with the notion that the perceptual priming depends on the specific features of the stimuli and task (Kristjánsson & Campana, 2010).

It is worth noting that participants responded with the index and middle fingers, with random allocation of the key to the two responses; therefore, half of them responded to the observation of an index finger movement by moving the same finger. However, reversing the response-key association had no effects on the priming effects, probably because of the difference between the finger movements that were observed (abduction) and executed (finger flexion), which triggered the access to different action representations. This is in keeping with the findings that reducing the ideomotor compatibility between observed and executed actions hinders the automatic imitation effects (Brass et al., 2000).

In sum, Experiment 1 provided evidence of perceptual priming effects that were specific for the processing of actions and independent of the perceptual awareness of the participants and of the type of motor response being prepared. Three possible limitations, however, need to be addressed. First, congruent finger movements also occurred in the same portion of the space; therefore, spatial compatibility could explain the results. Second, since we used only one finger movement, we could not establish whether the prime representation contained general dynamic information (i.e., something is moving) which facilitated the detection of movements in subsequent stimuli, or whether it contained specific information on the moving finger. Finally, since we did not have a neutral condition, we could not determine whether the priming effects were related to facilitation for congruent stimuli or interference for incongruent stimuli or both. Experiment 2 was aimed at addressing these issues.

2.3.2 Experiment 2

In Experiment 2, we tested whether visuo-perceptual priming effects could be ascribed solely to action congruence or whether some contribution of the spatial compatibility between the location occupied by the moving finger in the prime and the probe should be considered. To this end, we changed the orientation of the hand to independently manipulate the compatibility between the identity of the moving finger and its spatial position in the prime and in the probe stimuli. The prime and the probe hands could be presented from the same perspective or different perspectives (with the finger pointing upward or downward; Fig. 2A), but they always depicted a right hand, thus ensuring that the two views recruited the same hand motor representation (Shmuelof & Zohary, 2006, 2008; Vainio & Mustonen, 2011). Additionally, we presented hand pictures depicting an index or a little finger abduction (Fig. 2B). We used upward and downward hands because the abduction of the index finger occurs in the left hemifield for the upward perspective and in the right hemifield for the downward perspective; the opposite holds true for the little finger abductions. We asked participants to report the moving finger by pressing one of two keys with the left or right thumbs (Fig., 2C). Therefore, participants used different fingers than those that were shown abducted in the stimuli; however, to control for any spatial compatibility effects between the side of the moving finger in the probe and the side of response, we counterbalanced between-participants the response-key association. In sum, the design was aimed at testing the relative effects of action and spatial compatibility between the prime and probe hands. Furthermore, using two finger movements, we were able to test whether the priming representations contained specific information on the action being performed (index *vs.* little finger movements) rather than a general representation of a dynamic stimulus (i.e., moving *vs.* not moving). Finally, whereas the probe could depict only a hand with the index or little finger abducted, the prime could show a hand with congruent or incongruent finger abduction or a still hand, thus allowing us to test both facilitation and interference priming effects with respect to the neutral, still-hand condition. We expected that viewing an implied-action prime should facilitate the discrimination of congruent probes and interfere with the discrimination of incongruent ones. Furthermore, both facilitation and interference effects should occur irrespective of the visibility of the prime (as in Experiment 1) and the spatial compatibility between the side of the space occupied by the two fingers (as in Catmur & Heyes, 2011).

2.3.2.1 Method

Participants. Twenty-eight students (14 females) of the University of Verona (mean age=26.78 years) participated in the experiment. All were native Italian speakers of Caucasian ethnicity, right handed, and reported having normal or corrected-to-normal visual acuity. No participants took part in the previous experiment and recruitment procedures were as in the previous experiment.

Stimuli. We used the digital pictures depicting the right hand of a new group of 8 models (4 females, aged 20-23 years). The models' hands were pictured in three positions: i) with maximum index finger abduction; ii) with maximum little finger abduction; and iii) still. To preserve the appearance of naturalistic movement, each picture was taken while the model was actually moving the finger. The same pictures were used in the two perspectives and upward and downward stimuli were obtained by vertically flipping the pictures (Fig. 2A). Light conditions were kept constant across the three images of each model and the remaining luminance differences were manually corrected using Corel Paint Shop Pro X (Corel Inc., Mountain View, CA, USA). Stimuli were presented with a 60Hz CRT monitor (resolution 1024×768 pixels) and subtended a 6°×8.5° region.

Procedure. Participants were seated at a distance of 57 cm from the computer screen while their head was restrained by means of a head-and-chin rest. As schematized in Figure 2B, the general procedure involved the presentation of a central luminous dot serving as fixation point for 250 ms; then a picture of a still hand (sample) appeared on the screen for 250 ms and was followed by the mask consisting of the scrambled version of the prime for 100 ms (forward mask); then the prime hand, which could be still or with the index or little finger abducted, appeared for 17 ms or 50 ms and was subsequently masked for 130 ms (backward mask); then, the probe hand, which could show either index or little finger abduction, was presented for 250 ms, to which a blank screen followed and remained on the screen until response or for a maximum of 1,500 ms. Responses were recorded when provided within the 1,500 ms period after probe offset. The sample hand was always in the same perspective as the probe hand, whereas the prime hand could be in the same or different upward or downward perspective with respect to the probe. The maintenance of fixation during the trial was monitored via an infrared television camera (ASL Eye-Trac, Applied Science Laboratory, Bedford, MA). Participants were asked to identify the finger that was abducted in the probe hand by pressing one of two keys of a computer keyboard with the right or left thumbs (Fig. 2C). Half of the participants used the left thumb to report an index finger movement probe and the right thumb to report a little finger movement; the opposite response-key association was used for the remaining participants. In total we had 768 trials, 384 trials for each prime duration block; in each block, there were 32 repetitions for each of the 12 possible combinations between the three prime types, the two probe types and the two perspectives. The different prime-probe combinations were randomly presented in each block, whereas the order of prime-duration blocks was fixed, presenting first the low-visibility block (17 ms) and then the high-visibility block (50 ms). At the beginning of each block we administered 16 practice trials. Furthermore, at the end of the experimental session, participants were requested to retrospectively report on the subjective perception of the prime in each block; this allowed us to establish whether the participants noticed the presentation of the prime. All participants reported to have not seen the prime in the 17 ms prime duration block and to have seen it in the 50 ms ones.

Data analysis. One subject had two anticipations (RTs < 120 ms) and these trials were excluded from the mean calculation of the corresponding conditions. ERs were low for all participants. ERs and mean RTs for correct responses were used for the analysis. Preliminary analyses showed that there were no overall differences between the trials with upward and downward hands. Thus, data were coded on the basis of the congruence between the movement of the prime and of the probe (congruent index or little finger movements; incongruent index or little finger movements; and neutral static primes) and between the perspective of the prime and of the probe (same *vs.* different upward or downward hand directions). Data were entered into three-way repeated-measures ANOVAs. The study used a 2×2×3 design with three repeated-measures variables: Prime duration (low-, high-visibility), Perspective congruence (same or different), and Action congruence (congruent, incongruent and neutral). All pair-wise comparisons were performed using the Newman-Keuls post-hoc test. A significance threshold of $P < 0.05$ was set for all statistical analyses. Effect sizes were estimated using the partial eta squared measure (ηp2).The data are reported as mean ± standard error of the mean (SEM).

2.3.2.2 Results

RTs. The 3-way ANOVA on RTs (Fig. 2D) revealed a significant main effect of Perspective congruence (F1,27=111.480, $p < 0.001$, ηp2=0.805), because RTs were faster when probes and primes were in the same (602.36 ± 13 ms) rather than different perspective (628.94 ±12.27 ms). The main effect of Action congruence was also significant (F2,54=89.422, $p < 0.001$, ηp2=0.768), revealing that RTs in congruent trials were faster (600.99 ± 12.68 ms) than RTs in incongruent (631.85 ±12.33 ms; $p < 0.001$) and neutral trials (614.11 ±12.93 ms; $P < 0.001$); RTs in incongruent trials were also slower than RTs in neutral trials ($P < 0.001$). The 2-way interactions Prime duration × Perspective congruence (F1,27=85.09, $P < 0.001$, ηp2=0.759), Prime duration × Action congruence (F2,54=54.635, $P < 0.001$, ηp2=0.669) and Perspective congruence × Action congruence (F2,54=45.150, $P < 0.001$, ηp2=0.625) were also significant and were further qualified by a significant, 3-way interaction Prime duration × Perspective congruence × Action congruence (F2,54=37.853, $P < 0.001$, ηp2=0.583). Thus, the congruence between the prime and probe actions exerted different effects on performance according to the compatibility of their perspective and to prime duration.

To explore the significant three-way interaction we ran two separate, two-way ANOVAs, directly testing the effects of Perspective and Action congruence in each visibility condition. The ANOVA on the low-visibility condition revealed a significant main effect of Action congruence (F2,54=6.055, P=0.004, ηp2=0.183), with responses to congruent trials (602.08 ± 14.19 ms) being faster than those to incongruent (610.90 ± 13.41 ms, P=0.004) and neutral trials (608.91 ± 14.60 ms, P=0.013), which in turn were not different (P=0.458). The non-significant effects of Perspective congruence (F1,27=1.517, P=0.228, ηp2=0.053) and of the interaction Perspective congruence × Action congruence (F2,54=2.483, P=0.093, ηp2=0.084) showed that the compatibility between the viewing perspective of the probe and of the prime had no effect in the condition of low prime visibility. Conversely, considering the high-visibility condition, we found a significant interaction between Perspective congruence and Action congruence (F2,54=74.547, P < 0.001, ηp2=0.734). Newman-Keuls post-hoc analyses indicated that when the prime and probe were viewed from the same perspective, RTs were faster in the congruent trials (552.09 ± 13.46) than in both incongruent (649.91 ± 13.97; P < 0.001) and neutral trials (595.26 ± 14.11; P < 0.001); also RTs were faster in neutral than incongruent trials (P < 0.001). Thus, both facilitation and inhibitory effects were obtained, respectively, for congruent and incongruent combinations of prime and probe hand actions when they were viewed from the same perspective. In contrast, when the prime and probe hands were viewed from different perspectives, we did not find any difference between congruent, incongruent and neutral trials (All P >0.09).

ERs. The 3-way ANOVA on ERs (Table 1) yielded a significant main effect of Action congruence (F2,54=13.177, *p* < 0.001, ηp2=0.327), revealing that ERs in incongruent trials were higher (4.9% ± 0.5) than ERs in congruent (3.44% ±0.5; *p* < 0.001) and neutral trials (3.46% ±0.4; P < 0.001); ERs in congruent trials were not different from ERs in the neutral condition (P=0.95). The main effect of Perspective congruence was not significant (F1,27 < 1). The 2-way interactions Prime duration × Action congruence (F2,54=6.421, P=0.003, ηp2=0.192) and Perspective congruence × Action congruence (F2,54=6.291, P=0.003, ηp2=0.188) were also significant and were further qualified by a significant three-way interaction (F2,54=12.826, P < 0.001, ηp2=0.322). To explore the significant three-way interaction we ran two separate, two-way ANOVAs, directly testing the effects of Perspective and Action congruence in each visibility condition. Non-significant effects were found in the low-visibility condition (All F < 1), while a significant interaction between Perspective congruence and Action congruence was obtained for the high-visibility condition (F2,54=15.479, P < 0.001, ηp2=0.364). Post-hoc analysis indicated that when the prime and probe were viewed from the same perspective, ERs were higher in the incongruent trials (7.3% ± 0.9) than in both

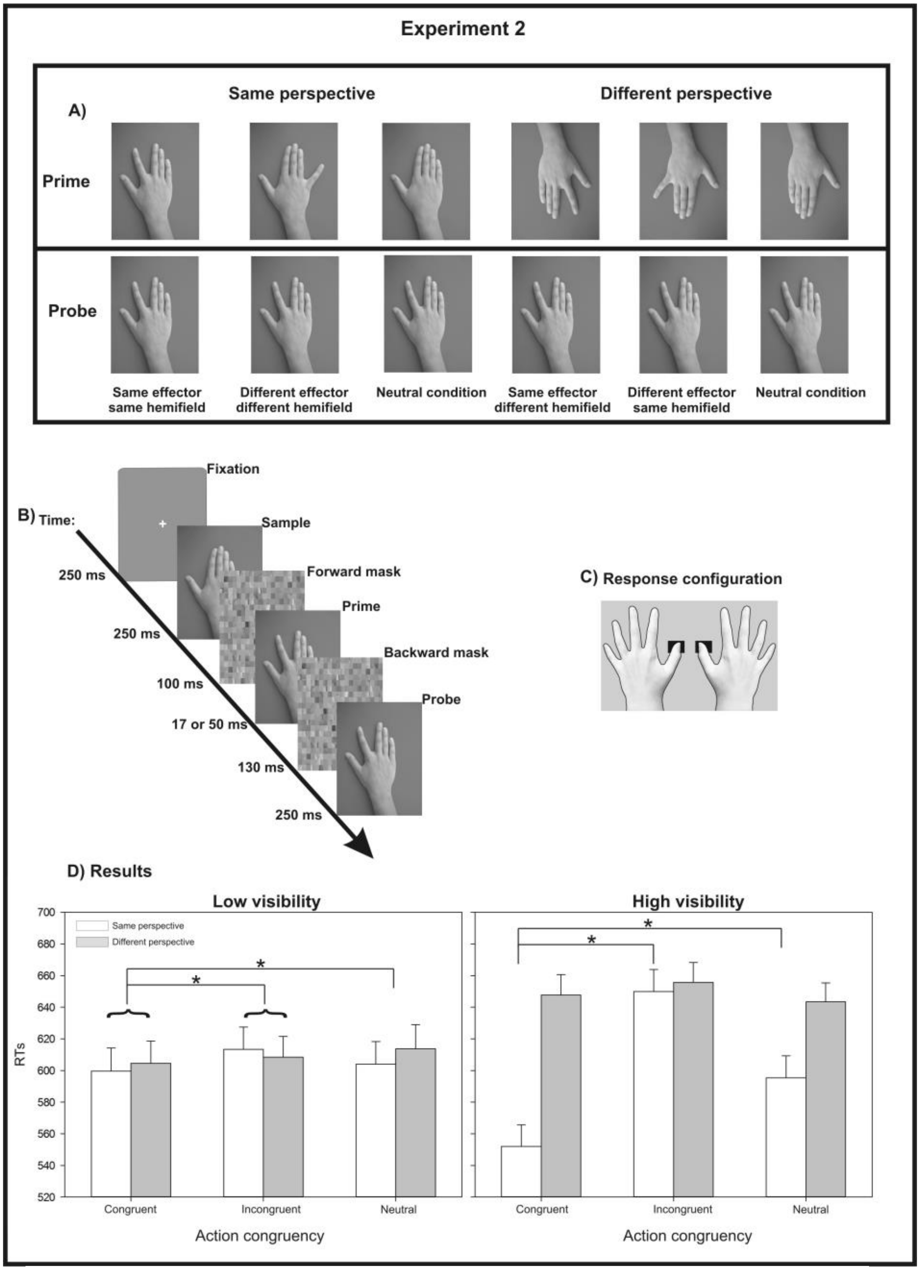


Figure 2. Trial structure (a), response configuration (b) and results (c) of experiment 2.

congruent (2.2% ± 0.4; $P < 0.001$) and neutral trials (2.5% ± 0.4; $P < 0.001$), which in turn did not differ from each other ($P=0.616$). In contrast, when the prime and probe hands were viewed from different perspectives, we did not find any effects (All $P > 0.72$).

2.3.2.3 Discussion

The results of Experiment 2 showed that the congruence between the prime and the probe actions affected the participants' responses in both low and high prime visibility conditions. When compared to neutral, still-hand primes, the observation of incongruent action primes induced interference (incongruent slower than neutral) and the observation of congruent action primes induced facilitation of the responses to the probe (congruent faster both than neutral and incongruent). Interference and facilitation effects, however, were both present only when the prime was consciously perceived (high-visibility condition). When the prime was not consciously perceived (low-visibility condition), we obtained only a facilitation for congruent *vs.* incongruent and neutral primes, but no interferential effects for viewing incongruent *vs.* neutral primes. This pattern of results was also confirmed by the analysis of ERs, which showed interference, but not facilitation, effects in the high-visibility condition, whereas no effects at all were obtained in the low-visibility condition. These results are in line with that of Experiment 1, providing evidence of action specific congruence-related facilitation of speed, but not accuracy of responses in the condition of low-visibility of the prime. Interference effects were found only in the condition of high visibility of the prime and were not present when the prime duration was too short (17 ms) to allow conscious perception, probably because there was no need to suppress a weak and rapidly decaying representation (see Vainio, 2011).

Experiment 2 also showed that the facilitation effects of viewing congruent prime-probe combinations are independent of the spatial compatibility between the positions occupied by the moving finger in the two stimuli. Indeed, since in the trials with the same action but different perspectives the finger movement occurred in opposite hemifields, spatial compatibility cannot explain the effects of action congruence in the low-visibility condition. Action congruence effects, however, were affected by the compatibility between the perspective of the probe and that of the prime in conditions of high prime visibility. Indeed, whereas bidirectional action priming effects were found when the prime and probe hands were viewed from the same perspective and action and spatial congruence effects were in the same direction, no facilitation or incongruence effects were found when the prime and the probe had different perspectives and there was a conflict between the direction of the action congruence and that of the perspective congruence. In a similar vein, while clear interference on accuracy was found for the high-visibility, same-perspective condition, no effect was obtained for different perspective trials. It is important to note, however, that in no conditions did we find evidence of facilitation or interference of responses according to the spatial compatibility between the side of the moving finger in the prime and in the probe (i.e., inversion of the action congruence effect with different perspective trials). Thus, spatial compatibility did not induce per se facilitation or interference effects on the responses to the probe, but attenuated the effect of the action priming, in particular in conditions of high-visibility.

In sum, the results of Experiment 2 provide evidence for genuine visuo-perceptual action congruence priming effects that are independent of perceptual awareness. They also suggest that action specific representations are affected by the compatibility between the perspective of the prime and probe hands in conditions of high, but not low visibility of the prime.

2.3.3 Experiment 3

The previous experiments demonstrated that masked presentations of implied-action hands facilitate the responses to congruent *vs.* incongruent and neutral action stimuli. This action congruence facilitation is independent of perceptual awareness (Experiments 1 and 2) and cannot be ascribed to spatial compatibility (Experiment 2). However, the prime stimulus was presented in a very short time (17 ms) and, thus, it was unclear whether the difference between the low- and high-visibility conditions was due to the short stimulus duration per se or to the fact that the mask prevented conscious perception (Vainio, 2011). To further investigate the effects of unconscious processing of action primes, in Experiment 3 we introduced a rotating mask to prevent conscious perception of the prime with high presentation times, which were comparable to the high-visibility condition in Experiments 1 and 2. Furthermore, we asked our participants not only to report their subjective perception of the prime, but also to try and guess to discriminate the prime in a control task run at the end of the experimental session, after participants were informed of the prime presence. This allowed us to study the visibility of the prime objectively. Finally, we also tested the interaction between visuo-perceptual and visuo-motor priming within the same group of participants and in the same behavioral task directly (Brass et al., 2000; Catmur & Heyes, 2011; Gowen & Poliakoff, 2012). Participants were required to report the presence of abduction of the index or little finger in the probe hand by performing, in different blocks, an abduction movement of the index or little finger and to report the absence of any finger abduction with the other finger. Therefore, to avoid any explicit response bias (Di Pace, Marangolo, & Pizzamiglio, 1997; Soutschek, Taylor, Mu, & Schubert, 2013), participants were asked to report the presence *vs.* absence of implied action, as in Experiment 1, rather than discriminating the moving finger, as in Experiment 2. In sum, Experiment 3 was aimed at testing the effects of the congruence between the prime and the probe (visuo-perceptual priming) and between the probe and the manual response (visuo-motor priming), when the prime remained unnoticed despite relatively high presentation times. We expected comparable facilitation effects when the prime was congruent *vs.* incongruent or neutral with respect to the probe and/or the manual response.

2.3.3.1 Methods

Participants. A new group of 27 students (6 men) of the University of Udine (mean age=22.44 years, standard deviation=3.96) participated in the experiment. All participants were native Italian speakers of Caucasian ethnicity, were right-handed and reported having normal or corrected-to-normal visual acuity. The recruitment procedures were as in the previous experiments.

Stimuli. We used the same hand stimuli as Experiment 2. In addition, a rotating mask was prepared by overlapping two identical star-like geometrical figures that were textured with a scrambled version of the hand pictures using the Bryce 3D software (DAZ Productions, Inc, Salt Lake City, UT, USA). To mask any dynamic cues related to the prime, the two mask figures rotated in opposite directions. We prepared two different versions of the mask that were presented randomly in different trials. The foreground figure rotated clockwise, while the background figure rotated counterclockwise in one version and vice versa in the other.

Procedure. Visual stimulation was performed on a computer screen (75Hz CRT), which the participants looked at in binocular vision from a distance of 57 cm while their head was restrained by means of a head-and-chin rest. As schematized in Figure 3A, the general procedure involved the presentation of a central luminous dot serving as fixation mark for 253 ms; then a picture of a still hand (sample) appeared on the screen for 253 ms and was followed by a rotating mask (forward mask). The duration of the forward mask randomly varied between 106 and 265 ms (in 53 ms steps) to prevent predictability of prime presentation. After the forward mask, the prime hand appeared for 53 ms and was subsequently masked with a rotating mask (backward mask) for 133 ms; then the probe hand was presented for 253 ms, to which a blank screen followed until response or for a maximum of 1,507 ms. Responses were recorded when provided within the 1,507 ms period after probe offset. The sample was always a still hand, whereas both the prime and probe hands could be still or with the index or little finger abducted. Participants were required to report the presence or absence of implied movement in the probe hand using the index finger or little finger. The response keys were placed, respectively, 2 cm to the left of the index finger and 2 cm to the right of the little finger of the participant’s right hand (Fig. 3B). This configuration forced participants to respond performing abduction movements similar to the ones depicted in the implied motion stimuli. This ensured the responses were congruent or incongruent with the specific movement shown in the prime and/or probe hand. All participants performed 2 blocks: one block was performed using the index finger to report the presence of implied-action and the little finger to report its absence; the other block was performed with the opposite key-response association. The order of the two key-response associations was varied between participants.

At the end of the two blocks, the participants were interviewed about their subjective perception of the prime. Additionally, in the present experiment, after having been explicitly informed of the presence of the prime, participants underwent an objective assessment of the prime visibility in a forced-choice manual response task using the same experimental procedure as the main experiment. This allowed us to ensure that participants could not perceive consciously the prime action despite relatively high presentation times. In this task, the participants were asked to indicate whether the prime showed a still hand or a hand with the index finger or little finger abducted; they responded by pressing one of three keys on a computer keyboard. They were instructed to answer “by feeling” and to guess for every trial in which they did not notice the presence of the prime. The trial structure used was identical to that of the experimental session, with the exception that the blank screen was replaced by the request for a response in the middle of the screen. This ensured that participants were faced with exactly the same conditions as in the main experiment. No time limit was given for the participants’ responses. The next trial started immediately after the response. All 384 trials of the experimental session were presented and randomized in 2 blocks of 192 trials each. The control task lasted approximately 4 min.

Data analysis. All the participants performed the experimental task without anticipations (< 120 ms) and with low ERs. Two participants reported having noticed the prime during the experiment and were excluded from the analyses. ERs and mean RTs for correct responses of the remaining participants were entered into a three-way, repeated-measures ANOVA. The study used a 2×3×3 design with three repeated-measure variables: Effector (implied-action responses given with the index or the little finger), Probe (index finger abduction, little finger abduction, or still hand), and Prime (index finger abduction, little finger abduction, or still hand). All pair-wise comparisons were performed using the Newman-Keuls post-hoc test. A significance threshold of $P < 0.05$ was set for all statistical analyses. Effect sizes were estimated using the partial eta squared measure ($\eta p2$). Data are reported as mean ± standard error of the mean.

2.3.3.2 Results

The 3-way ANOVA on RTs revealed a significant main effect of Effector ($F1,24=10.269$, $p=0.003$, $\eta p2=0.299$), which was further qualified by a significance 2-way interaction Effector × Probe ($F2,48=27.395$, $P < 0.001$, ηp2=0.533), showing automatic imitation effects (Heyes, 2011) in relation to the probe. Indeed, when participants reported implied-action probes with the index finger, RTs were slower for the little finger (783.04 ±21.63 ms) than index finger (720.22 ±21.88 ms, $P < 0.001$) probes. The opposite pattern was obtained when participants reported the presence of an index or little finger movement with the little finger: RTs were slower for the index finger (744.53 ±23.46 ms) than little finger (679.17 ±20.10 ms; $P < 0.001$) probes. Since the responses to the still probe were given using a different finger from those given to implied-action probes, directly comparing the static and implied motion probes might be affected by intrinsic differences in finger movement speed. However, slower RTs to incongruent implied-action than still-hand probes were obtained for both index (730.44 ±20.53 ms, $P < 0.001$) and little finger (706.61 ±20.74 ms, P=0.018) effector trials. In sum, the results showed clear interferential visuo-motor effects when participants were requested to report the presence of an implied-action hand by performing a finger movement that was incongruent with the movement depicted in the observed hand. Such interferential effects for incongruent probes were significant when compared to both the responses to congruent implied-action probes and those to still-hand probes.

Despite a clear visuo-motor priming in relation to the probe, no visuo-motor priming effect was obtained in relation to the prime, because the two-way interaction between Prime and Effector ($F < 1$) and the three-way interaction of Probe, Prime and Effector (F4,96=1.579, P=0.186, ηp2=0.061) were not significant. This cannot be ascribed to the fact that the prime had no effect at all, because the main effect of Prime (F2,48=15.707, $p < 0.001$, ηp2=0.395) and the 2-way interaction Probe × Prime (F4,96=40.802, $p < 0.001$, ηp2=0.629) were significant, showing evidence of visuo-perceptual priming effects in relation to action primes that were not consciously perceived. When the probe depicted a static hand, RTs for static prime trials (659.55 ± 19.77 ms) were faster than RTs for both index (749.08 ± 20.97 ms, $P < 0.001$) and little finger prime trials (746.95 ± 20.26 ms, $P < 0.001$), which in turn did not differ from each other (P=0.804). When the probe depicted an index finger abduction, RTs for index finger prime trials (703.49 ± 23.15 ms) were faster than RTs for both still hand prime (735.39 ± 20.75 ms, $P < 0.001$) and little finger prime trials (758.30 ± 23.73 ms, $P < 0.001$), which in turn did not differ from each other (P=0.08). When the probe depicted a little finger abduction, RTs for little finger prime trials (713.79 ± 21.59 ms) were faster than RTs for both still (740.78 ± 18 ms, P=0.011) and index finger primes (738.75 ± 17.39 ms, P=0.012), which, again, did not differ from each other (P=0.81). Thus, with respect to the neutral, still hand condition, the results provided evidence of facilitation for congruent prime-probe pairs, but no interference for incongruent prime-probe pairs when the prime was not consciously perceived by the observer.

ERs. The 3-way ANOVA on ERs revealed a significant main effect of Prime (F2,48=3.727, *p* =0.031, ηp2=0.134), because ERs were higher for little finger (4.09 ± 0.83%) than still hand primes (2.99 ± 0.69%). The 2-way interaction Effector × Probe (F2,48=7.779, P < 0.001, ηp2=0.244) and Probe × Prime (F4,96=3.17, P=0.017, ηp2=0.116) were significant and were qualified by significant 3-way interaction Effector × Probe × Prime (F4,96=2.986, P=0.022, ηp2=0.110). Follow-up Probe × Prime two-way ANOVAs, conducted on each block, showed that the interaction was significant (F4,96=4.39, P=0.003, ηp2=0.154) only when the participants used the index finger to report the presence of implied-action probes; in this block, when the prime was a still hand, participants committed significantly more errors in responding to little finger implied-action probes than to index finger implied-action (P=0.007) and still hand probes (P=0.004). Conversely, no effects were obtained when the prime depicted an implied-action hand (all P >0.1), suggesting that the interaction between the prime and probe masked the effects of the visuo-motor priming for ERs. Only a significant main effect of Probe was obtained when participants used the little finger to report the presence of implied-action hands (F2,48=8.35, P < 0.001, ηp2=0.258), with lower ERs for little finger than index finger (P < 0.001) and still hand probes (P=0.009). As the number of errors committed by the participants was very low in this experiment (Table 1), however, any interpretation of these effects should be cautious.

Forced-choice prime discrimination. A 3 × 3, Probe × Prime repeated-measures ANOVA was performed on the participants' prime discrimination accuracies in the post-experimental session (Table 2). The main effects were not significant (All P

>0.07), while the interaction was significant (F(4,96)=2.733, P=0.02; ŋp2=0.102). Post-hoc tests showed that the interaction could be explained by the fact that participants were more accurate in reporting still-hand than little-finger (P=0.02) primes when the probe depicted a still hand. All other comparisons were not

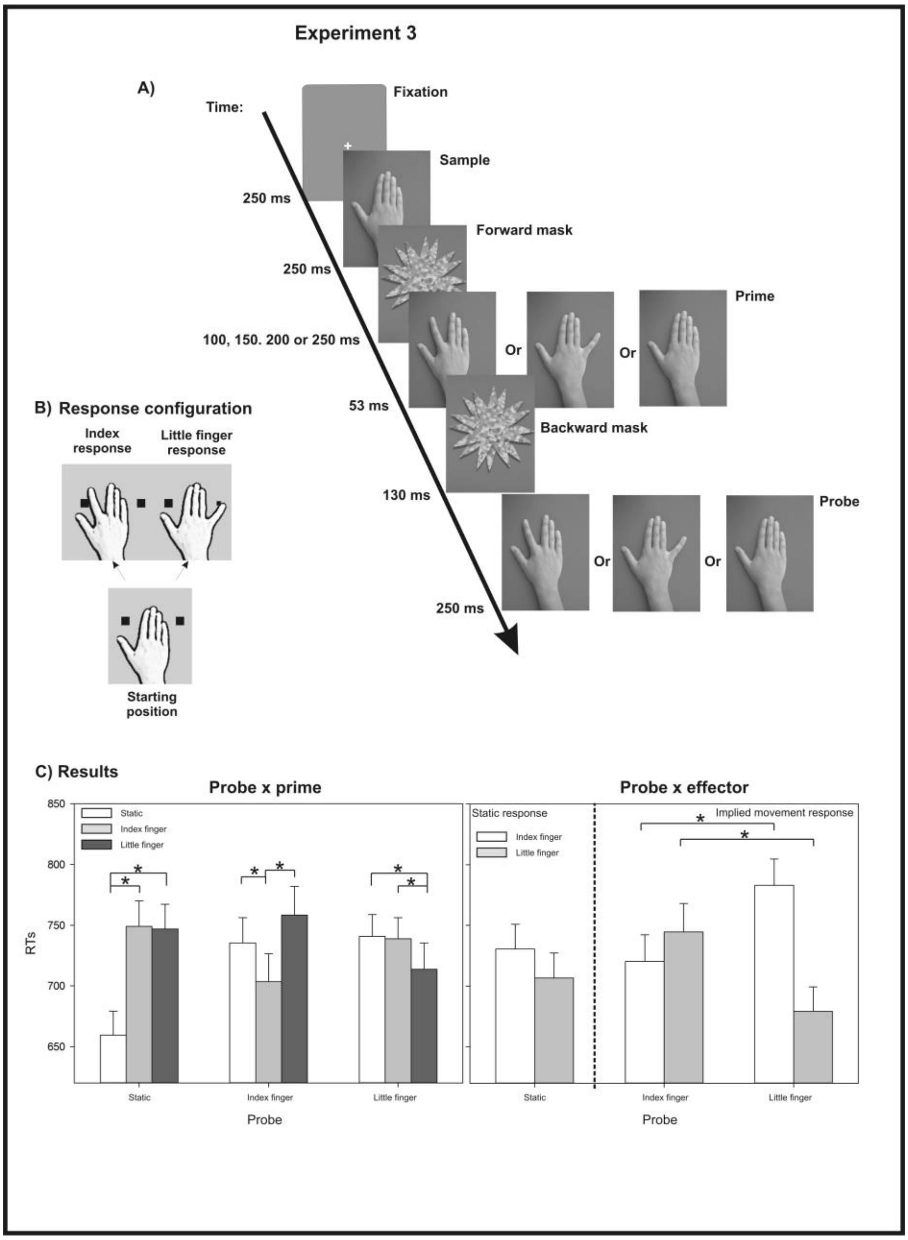


Figure 3. Trial structure (a), response configuration (b) and results (c) of experiment 3.

significant (All P >0.15). Furthermore, testing with one-sample t-tests whether the participants' prime discrimination performance was better than that expected by chance (33%) revealed above-chance levels only when both the prime and the probe depicted the same index finger abduction (t(24)=2.482, P=0.02) or the same still hand (t(24)=5.04, $P < 0.001$). All together, these results suggest that, even when participants were informed about the presence of the prime and were explicitly focused on its identification, they reported the probe and not the prime action and were thus more accurate when the prime was congruent with the probe. These results corroborate the participants' subjective reports showing that the masked action primes were not consciously perceived and could not be explicitly discriminated in a forced choice task.

2.3.3.3 Discussion

In Experiment 3, we investigated visuo-perceptual and visuo-motor priming when action primes were not consciously perceived. We used forward and backward dynamic masking procedures to present the prime for a relatively long time (53 ms) but nonetheless prevent conscious perception by all participants. When we asked our participants whether they saw anything during presentation of the rotating mask, most of them (25 out of 27) affirmed they had seen nothing during mask presentation. This subjective report was confirmed by the forced discrimination task conducted at the end of the main experiment. Indeed, even when participants were explicitly informed about the presence of the prime and were required to discriminate whether it depicted a still hand or an index or little finger abduction, their discrimination abilities were random and they responded on the basis of the probe type. This effect is probably due to the masking procedure, because the rotating star-like figure and the following probe hand tended to mask not only the perception of the hand shape but also the flickering of the moving finger.

Although the action depicted by the prime could not be consciously perceived, it affected the responses to the probe. We found, indeed, facilitation effects when the prime was congruent with the action depicted in the probe. In keeping with the results found in the low-visibility conditions of the previous experiments, no interference effects were found when the masked prime depicted an incongruent action with respect to a neutral, static hand. Thus, the results showed evidence of visuo-perceptual action facilitation induced by action primes even when they were not consciously perceived.

The congruence between the effector and the probe affected RTs, independently of the prime, since responses were interfered with when provided with an action that was incongruent *vs.* congruent with the probe. On the other hand, no direct effect of the compatibility between the effector and the prime was found, suggesting that the (unconscious) visual representation of the prime movement affected the (conscious) visual processing of the probe but not the (conscious) motor representation of the responding finger. In other words, results provide evidence for unconscious visuo-perceptual but not visuo-motor action priming effects.

2.3.4 Experiment 4

In Experiment 4 we tested whether the absence of visuo-motor priming for unconsciously perceived primes was due to the interference induced by the simultaneous visuo-perceptual priming related to the combination of the prime and probe actions. We used the same still, index or little finger action primes of Experiment 3 in a standard paradigm for visuo-motor priming in which participants respond to symbolic cues. The participants had to respond to colored frame probes performing abduction movements of the index or little finger, which were congruent or incongruent with the prime action. In two consecutive blocks, the prime was presented in conditions of low and high visibility. In keeping with the results of Experiment 3, we expected that the congruence between the prime action and the manual response should affect performance in conditions of high, but not low, prime visibility.

2.3.4.1 Methods

Participants. A new group of 20 students (6 men) of the University of Udine (mean age=23.50 years, standard deviation=3.33) participated in the experiment. All participants were native Italian speakers of Caucasian ethnicity, were right-handed and reported having normal or corrected-to-normal visual acuity. The recruitment procedures were as in the previous experiments.

Stimuli. We used the same stimuli of Experiment 3, which were presented with a 60Hz, 19 inch CRT monitor (resolution 1024×768 pixels).

Procedure. The general procedure was the same as in Experiment 3, except that the prime could depict a hand with the index or little finger abducted (i.e., no still hand was presented) and the probe always depicted a still hand presented in a blue or red frame. The sample, prime and probe hands could be presented with the fingers pointing upward or downward, thus in a position that was congruent or incongruent, respectively, with the posture of the participant's hand. All the three hands in each trial were presented in the same perspective. Participants were required to respond to the color of the frame probe by pressing one of two keys with the right index or little finger. The keys were positioned in a way that forced participants to answer performing movements that were congruent or incongruent with the prime action. The association between the keys and the frame colors was counterbalanced between participants. All participants performed 2 consecutive blocks: the first with the prime presented in a condition of low-visibility (33 ms) and the second with the prime presented in a condition of high visibility (66 ms). In the low-visibility condition, we reduced the duration of the prime with respect to that of Experiment 3 in keeping with pilot data showing that participants could often notice prime presentations of 53 ms when the probes always depicted a still hand. Indeed, it is likely that the presentation of the implied-action probes in Experiment 3 might have contributed to suppressing the conscious perception of the prime with relatively high presentation times. Reducing the prime duration in the low-visibility condition ensured that prime presentation was not noticed by any participants after the low-visibility block, whereas all of them reported having seen it in the high-visibility condition.

After the experimental session, participants were debriefed about the presentation of the prime hand and were requested to perform a control, forced-choice task to determine its discriminability. As in Experiment 3, in the forced-choice task participants were presented with the experimental trials, and after each trial, they were asked to press one of two keys to report whether the prime showed a hand with the index finger or with little finger abducted. The trial structure was similar to that used during the experimental task, with the exception that a response prompt appeared in the middle of the screen after the probe. This ensured that participants were faced with exactly the same conditions as in the main experiment. No time limit was given for the participants' responses. The next trial started immediately after the response. Two blocks of 136 trials each were presented to the participants in sequential order, the first with the prime presented in condition of low-visibility and the second in condition of high-visibility. The control task lasted approximately 8 min.

Data analysis. Two participants had one anticipation (RTs < 120 ms) each and the corresponding trial was excluded from the computation of the individual ERs and RTs mean. All participants had a good performance in all conditions, with ERs < 4% (Table 1). Thus, only mean RTs of correct responses were used for the analyses. RTs data were entered into a three-way, repeated-measures ANOVA. Considering the congruency between the prime implied-action and the finger response, the study used a 2×2×2 design with three repeated-measures variables: Prime duration (33 ms, 66 ms), Perspective (upward, downward) and Action congruency (congruent, incongruent). All pair-wise comparisons were performed using the Newman-Keuls post-hoc test. A significance threshold of P < 0.05 was set for all statistical analyses. Effect sizes were estimated using the partial eta squared measure (ηp2). Data are reported as mean ± standard error of the mean.

2.3.4.2 Results

RTs. The 3-way ANOVA on RTs revealed a significant main effect of Prime duration (F1,19=9.724, P=0.005, ηp2=0.338), because responding in the low-visibility condition was faster (523.71 ± 21.73 ms) than responding in the high-visibility condition (551.89 ± 21.28 ms). The main effect of Action congruence was not significant (F1,19 < 1, ηp2=0.026), but a significant two-way interaction Prime duration × Action congruency (F1,19=5.286, P=0.033, ηp2=0.217) showed that the visuo-motor action priming effect was modulated by prime visibility. Indeed, whereas in the low-visibility condition we did not obtain any difference between congruent and incongruent primes (P=0.275), in the high-visibility condition RTs for congruent primes (545.35 ± 20.24 ms) were faster than RTs for incongruent primes (558.43 ± 22.86 ms, P=0.046). The perspective of the prime did not affect the visuo-motor priming effect, as the main effect of Perspective and all the two-way (All F1,19 < 1) and three-way (F1,19=1.231, P=0.280, ηp2=0.060) interactions involving the effect of Perspective were not significant.

Forced-choice prime discrimination task. A 2 × 2 repeated measures ANOVA with Prime duration and Perspective as within-subjects variables was performed on the participants' prime discrimination accuracies in the forced-choice prime discrimination task (Table 2). Only the main effect of Prime duration was significant (F(1,19)=20.927, P < 0.001; ηp2=0.524), with higher discrimination

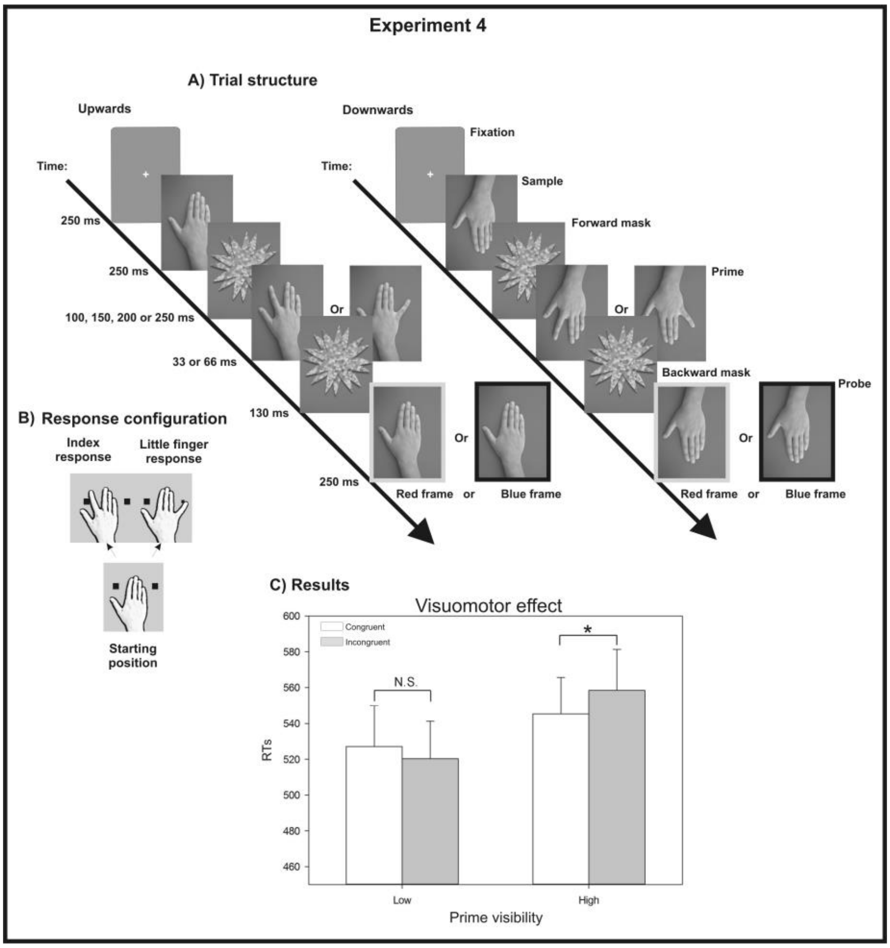


Figure 4. Trial structure (a), response configuration (b) and results (c) of experiment 1.

performance in the high- than low-visibility condition, whereas all other effects were non-significant (All $F < 1$). Comparing the discrimination performance in each condition against the chance level (i.e., 50%) showed that only in the high-visibility condition did accuracy exceed the chance level for both upward ($t(19)=5.432$, $P < 0.001$) and downward ($t(19)=4.242$, $P < 0.001$) perspectives. Conversely, performance was at chance for both perspectives in the low-visibility condition. These results confirm the participants' subjective reports that the prime was not consciously perceived in the low-visibility condition and was consciously perceived in the high-visibility condition.

2.3.4.3 Discussion

In Experiment 4 we used a standard visuo-motor priming paradigm in which participants executed manual responses in response to symbolic cues. The manual responses were congruent or incongruent with the prime actions, which were task irrelevant and could be presented in conditions of low and high visibility. The results corroborated those of the Experiment 3 in showing that observed actions affected motor preparation and execution processes only when they were consciously perceived (i.e., the prime in the high-visibility condition in Experiment 4 and the probe in Experiment 3), but not when they were not consciously perceived (i.e., the prime in the low-visibility condition in Experiment 4 and in Experiment 3).

2.3.5 Experiment 5

In Experiment 5 we tested whether the absence of visuo-motor priming for unconsciously perceived primes was due to different durations of the priming effects in low-visibility and high visibility conditions. Previous studies have shown that visuo-motor priming effects are dependent from the time elapsing between the prime and the response to the probe (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003; Summer 2007). Thus, in Experiment 5 we used the same stimuli and procedure of Experiment 4 in a standard paradigm for visuo-motor priming in which participants respond to symbolic cues, but we recorded also the time to initiate the response rather than only the time to complete the response (i.e., RT). Furthermore, we measured the response initiation times at two stimulus onset asynchronies (SOAs) between prime and probe: one was set at 166 ms (short SOA) and the other one was set at 250 ms (long SOA). In three consecutive blocks, the prime was presented in conditions of low (33 ms), periliminal (66 ms) and high visibility (99 ms). We included the 99 ms prime duration, along with the 33 and 66 ms durations used in Experiment 4, in keeping with pilot data showing that participants could not notice prime presentations of 66 ms in the new experimental setting that required recording initiation times.

In keeping with the results of Experiment 4, we expected that the congruence between the prime action and the manual response should affect performance in conditions of high, but not periliminal or low prime visibility.

2.3.5.1 Methods

Participants. A new group of 20 students (4 men) of the University of Udine (mean age=24.10 years, standard deviation=6.51) participated in the experiment. All participants were native Italian speakers of Caucasian ethnicity, were right-handed and reported having normal or corrected-to-normal visual acuity. The recruitment procedures were as in the previous experiments.

Stimuli. We used the same stimuli of Experiment 4, which were presented with a 60Hz, 19 inch CRT monitor (resolution 1024×768 pixels).

Procedure. The general procedure was the same as in Experiment 4, except that the probe was a small, colored square appearing at the center of the hand image; this ensured that participants were fixating at the center of the images during prime presentation rather than paying attention to any part of the image borders. The trial structure was similar to that used in Experiment 4, but the duration of the events was adapted according to the manipulation of prime visibility (33 ms, 66ms, or 99 ms) and SOA (166 ms or 250 ms). The forward mask could last 66 ms or 150 ms to prevent anticipation of prime presentation, while the duration of the backward mask was dependent from the duration of the previous events and was varied from 66 ms to 217 ms such that the total duration of the sequence ‘forward mask – prime – backward mask’ was 315 ms in all trials (Fig. 5A). A black square was presented from the beginning of the trial and the probe stimulus corresponded to a change of its color to blue or red. In keeping with Experiment 4, participants had to press one of two keys in response to the probe by performing movements that were congruent or incongruent with the prime action. Differently than in Experiment 4, however, at the beginning of each trial participants were required to press with the index and little fingers two start keys positioned centrally with respect to the response keys; thus, responding to the probe required the release of one of the two start keys (depending on the response prompted by the probe) and then to press the corresponding response key (see. Fig. 5B). This way, we were able to record for each trial both the response initiation time (i.e., the time elapsed between onset of the probe and release of the start key) and the response execution time (i.e. the time elapsed between release of the start key and press of the response key). The association between the keys and the frame colors was counterbalanced between participants. All participants performed 3 consecutive blocks: the first with the prime presented in condition of low-visibility (33 ms), the second with the prime presented in condition of periliminal visibility (66 ms), and the third with the prime presented in condition of high visibility (99 ms).

After the experimental session, participants were debriefed about the presentation of the prime hand and were requested to perform a control, forced-choice task to determine its discriminability. As in Experiment 4, in the forced-choice task participants were presented with the experimental trials, and after each trial, they were asked to press one of two keys to report whether the prime showed a hand with the index finger or with little finger abducted. The trial structure was similar to that used during the experimental task, with the exception that a response prompt appeared in the middle of the screen after the probe. This ensured that participants were faced with exactly the same conditions as in the main experiment. No time limit was given for the participants’ responses. The next trial started immediately after the response. Three blocks of 160 trials each were presented to the participants in sequential order, the first with the prime presented in condition of low-visibility, the second in condition of periliminal-visibility, and the third in condition of high-visibility. The control task lasted approximately 12 min.

Finally, in a stimulus evaluation phase administered at the end of experiment we asked participants to evaluate the implied-motion evoked by each experimental stimulus. Each of the 48 stimuli was randomly presented in two blocks for a total of

96 trials. The trials started with the presentation of a central fixation point lasting 500 ms, followed by the hand image stimulus presented for 2,000 ms at the center of the screen. After the stimulus, the question "How much does it imply movement (Quanto implica movimento in Italian)?" appeared on the screen with a vertical, 10-cm Visual Analogue Scale (VAS) ranging from "much (molto)" (score=100) to "little (poco)" (score=0). The top or bottom position of the two extremes was balanced between participants. The participants were asked to express an implied-motion judgment on the hand stimuli by moving the mouse cursor onto the point of the VAS corresponding to their opinion. The evaluation phase lasted approximately 5 min.

Data analysis. No participant showed any response anticipation and all had good performance in all conditions, with ERs < 4.2% (Table 1). Considered the ceiling effects in accuracy, we did not analyze further the ERs, but mean response initiation times and response execution times of correct responses were used for the analyses. Data were entered into a three-way, repeated-measures ANOVA. Considering the congruency between the prime implied-action and the finger response, the study used a 3×2×2 design with three repeated-measures variables: Prime duration (33 ms, 66 ms, 99 ms), SOA (short, long) and Action congruency (congruent, incongruent). All pair-wise comparisons were performed using the Newman-Keuls post-hoc test. A significance threshold of $P < 0.05$ was set for all statistical analyses. Effect sizes were estimated using the partial eta squared measure (ηp2). Data are reported as mean ± standard error of the mean.

2.3.5.2 Results

Response initiation times. The 3-way ANOVA on response initiation times revealed a significant main effect of Action congruence (F1,19=6.431, P=0.020, ηp2=0.252), because responding in the congruent condition was faster (467.11 ± 13.68 ms) than responding in the incongruent condition (470.47 ± 13.76 ms). The main effect of Prime duration was not significant (F2,38 = 1.236, p >0.30, ηp2=0.061), but a significant two-way interaction Prime duration × Action congruency (F2,38=5.594, P=0.007, ηp2=0.227) showed that the visuo-motor priming effect was modulated by prime visibility. Indeed, whereas in the low- and periliminal-visibility conditions we did not obtain any difference between congruent and incongruent primes (all P >0.365), in the high-visibility condition RTs for congruent primes (468.20 ± 13.51 ms) were faster than RTs for incongruent primes (482 ± 16.36 ms, P=0.005). The SOA did not affect the visuo-motor priming effect, as the main effect of SOA and all the two-way (All F < 1.143, P >0.329, ηp2 < 0.056) and three-way (F2,38 < 1) interactions involving the effect of SOA were not significant.

Response execution times. The 3-way ANOVA on response execution times revealed significant main effect of Prime duration (F2,38=4.989, P=0.011, ηp2=0.207), because responding in the high-visibility condition was faster (116.18 ± 12.61 ms) than responding in the low-visibility condition (134.15 ± 16.50 ms, P=0.009), but it was not different from responding in the periliminal condition (122.99 ±14.14 ms, P=0.243); furthermore, responding in the periliminal-visibility condition tended to be faster than responding in the low-visibility condition (P=0.059). No other effects were significant (all F < 2.742, P >0.077).

Forced-choice prime discrimination task. A 3 × 2 repeated measures ANOVA with Prime duration and SOA as within-subjects variables was performed on the participants' prime discrimination accuracies in the forced-choice prime discrimination task (Table 2). Only the main effect of Prime duration was significant (F(2,38)=100.438, P < 0.001; ŋp2=0.840), with higher discrimination performance in the high- (81.12 ± 0.02 %) than both periliminal- (59.40 ± 0.01%, P < 0.001) and low-visibility conditions (49.90 ± 0.008%, P < 0.001) and higher discrimination performance in the perilimininal- than low-visibility condition (P < 0.001). The main effect of SOA was not significant (F(1,19)=3.490, P >0.07; ŋp2=0.155), whereas the two-way interaction Prime Duration × SOA was significant (F(2,38)=4.747, P=0.014; ŋp2=0.199). The Post-hoc analysis revealed that only in the high visibility condition the SOA modulated the discrimination of the prime with higher scores in the long (83.45 ± 0.02 %) than in the short SOA (78.80 ± 0.02 %, P=0.005). Comparing the discrimination performance in each Prime duration against the chance level (i.e., 50%) showed that performance exceeded the chance level in the high- (t(20)=11.786, P < 0.001) and periliminal-visibility (t(20)=4.748, P < 0.001) conditions, but was at chance for the low-visibility condition (t(20)=-0.119, P=0.905). These results show that participants did not subjectively report primes presented for 33 ms and were not able to discriminate them when their attention was explicitly directed to prime presentation; with 66 ms prime duration, participants failed to report prime presentation but, as in Experiment 4, were able to discriminate above chance the prime type in the forced-choice prime discrimination task; only with the 99 ms prime duration did the participants demonstrate conscious prime perception in both the subjective and objective tests of prime perception.

Stimuli evaluation phase. A 3 × 2 repeated measures ANOVA, with Action posture (index finger abduction, little finger abduction, still hand) and Perspective (upward, downward) as within-subjects variables, was performed on the participants' implied-motion judgment. Only the main effect of Action posture was significant (F(2,38)=108.170, P < 0.001; ŋp2=0.850); the post-hoc analysis indicated that the VAS implied-motion judgments for both index finger (57.18 ± 4.55 mm) and little finger (59.73 ± 4.40 mm) abduction stimuli were higher than those for still hand stimuli (9.00 ± 1.64 mm; all *p*s < 0.001). No difference was observed between the implied motion evoked by index and little finger abduction stimuli (*p* >0.515). The main effect of Perspective and the two-way interaction were not significant (All Fs < 1.71, *p* >0.193). Thus, the results of the stimuli evaluation phase confirmed that pictures depicting index or little finger abduction implied more movement than those depicting a resting relaxed hand.

2.3.5.3 Discussion

As in Experiment 4, in Experiment 5 we used a standard visuo-motor priming paradigm in which participants executed manual responses to symbolic cues. We collected the response initiation times at two different SOAs between prime and probe. The results corroborated those of the Experiment 4 in showing that observed actions affected motor preparation and initiation processes only when they were consciously perceived, but they did not exert any effects when they were not consciously perceived. Furthermore no visuo-motor priming effects was obtained, independently from prime visibility, on the time needed to execute the movement, suggesting that observed actions affect the preparation and initiation phases, but not the execution phase of motor responses. Finally, the manipulation of the time elapsing between presentation of the action prime and triggering of the response (i.e., SOA) revealed no effect, suggesting that the priming induced by consciously perceived actions was still present after 250 ms from the prime onset. On the other hand, no effects were observed for action primes that were not consciously perceived, when the priming effects were probed either early on response initiation times or later on RT and longer SOAs. It is also worth noting that in the present experiment we had to increase the duration of the prime up to 99 ms in order to ensure all participants noticed its presentation. Indeed, at 66 ms duration, which allowed most participants of Experiment 4 to be aware of the prime, participants of this experiment failed to notice it. This may be due to the experimental setting needed to record response initiation times, since participants had to keep pressing the start keys during the whole ‘forward-mask – prime – backward mask’ sequence, which might be expected to be more distracting than keeping a relaxed hand before responding. This further corroborates the claim that observer’s visual awareness of the stimuli rather than prime duration or SOA per se determines whether observed actions affects motor preparation and initiation processes.

2.3.6 General Discussion

In the present study we tested how the effects of action observation on subsequent action perception (visuo-perceptual priming) and action preparation (visuo-motor priming) are modulated by the reduction of visibility of the prime and by the spatial compatibility between the prime and probe actions. Previous studies have shown that conscious action observation facilitates the perception (Costantini et al., 2008; Finke & Freyd, 1985) and the execution (Brass et al., 2000; Heyes, 2011; Kilner et al., 2003; Stürmer et al., 2000) of congruent *vs.* incongruent actions, thus providing evidence of visuo-perceptual and visuo-motor action priming. These effects suggest that viewing an action activates its perceptuo-motor representations, affecting subsequent perceptual and motor processing. In these previous studies, however, the priming action was always presented in conditions of high-visibility, and the participants were aware of its presentation. It was thus unclear whether perceptuo-motor action representations require perceptual awareness.

Table 1. Accuracy (mean % ± standard deviation) for each condition of the four experiments

		Experiment 1					
Action congruence		Action task			Form task		
		Prime visibility			Prime visibility		
		Low	High		Low	High	
	Congruent	92 ± 8.54	96 ± 3.88		67 ± 12.4	79 ± 17.1	
	Incongruent	92 ± 6.12	88 ± 9.98		65 ± 13.8	78 ± 12.1	
		Experiment 2					
Action congruence		Perspective					
		Congruent			Incongruent		
		Prime visibility			Prime visibility		
		Low	High		Low	High	
	Congruent	96 ± 4.41	98 ± 2.35		96 ± 3.99	96 ± 4.03	
	Incongruent	96 ± 2.73	93 ± 4.86		96 ± 3.98	96 ± 4.31	
		Experiment 3					
Prime		Effector					
		Index finger			Little finger		
		Probe			Probe		
		Static	Index finger	Little finger	Static	Index finger	Little finger
	Static	99 ± 2.52	98 ± 3.24	93 ± 12.28	98 ± 3.43	96 ± 4.92	98 ± 2.77
	Index finger	96 ± 4.78	98 ± 4.64	96 ± 7.13	95 ± 7.11	95 ± 7.48	99.9 ± 1.4
	Little finger	94 ± 7.54	98 ±3.92	96 ± 6.55	96 ± 6.43	94 ± 7.18	97 ± 5.20
		Experiment 4					
Action congruence		Perspective					
		Congruent			Incongruent		
		Prime visibility			Prime visibility		
		Low	High		Low	High	
	Congruent	99 ± 1.65	99 ± 1.33		99 ± 1.65	99 ± 1.33	
	Incongruent	99 ± 1.56	99 ± 1.97		99 ± 1.33	99 ± 1.65	

2.3.7 Visuo-perceptual action representations do not require perceptual awareness

In Experiments 1-3 we tested the modulation of visuo-perceptual action priming according to the visibility of the prime and the type of task. We found reliable evidence across experiments of action priming in conditions of high and low prime visibility, suggesting that viewing an action activated its perceptual representation and allowed a more efficient perceptual processing of subsequent actions (Finke and Freyd, 1985). This perceptual action representation was activated automatically, for the participants were not requested to process the prime stimulus, and unconsciously, for priming effects were found even when the participants remained unaware of prime presentation. Increasing the visibility of the prime only had the effect of increasing the congruence-facilitation effects, but perceptual awareness was not a condition of their appearance.

Action primes, independently of their visibility, exerted specific effects on the processing of the action displayed by the probes, while they had no effects on the perception of the same stimulus when the task required processing body form cues. This suggests that the prime established action-specific representations. Then again, action primes facilitated action processing both in an action detection task, when participants were required to detect the presence of an implied-action hand *vs.* a still hand (Experiments 1 and 3), and in an action discrimination task, when participants were requested to discriminate between index *vs.* little finger abductions (Experiment 2). In the latter case, the prime and the probe were related for both perceptual similarity and association with the same response (i.e., reporting index or little finger movements). Conversely, in the first case, the two finger abduction stimuli were associated with exactly the same response (i.e., reporting an implied-action hand) and the priming effects were only based on perceptual similarity. In keeping with the perceptual priming effects (Sumner, 2007; Tulving & Schacter, 1990), when compared to the neutral condition, unconscious processing of action primes in Experiment 3 induced only facilitation of response to congruent probes, but not interference of responses to incongruent pairs. In Experiment 2, when both perceptual similarity and motor-response compatibility were at handle, we found both facilitation and interference effects. This is in keeping with the notion that the priming related to perceptual similarity induces only facilitation effects, while the priming related to the association with the same motor response induces both facilitation and interference effects (Sumner, 2007; Tulving & Schacter, 1990). It is worth noting, however, that the interference effects in Experiment 2 were only obtained when the prime was presented in conditions of high visibility; conversely, only facilitation for congruent actions was found for low-visibility primes. All in all these results suggest that unconscious processing of body actions activates perceptual action representations that facilitate the processing of similar stimuli.

2.3.8 Visuo-motor action representations require perceptual awareness

In contrast to the evidence of perceptual facilitation induced by unconscious action processing, we did not find any indication of visuo-motor priming in conditions of low prime visibility. This suggests that the influence of action observation on motor representations requires perceptual awareness. When the action stimuli were presented in conditions of high visibility, namely for the probes in Experiment 3 and the high-visibility primes in Experiment 4, the responses provided with incongruent movements were interfered with, as compared to those provided with congruent movements. Thus, in keeping with previous studies on the automatic imitation effect (Heyes, 2011), action observation automatically triggered the motor representation of the same action, which conflicted with the execution of incongruent movements. The effect was automatic, since it was obtained both when the participants were requested to respond to the action stimuli (Experiment 3) and when they responded to non-spatial symbolic cues (colored squares) and had to ignore the action stimuli (Experiment 4 and 5). Comparing the effects on the time needed to initiate the response or to execute it in Experiment 5 also revealed that observed actions affect motor preparation and initiation processes but not the actual implementation of the motor program. Furthermore, in keeping with the visuo-perceptual priming, the visuo-motor priming effect was independent of the association of the two actions to the same or different task responses. Indeed, in Experiment 3, the probes depicting an index or little finger abduction were associated with the same response, namely reporting an implied-action hand by abducting the index or little finger. Nevertheless, index finger movements were slower in response to little than index finger probes, while little finger movements were slower in response to index than little finger probes. This suggests that the association between the stimulus and the motor responses relied on representations that pre-existed the experimental task and were likely to have been established after the repeated experience of the visual consequences of one’s own movements. According to the associative sequence learning hypothesis (Catmur, Walsh, & Heyes, 2009; Heyes, 2011) perceptuo-motor representations of actions emerge from sensorimotor learning processes that associate motor preparation and execution representations with the contingent (Cook, Yip, & Goldin-Meadow, 2010) and contiguous (Keysers & Perrett, 2004) perception of the sensory (kinesthetic and visual) consequences of movements in the actor’s body and/or of the sensory (visual) signals coming from the body of other individuals performing similar actions in imitative settings. Evidence favoring this view comes from the finding of a reversal of the typical automatic imitation effects after repeated exposure to incongruent associations of movement execution and action observation (e.g., making an index finger movement while seeing a little finger movement; Heyes, Bird, Johnson, & Haggard, 2005). Although also in our experimental sessions participants were presented with an incongruent association between action observation and a given motor response (e.g., abducting the index finger to report both index finger and little finger implied action probes), it was probably too short a training to substitute or superimpose the new task-related association to the long-lasting perceptuo-motor associations of congruent movements and visual feedbacks.

The responses to visual targets following masked primes are generally modulated in a biphasic pattern, depending on the SOA between the prime and the target. Indeed, with respect to a neutral condition with no prime-target association, facilitation for congruent and interference for incongruent pairs (positive prime effects) are obtained if the target is presented within 60 ms from the prime onset. Conversely, when the target is presented after longer delays from the prime onset (100-200 ms), an opposite pattern is obtained, with interference for congruent and facilitation for incongruent prime-target pairs (negative prime effects) as compared to the neutral condition. The positive and negative prime effects are thought to reflect, respectively, an initial facilitation of the motor response activated by the prime, which is soon followed by self-inhibition mechanisms within the motor system that suppress unwanted motor responses (Boy & Sumner, 2011; Eimer & Schlaghecken, 1998, 2003; Sumner, 2007). The interference for incongruent *vs.* congruent motor responses obtained in Experiments 3 and 4 is in keeping with the positive priming effects induced by high-visibility primes. On the other hand, the fact that we did not find any positive or negative priming effects in condition of low prime visibility cannot be ascribed to insufficient time for the manifestation of the visuo-motor priming effects (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003), because the SOA was 183 ms in Experiment 3, 163 ms in Experiment 4 and 166 ms and 250 in Experiment 5 thus being, for all Experiments, in line with the SOA at which negative priming effects are typically obtained

(Eimer and Schlaghecken, 2003). Furthermore, the absence of visuo-motor priming effects for subliminal condition on either response initiation or completion times suggest that the results are unlikely to be ascribed to different time courses of the effects of consciously and unconsciously action primes. However, an important factor that must be considered is that negative visuo-motor prime effects strictly depend on the selection of the motor response concurrently required by the explicit task (Eimer and Schlaghecken, 1998, 2003) and seem to reflect the association of the prime and target with the same or different lateralized motor responses. In contrast, in our study, the two action primes were associated to the same motor response in the task administered in Experiment 3 (i.e., reporting implied-action hands) and were task-independent in Experiment 4 and 5 (i.e., discriminating the frame color).

Automatic imitation may involve different processes from those explaining the visuo-motor priming of responses to spatial cues.

2.3.9 Spatial compatibility affects visuo-perceptual, but not visuo-motor action representations

A further aim of the present study was to clarify and dissociate spatial compatibility and action-specific representations in visuo-perceptual and visuo-motor action priming. To this end, we presented the prime hand in a perspective that was congruent or incongruent with the perspective of the probe hand (in Experiment 2, testing visuo-perceptual priming) or with the posture of the participant's responding hand (in Experiment 4, testing visuo-motor priming). Such manipulation changed the side of the space in which the finger movements occurred, reversing spatial and action congruence, without changing the identity of the depicted hand. In Experiment 2, we found that spatial compatibility between the prime and the probe action modulated the visuo-perceptual action priming in conditions of high but not low prime visibility. Whereas action-congruence facilitation with low-visibility primes was obtained independently of perspective compatibility, facilitation for congruent prime-probe pairs and interference for incongruent prime-probe pairs (with respect to neutral trials) were obtained only when the prime and probe perspectives were compatible. The null effect in condition of incompatible perspective might reflect the interaction between action and spatial congruence, which cancelled each other out when the same moving finger occupied opposite positions in the prime and in the probe. Such interaction, however, was present only when the prime was consciously perceived. This suggests that, whereas perceptual action representations are activated at a completely unconscious processing level, the orienting of spatial attention is not activated by such low-visible primes that could not be detected by the participants even when they were directly prompted to it. In the same way, previous studies (Ivanoff & Klein, 2003; Mele, Savazzi, Marzi, & Berlucchi, 2008) investigating the effects of spatial attention on the detection of visual targets presented to the left or right side showed that lateralized cues induced facilitation for cued locations only when they were presented in conditions of high-visibility, but no effects were induced by low-visibility cues. Importantly, the spatial-compatibility facilitation was obtained when the cue-target SOA was between 105-150 ms, which is similar to our prime-probe SOA, while inhibition for detecting targets at cued locations and facilitation for detecting targets at uncued locations (the so called inhibition of return effect; Berlucchi, 2006; Posner, Rafal, Choate, & Vaughan, 1985) were found for both low- and high visibility cues when the cue-target SOA was 750 ms or longer. This suggests that spatial compatibility, also in conditions of low prime visibility, might affect visuo-perceptual action priming at longer SOAs than those used in this study, with the expected outcomes of aiding to it for incongruent perspectives and hindering it for congruent perspectives.

Although spatial compatibility affected visuo-perceptual action priming in conditions of high prime visibility, no spatial compatibility effects were obtained for visuo-motor priming in Experiment 4. Indeed, no effects were obtained for low-visibility primes, independently from their perspective; conversely, comparable visuo-motor priming effects were obtained for high visibility primes when the perspective of the prime hand was both congruent and incongruent with the participants' hand. This is in keeping with previous findings that automatic imitation is independent of spatial compatibility (Catmur & Heyes, 2011; Heyes, 2011). Notably, while previous studies have controlled spatial compatibility effects by presenting left and right hands, we always presented right hand stimuli viewed with the fingers pointing upward or downward. This is crucial to ensure exact mapping of the same hand actions in the prime and in the response. However, previous neuroimaging (Shmuelof & Zohary, 2006, 2008) and behavioral (Vainio and Mustonen, 2011) studies have shown an inversion motor hand representation and of the visuo-motor priming for lateralized motor responses when the hand was shown in allocentric with respect to egocentric perspective. However, the inversion of the visuo-motor priming effects was only reported when the priming hand was presented for long presentation times (more than one second), whereas a negative priming effect on lateralized motor responses has been obtained also for egocentric views of hand primes presented for short presentation times (Vainio, 2011; Vainio & Mustonen, 2011). On the other hand, although previous studies have shown that motor activation during action observation is higher for actions viewed from a spatial perspective which is compatible rather than incompatible with the observer’s posture, they have also consistently shown that the occurrence of such motor activation is independent of the action perspective (Alaerts et al. 2009; Maeda et al. 2002; Urgesi, Candidi et al. 2006). At the behavioral level, our data are in keeping with previous evidence (Bortoletto, Mattingley, & Cunnington, 2013) of visuo-motor priming effects in both egocentric and allocentric views and further suggest that they occur even when the observer has to respond to a symbolic, non-spatial cue and has to ignore the action stimuli (Experiment 4 and 5). Furthermore, the results suggest that visuo-motor interaction in representing observed actions, no matter of their viewing perspective, requires perceptual awareness.

2.3.10 Multiple perceptual and motor action representations

One may argue that our claim that visuo-motor interaction requires the conscious processing of observed actions is based on a null result, which always leaves open the possibility that other manipulations of stimuli visibility and task response might lead to different results. Obviously, this argument is an inevitable corollary of any report of absent modulation following the manipulation of stimulus visibility (or other variables) and would make it virtually impossible to demonstrate that action observation requires perceptual awareness. It should be noted, however, that the same manipulation of the visibility of action primes did not hinder their effects on action perception, because visuo-perceptual action priming was consistently obtained during various action perception tasks (action detection or discrimination) even in low-visibility conditions. Furthermore, the same task responses were affected by action stimuli that were consciously perceived independently of their role in the task (i.e., the probes in Experiment 3 and the high-visibility primes in Experiment 4 and 5). Finally, not only were visuo-perceptual and visuo-motor action-priming effects affected differently by the reduction of stimulus visibility; they were also affected differently by spatial compatibility, with interacting effects for the first and no modulation for the latter. Thus, the most tenable interpretation of the data is that action observation affects subsequent action perception and action execution via different processes. This does not hamper the general notion of common-coding hypotheses (Hommel & Müsseler, 2001; W. Prinz, 1997) that observed actions are perceived using internal models of the sensory consequences of executed actions, but it argues against a complete isomorphism between perceptual and motor action representations. Our results are in keeping with multiple perceptual and motor representations of actions, which only partially overlap, may interact in certain circumstances and not in others, are affected differently by perceptual awareness and spatial compatibility and may ultimately serve different functions.

Considering the action priming effects at the functional level, an important factor that needs to be considered is the level of action representation that was tested in the present study as in other automatic-imitation paradigms (Heyes, 2011). Indeed, the association between the prime and probe stimuli and between the prime and the manual response concerned the specific kinematics of intransitive movements. In hierarchical models of action representation (Grafton & Hamilton, 2007; Keele, Cohen, & Ivry, 1990) this corresponds to the first level of movement implementation (e.g., abducting or flexing a specific finger) as compared to that of action (e.g., reaching or grasping an object), immediate (e.g., pressing a button or taking an object) and remote goal (e.g., switching the light or feeding). Thus, while the present study suggests that at least partially different processes are involved in the influences of action observation on action perception and execution at the movement level, this does not rule out that common perceptual and motor coding is involved in representing actions at more abstract levels.

Previous studies (Costantini et al., 2008) have shown that action observation may prime subsequent action perception independently of the specific effector used (e.g., taking an object with the hands or the feet). In a similar way, the observation of object-directed actions executed with different effectors induced similar activation of the motor representation of the muscles typically involved in achieving the observed goal (Senna, Bolognini, & Maravita, 2013). Such coding of action end-goals or effects has been also called into action to explain the interaction between language and motor processing, as demonstrated for example with the action-sentence compatibility effect (e.g., Diefenbach, Rieger, Massen, & Prinz, 2013; Ibáñez et al., 2013). In this paradigm, processing sentences that describe motor actions (e.g., moving an object away from the body) affects the execution of motor responses whose effects are congruent vs incongruent to the direction of the action effects described in the sentences. This action-sentence compatibility effect is independent from the specific body movements performed to obtain the action effects, suggesting that it involves common-code representation of action goals (or effects), rather than of specific motor programs, during language and motor processing (Diefenbach et al., 2013). Furthermore, recording of cortical dynamics during the action-sentence compatibility task has shown that such language-motor interaction is reflected into modulation of neural activity in both motor- and semantics- related areas (Aravena et al., 2010; Ibáñez et al., 2013). Overall, these studies point to the existence of an abstract, effector’s independent representation of the goal of observed and executed actions, which might allow the direct understanding of others’ behavior (Rizzolatti & Sinigaglia, 2010). It is unlikely, however, that such abstract goal-representation was activated by observing the simple, intransitive finger movements used in the present study as well as in previous automatic imitation paradigms (Heyes, 2011). Thus, we argue that the visuo-perceptual and visuo-motor priming reported here were based on the coding of the movement kinematics of observed actions. At the perceptual level, the activation of movement-specific representations might serve the dynamic integration of different movement phases into a unitary, smooth perception of biological motion, a process that may occur at an unconscious level of perception (Güldenpenning, Kunde, Weigelt, & Schack, 2012). At the motor level, the specific representation of the movement kinematics might serve the replica of the same movements (i.e., imitation), a process that seems to proceed in an automatic manner, independently of the observer’s task, but requires perceptual awareness.

In conclusion, the absence of any effect of the congruence between the specific prime action and the executed motor responses in the low-visibility condition of our study suggests that automatic imitation effects require perceptual awareness and operate at a conscious level of action representation. Such only conscious motor processing of others' actions may allow us to simultaneously address numerous agents and multiple and possibly incongruent actions that we must flexibly imitate, complement or react to (Sartori, Cavallo, Bucchioni, & Castiello, 2012) without being overloaded by unwanted and uncontrollable automatic imitation events.

2.4 Conscious and unconscious representations of observed actions in the human motor system

In this study, published in Journal of Cognitive Neuroscience (Mattiassi, Mele, Ticini, & Urgesi, 2014), my colleagues and I tested the modulation of corticospinal activity of individuals that passively observed masked hand action stimuli to investigate the impact of the unconscious perception of actions on motor resonance responses.

2.4.1 Methods

§ Subjects

Twenty-two healthy volunteers (11 females and 11 males) aged 19-34 years (mean = 23, standard deviation, SD = 4) participated to the experiment. Participants had normal or corrected-to-normal visual acuity and were all right-handed according to a standard handedness inventory (Briggs & Nebes, 1975). All participants were naive to the purpose of the experiment but received detailed information about the procedures. Participants gave written informed consent and received course credit for their participation in the study. The procedures were approved by the ethics committee of the Scientific Institute E. Medea (Bosisio Parini, Como, Italy) and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. None of the participants had neurological, psychiatric, or other medical problems or any contraindications to TMS (Wasserman, 1998). There were no reports or observations of any discomfort or adverse effects during TMS.

Stimuli

Stimuli were color pictures taken with a digital camera during the execution of abduction movements of the right index or little finger. Pictures from eight models (4 females and 4 males, aged 20-23 years) were used as stimuli to minimize habituation and loss of attention. For each model, three pictures of the hand were taken: a) a picture in a resting position; b) a picture with the index finger abducted (a movement that requires contraction of the first dorsal interosseous or FDI muscle); and c) a picture with the little finger abducted (a movement that requires the contraction of the abductor digiti minimi or ADM muscle). To preserve the appearance of naturalistic movement, each picture was taken while the model was moving the finger. Pictures were taken from an egocentric perspective in light of evidence of higher mirror-like motor facilitation in response to hand movements viewed from egocentric than allocentric perspective (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Maeda, Kleiner-Fisman & Pascual-Leone, 2002). Light conditions were kept constant across the three images of each model and the remaining luminance differences were manually corrected using Corel Paint Shop Pro X (Corel Inc., Mountain View, CA, USA). A rotating mask was prepared by overlapping two identical star-like geometrical figures that were textured with a scrambled version of the hand pictures using the Bryce 3D software (DAZ Productions, Inc, Salt Lake City, UT, USA). To mask the displacement of the fingers to the left or the right side of the screen, the two star-like figures rotated in opposite directions at 0.63 Hz (i.e., 3° every 13.33 ms refresh event), with a velocity almost comparable to that of the abduction/adduction displacement of the finger (2.8°-4.3° every 13.33 ms refresh event). This way, we were able to mask not only the perception of the form cues (hand shape) but also any motion cues induced by the apparent displacement of the index or little finger. We prepared two different versions of the mask that were presented randomly in different trials. In one version, the foreground figure rotated clockwise, while the background figure rotated counterclockwise and vice versa for the other version. Hand and mask stimuli were presented on a uniform background and subtended a central 6° × 8.5° region.

Procedure

Stimuli were presented in a subliminal masked priming paradigm (Fig. 5). Each trial started with a fixation cross presented in the center of the screen for 500 ms and proceeded to the successive presentation of the three following hand stimuli: a sample hand for 250 ms; a prime hand for 53 ms; and a probe hand for 250 ms. Prime duration was selected to be just below the threshold of conscious perception (i.e., subliminal) on the basis of preliminary behavioral data on a different group of individuals that could not report the presence of hand primes presented in the same paradigm as in this study. Pictures showing relaxed or abducted fingers were used instead of video clips since the stimulus duration required by subliminal masked presentations is too short for allowing even two-frame movement sequence at the typical 25 Hz video frame rate. Nonetheless, previous studies (Avenanti, Annella et al., 2013; Urgesi, Moro et al., 2006; Urgesi, Maieron et al., 2010) have provided evidence of muscle-specific, mirror-like facilitation in response to single frames depicting an implied action, thus supporting that our stimuli are adept to study motor resonance. The sample hand was always a still hand, while the prime and the probe stimuli could depict a still hand or a hand implying an abduction movement of the index or little finger. Prime presentation was forward and backward masked with the rotating star-like figure. The mask preceding the prime (forward mask) could rotate for 40, 80, 120 or 160 ms; the duration of the rotation was randomly selected for each trial and could not be predicted; random duration of the rotating forward mask was aimed at limiting anticipation of the time of prime presentation, which could be perceived by participants as a flickering of the mask. On the contrary, the mask following the prime (backward mask) presented a rotation of 120 ms, thus inducing constant backward masking effects. Notably, the rotation of the backward mask started from a point congruent to that expected from a continuous rotation of the star-like figure during the prime presentation time; this facilitated the perceptual fusion of the forward and backward mask rotation into a single, smooth movement, thus strengthening the possible masking effect. After a 2,000, 2,500, 3,000 or 3,500 ms delay following probe presentation (with delay duration randomly varying for each trial), a response screen was presented with the request to report whether a still or a moving probe (either index or little finger movement) was pictured in the preceding trial. In different trials, participants were asked: “Was the hand still or moving?”, “Was the hand moving or still?”, “Was the hand moving?”, or ”Was the hand still?”. In no trials were the participants asked to report whether the probe hand displayed movement of the index or little finger. The question was presented for 3,000 ms on the left of the response screen, while two possible answers (still or moving; yes or no) were simultaneously presented on the right. Subjects were instructed to report by means of a vocal response the position of the correct answer (up or down) based on the type of probe. The vertical position of the correct answer was randomly varied across trials. This procedure was chosen to prevent spurious priming effects on the size of motor evoked potentials (MEPs) such as sublexical processes that are known to activate M1 (e.g., McGettigan, Warren, Eisner, Marshall, Shanmugalingam, & Scott, 2012).

A single TMS pulse was delivered at one of two moments during the trial, either 133 ms (early delay) or 307 ms (late delay) after the onset of the probe, corresponding to 307 ms after the onset of prime in the early delay and 307 ms after the onset of the probe in the late delay. A blank screen was presented before the next trial to create interpulse intervals ranging from 11713 to 11833 ms (Brasil-Neto, Cohen, Panizza, Nilsson, Roth, & Hallett, 1992).

Participants were tested in a single experimental session lasting ~75 min. They sat in a dimly lit room 57 cm away from a 21-inch CRT monitor (resolution: 1024 x 768 pixels, refresh frequency: 75 Hz) with their heads positioned on a chin rest. Participants were instructed to pay attention to the sequence of hands presented on the screen but were informed only of the presence of the sample, mask, and probe hands. Thus, they were naïve regarding the presence of the prime hand.

The different conditions were presented in a randomized order in eight blocks of 48 trials each. In half of the trials, a still probe was presented, and in the other half, a moving probe was presented. Half of the moving probe trials displayed an index finger movement, and the other half presented a movement of the little finger. Thus, the same numbers of moving and non-moving trials were presented to avoid biasing the participants in the motion detection task. The TMS delay was randomly varied in each trial. In total, 384 MEPs were recorded from each muscle, with 192 still probe trials (32 trials for each of the 2 delays × 3 primes), 96 index finger movement probes (16 trials for each of the 2 delays × 3 primes) and 96 little finger movement probes (16 trials for each of the 2 delays × 3 primes). Two series of eight baseline MEPs were recorded at the beginning and at the end of the experimental session during which participants were required to look at the screen, but no stimuli were presented.

After the experimental session, participants were prompted to report any discrepancies between the instructions given and their understanding of the trial structure during the experiment. This allowed us to test for spontaneous reports of the prime presence. Following this report, the experimenter described the actual trial structure, including the presence of the prime. Participants were then asked for a confirmation of their previous report and were required to perform a control, forced-choice task to determine whether they could discriminate the type of prime after being informed of its presence. In this forced-choice task, participants were presented with the experimental trials, and after each trial, they were asked to press one of three keys to report whether the prime showed a still hand, a hand with the index finger abducted or a hand with the little finger abducted. They were instructed to answer “by feeling” and to guess for every trial in which they did not notice the presence of the prime. The trial structure used was identical to that used during TMS, with the exception that the response screen was replaced by a request for a button press in the middle of the screen. This ensured participants were faced with exactly the same conditions as in the main experiment. No time limit was given for the participants’ responses. The next trial started immediately after the response. All 384 trials of the experimental session were presented and randomized in 2 blocks of 192 trials each. The control task lasted approximately 4 min.

Electromyography recording and transcranial magnetic stimulation

To check for muscle specificity and for any modulation related to the different observational conditions, both FDI and ADM MEPs were simultaneously recorded. Surface Ag/AgCl disposable electrodes (1 cm diameter) were placed in a belly-tendon montage for each muscle and connected to a Biopac MP-36 system (BIOPAC Systems, Inc., Goleta, CA, USA) for amplification, band-pass filtering (5 Hz–20 kHz), and digitization of the EMG signal (sampling rate: 50 kHz).

A 70 mm figure-eight stimulation coil (Magstim polyurethane-coated coil) connected to a Magstim 200 Rapid (The Magstim Company, Carmarthenshire, Wales, UK) was used to perform focal TMS (maximum output: 2 T at coil surface, pulse duration: 250 µs, rise time: 60 µs). The coil was placed tangentially on the scalp, with the handle pointing backward and approximately 45° lateral from the midline such that coil was placed perpendicularly to the line of central sulcus (Di Lazzaro et al., 1998). The coil position was marked on the subjects' scalp. The coil was held on the scalp by a coil holder with an articulated arm, and the experimenter continuously checked the position of the coil with respect to the marks and compensated for any small movements of the participant's head during data collection. The exact position of the coil varied for each participant on the basis of the optimal scalp position (OSP), which was defined as the position from which MEPs from both the FDI and ADM muscles with maximal amplitude were recorded. The OSP was detected by moving the coil around the motor hand area of the left motor cortex projection on the scalp and delivering single TMS pulses of constant intensity. The resting motor threshold (rMT), defined as the lowest TMS intensity able to evoke MEPs with amplitudes of at least 50 µV after 5 out of 10 stimulations in the higher threshold muscle (ADM), was determined by holding the stimulation coil over the OSP. To record stable MEPs from both muscles, stimulation intensity during the recording session was 120% of the rMT and ranged from 50% to 84% (mean: 67%, SD: 8.46%) of maximum stimulator output. Importantly, the chosen scalp positions and stimulation intensities allowed us to record clear and stable EMG signals (10 MEPs from 10 TMS pulses) from both recorded muscles in all participants. During MEP recordings, the background EMG signal was continuously monitored, and when voluntary contractions of the recorded muscles were detected, participants were encouraged to fully relax their muscles. The peak-to-peak MEP amplitudes (in millivolts) were collected and stored on a computer for offline analysis.

Data handling

Five participants were excluded from the analysis because they reported the presence of the prime spontaneously or after receiving a description of the actual trial structure. This procedure is weak to false positives (i.e., reports of seeing the prime after the explanation of its presence by participants that were actually unaware of the prime) but not to false negatives (i.e., participants that were aware of the prime failing to report its presence). The remaining participants were entirely unaware of the presence of the prime. The peak-to-peak amplitude of each MEP was calculated, and trials with background activities greater than 50 µV, amplitudes less than or equal than 50 µV, or amplitudes greater or less than ± 2.5 SD from the mean were discarded. After this procedure, mean values were obtained from an average of 92.52% (SD: 7.31%) of the recorded MEPs per condition. The number of recorded MEPs did not vary across the different experimental conditions between the early and late delays (all Fs < 2.6), but there was a significant effect of muscle in the early delay MEPs; fewer MEPS from the little finger (mean: 91.87%, SD: 1.09%) than from the index finger (mean: 92.79%, SD: 1.02%) were used.

For each subject and each condition, the mean MEP amplitude for each muscle and for each TMS pulse delay was expressed as % change from the mean value of the baseline MEPs of that muscle (baselines were collapsed across the MEPs recorded at the beginning and at the end of the experimental session). This procedure allowed us to obtain a MEP ratio index of motor facilitation, hereafter referred to as the MEPratio, which takes into account inter-individual differences in baseline corticospinal excitability. The levels of the prime and probe for each experimental trials were coded into the following categories based on the correspondence between the muscle from which MEPs were recorded and the muscle that drives the observed movement: a) still —still hands for both muscles; b) related—index finger movements for FDI MEPs and little finger movements for ADM MEPs; c) unrelated—little finger movements for the FDI MEPs and index finger movements for ADM MEPs. It is worth noting that behavioral studies of visuomotor priming effects (eg., Brass, et al., 2000; Stürmer et al., 2000; Kilner et al., 2003) tend to code the conditions according to the congruency between the prime and the probe actions. However, since the critical measure in this study is the facilitation of the corticospinal excitability of a specific muscle, which action is shown and not whether prime and probe pairs are congruent or not is crucial for the effects. Thus, in keeping with previous single-pulse TMS studies of visuomotor interaction (Catmur Mars, Rushworth, & Heyes, 2011), we coded the prime and probe conditions in terms of whether they showed a static hand or an implied action that was related *vs.* unrelated to the motor role of the recorded muscle. Furthermore, since the action (i.e., index finger abduction) that is related to the FDI motor role is unrelated to the ADM motor role, and vice versa, expressing conditions in terms of related/unrelated actions, instead of index/little finger abduction, allowed us to directly test somatotopic motor facilitation (i.e., greater motor facilitation during observation of actions whose execution requires the recorded muscle versus observation of static hand and of actions that do not involve the recorded muscle), independently of which specific action and muscle were involved.

The MEPratios for each condition were entered into two separate 2 × 3 × 3 repeated-measures ANOVAs, one for each TMS delay, with muscle (FDI *vs.* ADM), prime (still *vs.* related *vs.* unrelated) and probe (still *vs.* related *vs.* unrelated) as within subject variables. Separate analyses for the two TMS delays were performed to avoid the spurious effect of the context in which the pulse was delivered: in the early condition the pulse was delivered during probe observation, while in the late condition the pulse was delivered during blank screen observation, thus confounding any possible comparison. Post-hoc multiple, pairwise comparisons were performed using the Duncan test. A significance threshold of $p < 0.05$ was set for all statistical analyses. Data are reported as the mean ± the standard error of the mean (s.e.m.).

We expected that, if motor facilitation is independent of perceptual awareness, muscle-specific motor facilitation should be obtained in response to both probe and prime action stimuli (main effects of prime and probe). Conversely, if the motor representation of observed actions is dependent on conscious processing, we expected to obtain motor facilitation in response to the probe but not the prime (main effect of probe). Finally, the masked action prime may not trigger motor facilitation per se, but it may modulate the response of the motor system to consciously perceived actions. In this case, we would expect an effect of the prime-probe congruence only for implied action probes that call for motor representations, i.e., only when the probe shows a movement related to the recorded muscle (prime × probe interaction). Thus, the presentation of congruent *vs.* incongruent prime-probe pairs should be specific for trials in which the probe shows an action that is related to the motor role of the recorded muscle (i.e., related prime and related probe pairs *vs.* unrelated or still prime and related probe pairs) but not when the probe shows an action that is not related to the motor role of the recorded muscle (i.e., related prime and unrelated probe pairs *vs.* unrelated or still prime and unrelated probe pairs). This would provide evidence that unconscious perception of the prime affected muscle-specific, mirror-like motor facilitation.

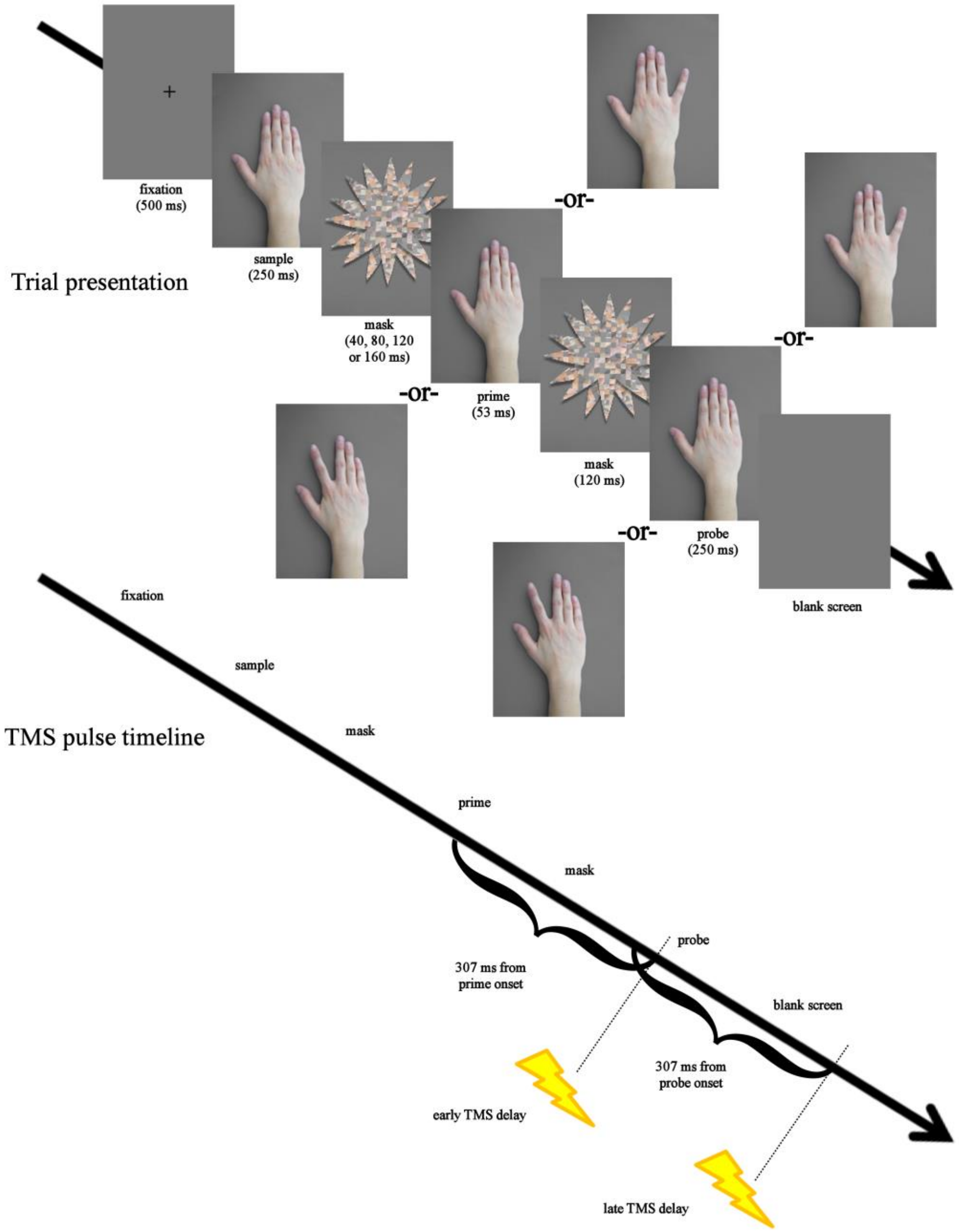


Figure 5. Trial structure of the experiment, including priming procedure and TMS timing.

2.4.2 Results

Behavioral data

Analysis of the behavioral responses of participants in the TMS session revealed that they paid attention to the stimuli and successfully discriminated whether the probe was moving or not (the mean accuracy in each condition ranged from 89.89% ± 2.66% to 96.69% ± 1.43%). No differences were obtained between the different experimental conditions (all Fs ≤ 2.22), suggesting that participants were equally accurate in both early and late delay trials, regardless of the prime or probe. In a similar vein, a signal detection analysis (Macmillan, & Kaplan, 1985) showed that participants had high sensitivity levels for detecting the probe motion when it was preceded by both still hand (d’ = 4.07 ± 0.24; one-sample t-test against 0: t(16) = 17.014, $p < 0.001$) and implied action primes (d’ = 3.57 ± 0.19; one-sample t-test against 0: t(16) = 18.62, $p < 0.001$), with the difference between the two conditions not reaching the significance threshold (t(16) = 1.781, $p = 0.094$). On the other hand no response bias was obtained when the probe was preceded by still (ln(ß) = -0.21 ± 0.63; one-sample t-test against 0: t(16) = -0.34, $p = 0.616$) and implied action primes (ln(ß) = 0.71 ± 0.38; one-sample t-test against 0: t(16) = 1.82, $p = 0.087$); no difference was obtained between the two prime conditions (t(16) = -0.909, $p = 0.151$).

The 17 participants who were entered into the analysis reported that they were unaware of the presence of the prime in the TMS session. Their overall discrimination accuracy in the post-TMS session was 39.22% (SD: 10.03%), which was not significantly different from chance (two-tailed one-sample t-test against 33.333%, t(16) = -1.895, $p = 0.076$, Cohen’s d = 0.47). Although such overall comparison showed that participants’ discrimination ability tended to be higher than that expected by guessing, effect size was small. More importantly, inspection of the mean accuracy values for each prime-probe pair (Table 1) revealed that such an effect was driven by apparently accurate responding when the prime and the probe actions were congruent but not when the probe depicted an action incongruent with the prime or a neutral, still hand. Indeed, a 3 × 3 repeated measures ANOVA of the participants’ prime discrimination accuracies with probe (still *vs.* index finger abduction *vs.* little finger abduction) and prime (still *vs.* index finger abduction *vs.* little finger abduction) as within-subjects variables showed that participants' response to the prime was modulated by the type of probe: the main effect of probe was significant (F(2,32) = 3.82; *p* = 0.033; ŋp2 = 0.1926) and was further qualified by the interaction between probe and prime (F(4,64) = 12.32; *p* < 0.001; ŋp2 = 0.4351). Post-hoc tests showed that, in still probe trials, participants were more accurate in discriminating still primes than primes showing index (*p* = 0.006) or little finger abduction movements (p < 0.001). The last two conditions did not differ from one another (*p* = 0.347). Furthermore, in the trials with probes showing an index or little finger abduction, participants were more accurate in identifying primes showing a movement congruent with the probe than they were for primes showing a still hand (index finger probes: *p* < 0.001; little finger probes: *p* = 0.013). Participants also tended to be more accurate for congruent than incongruent probe-prime movements, but this difference reached significance only for the index (p < 0.001) and not the little finger probes (*p* = 0.062). No difference was obtained between incongruent movement and still hand primes (index finger probes: *p* = 0.369; little finger probes: *p* = 0.461). Together, these results suggest that, even when participants were informed about the presence of the prime and were actively pursuing its identification, they tended to report the action showed by the probe and not that shown by the prime. This explains greater accuracy levels for congruent prime-probe pairs *vs.* incongruent ones and marginally above-chance overall accuracy levels. These results corroborate the participants' subjective reports showing that the masked action primes were not consciously perceived and could not be explicitly discriminated in a forced choice task.

Corticospinal excitability

The MEPs recorded from each muscle at the beginning and at the end of the experimental session were entered into a 2 × 2 repeated-measures ANOVA with muscle (FDI *vs.* ADM) and session (pre- *vs.* post-TMS) as within subject variables. A main effect of muscle was found (F(1,16) = 6.12; *p* < 0.001; ŋp2 = 0.5705): MEPs recorded from the FDI (1.811 ± 0.473 mV) were greater than MEPs recorded from the ADM (0.883 ± 0.131 mV, *p* = 0.025). The main effect of session and the interaction between muscle and session were not significant (all Fs < 1, ŋp2 < 0.01).

Table 2 shows the raw MEPs amplitudes (in millivolts) in the different experimental conditions. Inspection of Table 2 reveals that MEPs amplitude at both TMS delays was higher during the observational task than at baseline, independently of whether participants were fixating at a still hand or a hand performing a movement that was either related or unrelated to the motor role of the recorded muscles. This was confirmed by dependent-sample t-tests (one-tailed) comparing the average of raw MEPs during the 9 observation conditions at each TMS delay and for each muscle. Indeed, FDI MEPs amplitude was higher during observation than at baseline when TMS was delivered at either early (2.067 ± 0.511 mV; t(16) = 2.8, p=0.006) or late (2.039 ± 0.513 mV; t(16) = 2.52, *p* = 0.011) delay from stimulus onset; the same comparisons with baseline for the ADM muscle were only marginally significant (early: 1.078 ± 0.195 mV; t(16) = 1.69, *p* = 0.055; late: 1.066 ± 0.192 mV; t(16) = 1.61, *p* = 0.064). In a similar vein, dependent-sample t-tests (two-tailed) showed that no difference was obtained between MEPs amplitudes recorded at early and late TMS delays for either FDI (t(16) = 0.88, *p* = 0.39) or ADM (t(16) = 0.9, *p* = 0.38) muscle during the observation conditions. In sum, during observation of hand stimuli we found an overall increase of corticospinal excitability that was not specifically associated to implied actions as it also occurred for still hand images. This is in keeping with previous studies showing that body part observation activates the motor cortex more than baseline trials in which participants either keep the eyes closed or fixate at a blank screen (e.g., Borgomaneri, Gazzola, & Avenanti, 2012; Hodzic, Muckli, Singer, & Stirn, 2009; Raos, Kilintari, & Savaki, 2013; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006)

Modulation of motor facilitation

Previous analysis of raw MEP amplitudes showed that as compared to viewing a blank screen, observation of hand images increased corticospinal excitability. Since mirror-like motor facilitation is indexed by a greater activation during observation of dynamic (or implied action) bodies or body parts as compared to still bodies or body parts (Fadiga et al., 2005; Urgesi, Candidi, et al., 2006; Urgesi, Moro et al., 2006), in the successive analysis we tested how corticospinal excitability was modulated according to the hand image that was presented. We thus expressed

MEPs amplitude of each muscle as % change (MEPratio; Fig. 6) from that muscle baseline, averaging the baseline MEPs collected at the beginning and at the end of the experimental session. This gave a motor facilitation index of how much the motor cortex was facilitated during observation of hand images as compared to baseline. The MEPratio values for the two TMS delays were entered into two separate 2 × 3 × 3 (muscle × prime × probe) repeated-measures ANOVAs to test whether motor facilitation was greater during observation of related actions than still hands and unrelated actions depicted in either the probe or the prime.

The ANOVA for the early TMS delay condition yielded no significant effect (all Fs < 1.1; $p > 0.35$), suggesting that motor facilitation at this delay from stimulus onset was not specific for the action depicted in the images. The ANOVA for the late TMS delay condition yielded significant main effect of probe (F(2,32) = 5.6776; $p = 0.008$; ŋp2 = 0.2619). The main effect of prime was not significant (F(2,32) = 1.5; $p = 0.239$; ŋp2 = 0.086), but a significant interaction between prime and probe was found (F(4,64) = 3.23; $p = 0.017$; ŋp2 = 0.168), suggesting that motor facilitation during observation of muscle-related probe actions was modulated by masked prime actions. The three-way interaction was not significant (F(4,64) < 1; ŋp2 < 0.05), suggesting comparable patterns of results for the two muscles when movements that were related versus unrelated to their motor roles were observed. Simple effect analysis of mirror-like motor facilitation in response to related as compared to still and unrelated probes showed significant effects for still (F(1,16) = 9.09, $p = 0.008$) and related (F(1,16) = 11.76, $p = 0.003$) prime trials but not for unrelated prime trials (F(1,16) < 1). Thus, the observation of a probe stimulus implying a finger movement induced a significant facilitation of the corticospinal representation of the muscle involved in the execution of that movement when the probe was preceded by a still (neutral) prime and by a related (congruent) prime. In contrast, no mirror-like facilitation was obtained when the probe was preceded by unrelated primes, showing comparable motor facilitation for related than still and unrelated probes.. Pair-wise post-hoc analysis of the interaction between the probe and prime hands revealed no differences among the three prime types in the unrelated and still probe conditions (all $p > 0.102$). Conversely, when the probe was related to the recorded muscle, MEPratios in the unrelated prime trials (117.34 ± 10.89%) were lower than those in the related prime trials (130.9 ± 13.08%, $p =$

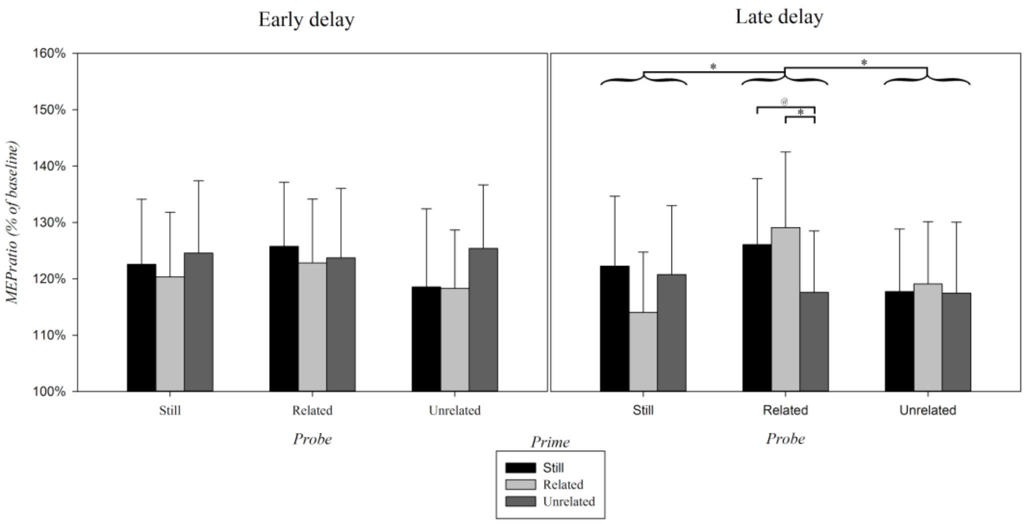


Figure 6. Results.

0.006) and marginally lower than the MEPratios in the still prime trials (126.66 ± 11.77%; $p = 0.059$); the related and still prime trials did not differ from each other ($p = 0.308$). Indeed, MEPratios in the related probe-unrelated prime condition were not significantly different from MEPratios in the still and unrelated probe conditions regardless of the prime type (all $p > 0.319$). Since motor facilitation for still hands and unrelated movements reflects non-specific activation in response to viewing body parts, no evidence of mirror-like motor facilitation was obtained when related movement probes were preceded by primes showing a movement that is unrelated to the motor role of the recorded muscle. Thus, presentation of an unrelated prime suppressed motor facilitation to a level that is expected in response to observation of body parts independently of movement information.

2.4.3 Discussion

In this study, we provide evidence that motor resonance, as indexed by greater motor facilitation in response to related than static hands and unrelated actions, is not elicited by unconscious action perception but requires perceptual awareness. Nevertheless, its expression in response to consciously perceived actions is modulated by unconscious perception of incongruent actions. We tested corticospinal excitability while participants passively observed static images of either still or moving hands preceded by masked primes of either the same or different movement. Our results show the following: i) observation of the action probe, which was consciously perceived, engendered a somatotopic activation of the cortical representation of the muscles actually involved in the same action when compared with observation of a still hand or of unrelated actions; ii) subliminal perception of the action prime did not increase motor facilitation more than observation of a still hand, suggesting that actions need to be consciously perceived to evoke mirror-like motor facilitation (motor resonance); and iii) unconscious priming of actions unrelated to the motor role of the recorded muscle interfered with mirror-like motor facilitation (motor resonance) in response to consciously perceived probe actions that are related to the motor role of the recorded muscle.

2.4.3.1 Conscious perception of implied actions activates the motor system

Several studies have shown that passive observation of dynamic displays (Fadiga et al., 2005; Urgesi, Candidi, et al., 2006; Avenanti, Bolognini, Maravita, & Aglioti, 2007; Avenanti & Urgesi, 2011; Tomeo, Cesari, Aglioti, & Urgesi, 2013) and static images of bodies in action (Urgesi, Moro et al., 2006, 2010; Proverbio, Riva, & Zani, 2009; Avenanti, Annella et al., 2013) triggers somatotopic activation of the motor system and thus facilitates the corticospinal representation of those muscles involved in the perceived actions; this effect is thought to reflect motor resonance. Hence, motor resonance is involved in the extrapolation of dynamic information from actual as well as implied action stimuli. Although static images were used in the present study, these images were presented in a sequence of three snapshots (i.e., sample, prime and probe) rather than in a single static frame. This sequence may have contributed to the apparent motion perception if the mask served as a temporal occluding object and the successive hand postures were amodally completed into a continuous perception of movement (Shiffrar & Freyd, 1993). If true, this interpretation is in keeping with the notion that the amodal completion of occluded actions may involve automatic motor resonance processes (Orgs, Bestmann, Schuur, & Haggard, 2011; Urgesi et al., 2010; Avenanti & Urgesi, 2011).

Importantly, the different delays of TMS stimulation allowed us to test modulation of motor facilitation during observation of still, related and unrelated actions after a comparable delay (307 ms) from prime (early delay) and probe (late delay) presentation. Thus, we could test muscle-specific, mirror-like facilitation separately for unconsciously and consciously perceived stimuli. Magnetoencephalographic (MEG) studies (Nishitani & Hari, 2000; Nishitani, Avikainen, & Hari, 2004) have found that the responses to action observation peak first in the visual occipital areas (at approximately 118 ms from the onset of the stimulus) before subsequent activation of the superior temporal sulcus, inferior parietal lobule, inferior frontal areas and, finally, M1 at approximately 300 ms. Similarly, a recent TMS study (Barchiesi & Cattaneo, 2012) found that muscle-specific effects in M1 were observed only 250 ms after action stimuli onset. Therefore, any direct motor response to unconscious prime perception (i.e., main effect of prime) was likely to occur in the early TMS delay, since in that case processing of the prime action, but not of the probe action was likely to have reached the motor cortex. In contrast we did not find any modulation of the corticospinal excitability for the unconsciously perceived prime at the early TMS delay independently of the type of probe presented; nor did we found any effect of prime presentation when the probe depicted a still hand or an unrelated action, thus ruling out that unconscious action prime action perception may increase motor facilitation in a muscle-specific fashion more than observation of a still hand. Conversely, the late TMS delay, when the TMS pulse was delivered after 307 ms from probe onset, allowed us to show that muscle-specific motor responses are facilitated for the consciously perceived probe. In sum, our finding that motor facilitation in response to consciously perceived probe actions was obtained at the late TMS delay corroborates the temporal dynamics of cortical activations reported in previous MEG and TMS studies and suggests a late involvement of M1 in mapping observed (implied) actions.

2.4.3.2 Motor resonance requires perceptual awareness

The main aim of the present study was to test whether perceptual awareness is a condicio sine qua non for the emergence of motor resonance responses, measured as a facilitation of corticospinal excitability during observation of actions that are related to the motor role of the recorded muscle as compared to observation of a still hand or of an action that is unrelated to the motor role of the recorded muscle. The forward and backward masking procedure allowed us to present the prime for a relatively long time (53 ms) but nonetheless prevented conscious perception by most participants (17/22 individuals). Indeed, even when these participants were explicitly informed about the presence of the prime and were required to discriminate whether it depicted a still hand or an index or little finger abduction, their discrimination abilities were at chance. This suggests that manipulation of the voluntary control of the attentional focus did not affect the perception of the prime, since prime discrimination was not possible even when subjects were actively pursuing it. This does not exclude, however, that presentation of the probe stimulus may have contributed to prevent conscious perception of the prime with automatic attentional shift. Whether the locus of prime perception disruption was at a perceptual or attentional level, our paradigm ensured that subjects remained completely unaware of the prime action.

In striking contrast with the muscle-specific response to the probe, no motor facilitation was measured in response to the presentation of the prime (independently of the probe type and TMS delay). The absence of motor responses to masked action primes cannot be ascribed to the interferential effect of probe movement presentation because M1 responses to the prime in the still-hand probe conditions were also absent. Nor can this absence reflect that the presentation of either static or implied action probes completely suppressed the early processing of the masked prime stimulus in the visual system, thus preventing the result of this processing to be forwarded to the motor system. Indeed, we have evidence that the prime was processed to a certain extent and the result of this processing affected the activation of the motor system, since the presentation of incongruent action primes suppressed the motor resonance to implied action probes (see below). Furthermore, it is also unlikely that the absence of motor responses to masked action primes was due to inappropriate timing of the TMS pulses; indeed, in both the early and late TMS delay conditions, corticospinal excitability was tested after the 250 ms threshold for the establishment of muscle-specific motor resonance responses to the prime (Barchiesi & Cattaneo, 2012). Given our experimental settings, however, we cannot exclude the possibility that masked action stimuli may have modulated motor cortex activity at earlier phases of stimulus processing, for example in the 60-90 ms time window in which a nonspecific activation of the motor cortex in response to action stimuli has been reported (Lepage, Tremblay, & Théoret, 2010). However, because this early activation lacks muscle specificity, it is unlikely to reflect motor resonance. Together, our data suggest that motor resonance requires awareness of the action stimuli.

Action stimuli with an emotional valence are known to activate the motor system in conditions of reduced visibility or when subjects are not aware of the stimuli. Emotional face and body expressions induce fast facial mimicry responses (Tamietto et al., 2009) (i.e., electromyographic preactivation of the muscles involved in the same expressions) and motor and premotor cortical activations (Van den Stock et al., 2011) even when presented in the blind hemifield of hemianopic patients or in masked presentation conditions in healthy individuals (Dimberg et al., 2000). Such affective facial mimicry responses, however, are not specific for the observed body parts because they also occur in response to whole-body emotional expressions and lack the muscle-specific properties of motor resonance responses. Thus, these responses seem to be mediated by the activation of subcortical structures in response to emotionally valenced stimuli and are not involved in nonemotional actions (Tamietto & De Gelder, 2010).

2.4.3.3 Unconscious presentation of incongruent actions inhibits motor resonance

Although the subliminal presentation of masked prime actions did not trigger motor facilitation per se, it affected the activation of the motor cortex in response to consciously perceived actions. In other words, masked prime actions that were incongruent with the probe interfered with motor facilitation in response to the probe. This evidence of the implicit effects of unconscious action perception on motor resonance suggests the dissociation between visual awareness and the perceptual effects of masked action primes (Van den Bussche et al., 2009). Thus, in keeping with the finding that unconscious prime perception may affect motor execution processes during visuomotor masked priming tasks (Eimer & Schlaghecken, 1998, 2003), we show evidence that masked primes can affect motor resonance.

The suppression of motor facilitation during action observation is unlikely to involve a specific exogenous inhibition of motor activation induced by the abrupt interruption of stimulus presentation, as reported in visuomotor masked priming tasks (Eimer & Schlaghecken, 1998, 2003). Indeed, motor facilitation was suppressed for incongruent presentations of prime and probe movements, whereas visuomotor masked primes tend to inhibit the execution of congruent actions. Because no facilitatory or inhibitory responses to the prime were obtained with neutral (i.e., still hand) probes, the interaction between the probe and prime does not seem to be due to the orienting of spatial attention to the one or to the other side of the space. Accordingly, previous single-pulse TMS studies have shown that motor facilitation during action observation is based on mapping the specific muscle involved in the actual execution of the action rather than on the spatial compatibility between the model's and observer's body part (Alaerts, Van Aggelpoel, Swinnen, & Wenderoth, 2009; Urgesi, Candidi, et al. 2006). Furthermore, behavioral studies have shown that visuomotor interference effects occurred when the observed and executed movements involved different hands (i.e., left *vs.* right hand; Bertenthal, Longo, & Kosobud, 2006; Brass et al., 2000; Catmur & Heyes, 2011) or the same hand viewed from different perspectives (egocentric *vs.* allocentric perspective; Bortoletto, Mattingley, & Cunnington, 2013) and thus occurred in the opposite sides of the space. Even when visuomotor interaction was affected by the spatial compatibility between the executed and observed movement, this resulted into inversion of the effect (i.e., facilitation for incongruent actions) rather than into its suppression (Vainio & Mustonen, 2011). As such, the suppression of mirror-like (i.e. muscle specific) facilitation obtained in this study is unlikely to be due to the effects of spatial attention. In a similar vein it seems untenable a pure attentional account for the suppression of motor resonance to the probe, according to which the presentation of the incongruent prime may have diverted the focus of attention away from processing the probe action. Indeed, on the one hand, the prime was not perceived consciously and could not be discriminated even when the focus of attention of the observer was explicitly focused on its presentation, thus ruling out a role for voluntary control of attention. On the other hand, although prime presentation may have influenced probe processing by causing automatic attentional shift, the results of the online task suggest that participants could easily detect the probe action independently from whether the action shown by the prime, thus ruling out that the prime disrupted conscious perception of the probe at an extent capable of explaining the complete suppression of mirror-like motor facilitation. Accordingly, previous studies showed that attentional modulation of action perception may modulate, but not suppress motor resonance (Muthukumaraswamy & Singh, 2008). Thus, it is likely the effects of unconscious perception of prime actions on motor resonance to probe actions are at least partially independent from attentional modulation processes.

The present single-pulse TMS study is not informative regarding the possible neural site of the interaction between subliminal and supraliminal action processing. We can speculate that such interaction likely involves an area or set of areas that have direct or indirect connections to the primary motor cortex and that process both supra- and sub-liminal presentations of actions, thus explaining the effects of the masked action prime. Considering the pattern of results, two possible scenarios can be hypothesized. On the one hand, the facilitation induced by supraliminal probe actions and its suppression by subliminal incongruent prime actions may be due to separate mechanisms operating within the motor system. A possible candidate is the ventral premotor cortex, which is strongly connected to M1 (Prabhu et al., 2009) and seems to be the main source of the motor-resonance facilitation responses observed in M1 (Avenanti et al., 2007; Avenanti, Annella, et al., 2013; Avenanti, Candidi, et al., 2013). There is evidence of pyramidal tract neurons in the macaque ventral premotor cortex (Kraskov, Dancause, Quallo, Sheperd, & Lemon, 2009; but see a similar finding in M1; Vigneswaran, Philipp, Lemon, & Kraskov, 2013) that may exhibit one of two main patterns of activity: while one pattern consists in facilitation of the hand motor-neurons that mirrors the observed action and corresponds to what is generally called motor resonance, the other consists in a number of neurons being suppressed during action observation. This suppression is thought to prevent overt movements during action observation, but since the same neurons showed inhibitory responses in a variety of conditions (e.g., grip with object, grip without object, concealed grip) it may be that this inhibitory mechanism is less selective with regard to the specific action observed when compared to classical mirror facilitation. Importantly, facilitation and suppression neurons seem to be part of two parallel mechanisms in the ventral premotor cortex and their possible differential sensitivity to perceptual awareness and attentional modulation may explain the pattern of results obtained in the present study in the terms of facilitation of cortico-spinal excitability. Indeed, assuming that suppression neurons may respond to observed actions independently of their perceptual awareness, suppression of motor activity in response to the prime and/or probe actions may remain unnoticed in a gross measure of cortico-spinal excitability as done with TMS-evoked motor potentials. Nevertheless, the inhibition of their activity after presentation of two incongruent actions, which is likely stronger as compared to presentation of a single action, may contribute to suppress the expression of facilitation neuron activity in response to consciously perceived probe actions.

On the other hand, the suppression of motor facilitation for incongruent prime-probe actions may stem specifically from the processing of the conflict between two incongruent action representations in areas beyond the motor cortex but directly or indirectly connected to it. The detection of a conflict in these areas may generate a signal that is sent to the motor system to suppress motor resonance in response to consciously perceived actions. Unconscious processing of the conflict between different action-related cues may involve several cortical and subcortical regions (D’Ostilio & Garraux, 2012). For example, the pre-supplementary motor area is involved in exerting control over voluntary actions during response conflict (Nachev, Wydell, O’neill, Husain, & Kennard, 2007) and may also subserve the suppression of incongruent motor resonance responses. Furthermore, controlling the automatic tendency to imitate other’s actions, as tested in the visuomotor priming paradigm, involves activation in the ventromedial prefrontal cortex and the temporo-parietal junction (Brass et al., 2009; Spengler, Brass, Kühn, & Schütz-Bosbach, 2010). These areas are implicated in higher level mentalizing abilities, such as the sense of agency, perspective taking and self-referential processing (Brass, Ruby, & Spengler, 2009) and seem to be also involved in preventing the coding of others’ movements to be translated into self-movements. Finally, inhibitory afferents to M1 via cortico-striatal pathways play a role in masked visuomotor priming effects (Bowman, Schlaghecken, & Eimer, 2006; D’Ostilio & Garraux, 2012) and may also be involved during action observation (Marceglia et al, 2009) and, especially, suppression of unwanted motor resonance responses.

In conclusion, we show that although motor resonance in response to non-emotional actions is automatic, it requires the perceptual awareness of actions and operates at a conscious level of motor representation. While the presentations of subliminal actions do not activate the motor cortex, they suppress motor resonance responses to incongruent actions that are consciously perceived. We suggest that this suppression reflects the processing of action conflicts in areas upstream of the motor cortex and may subserve a basic mechanism for dealing with the multiple and possibly incongruent actions of other individuals. Motor resonance responses, indeed, seem to endow the social brain with the ability of simulating anticipatory representations of unfolding actions ahead of their realization and in the absence of complete perceptual information from the environment (Wilson & Knoblich, 2005; Avenanti & Urgesi, 2011; Avenanti, Candidi et al., 2013). Such representations, however, need to be flexibly updated on the basis of upcoming information, to take into account not only actual deployment of actions but also their future phases, and to be modulated by the social context toward imitative or complimentary responses (Sartori et al., 2013). The results of the present study suggest that modulation of motor resonance according to the social context (in this case incongruent actions) may also occur at an implicit level and independently of observer's perceptual awareness.

2.5 Conclusions

With our behavioural study, we showed that automatic imitation requires perceptual awareness. With our neurocognitive study we showed that motor resonance occurs automatically, but non mentalized actions don't activate the motor cortex: indeed, our results suggest that it suppresses motor resonance to incongruent subsequent actions. Both studies' results suggest that mentalization of perceived actions is needed in order to trigger motor resonance and to activate motor cortex and as such suggest the presence of a basic, implicit mechanism for dealing with multiple, incongruent actions of other individuals in a crowded environment aimed at avoiding being overload by automatic imitation.

3

Automatic and controlled mechanisms of emotion regulation in social adaptation

3.1 Introduction to emotion regulation

An important feature for a social animal is the ability to regulate its own behaviour in order to cope in an optimal way with the social environment. While in the previous chapter I introduced and explored the ability to process social stimuli, in this chapter I'm going to explore the ability of humans to regulate their behaviour by means of modulating their automatic emotional responses in social situations.

3.1.1 Emotional responses

There is a huge and long lasting debate going on in the scientific and philosophical communities about what emotions are, what their purpose is and how they operate. However, from an evolutionary point of view emotions are generally thought as sets of programs that drive cognitive, physiological and behavioural processes when problematic situations are encountered and need to be solved in a highly adaptive manner (e.g., Tooby & Cosmides, 1990). According to cognitive theories of emotions, the specific emotion that is triggered by a stimulus is determined in an early phase after stimulus processing, before physiological responses occur (e.g., Roseman & Smith, 2001). In contrast, according to non-cognitive theories, this early phase of stimulus processing is reflex-like, for at least some emotion (e.g., Ekman, 1992). Cognitive and non-cognitive theories differ also for considering bodily (physiological, somatic) responses as, respectively, a consequence or a part of the emotion. Finally, somatic feedback theories state that the feedback regarding bodily changes constitutes what is called emotion (Damasio, 2001; J. J. Prinz, 2004).

A component process definition of emotions, like the one proposed by Scherer (2005), describes emotions as stimuli elicited and appraisal driven (meaning that emotions always follow an event and depend on the evaluation of its relevance to the organism), massively and rapidly activating different response systems (outlined in the next paragraph) and synchronizing them, and heavily impacting the behavior. General agreement is found upon distinguishing emotions from similar affective contracts like moods (affective that last longer, are less intense and are not strictly stimuli driven) or affect dispositions (not stimuli driven, long lasting, difficult to change)(see for example Scherer, 2005 within this theoretical framework).

3.1.2 Between systems coherence of response

Emotional responses are thought of as a synchronized, coordinated and interrelated set of changes that deliver on different levels the necessary elements for an optimal response to major concerns of the organism (Levenson, 2003; Scherer, 2005). Indeed, emotions involve changes across different response systems: experiential, physiological and behavioral. However, the coherence with which these different response systems are activated has often been assumed but is backed up with little empirical evidence (see Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005 for an outline of the debate). Sherer (2005) proposed a model of relationships between organic systems and functions of emotions that include five components:

1. the cognitive component, appraisal, that evaluates objects and events and involves the central nervous system;

2. the neurophysiological component (bodily symptoms), that supports the system regulation by involving central nervous, neuro-endocrine and autonomic nervous systems
3. the motivational component (action tendencies), playing the executive role in preparing and directing actions through central nervous system
4. the expressive component, including motor facial and vocal expressions, that communicates reactions and behavioral intentions and involves the somatic nervous system
5. the subjective experiential feeling component, including the mental state of the emotional experience, that supposedly monitors internal states and the subject-environment interaction and involves the central nervous system

However, as emotions activate all these different response systems on different domains, the regulatory strategies that are necessary in order to behave appropriately in daily-life contexts (Gross & Thompson, 2007) need to account for the variety in response systems and patterns of activation.

3.1.3 Gross model of regulation of emotional responses

An influential cognitive model of emotional regulation has been developed by Gross (Gross & Thompson, 2007; Gross, 1998, 1999), who posits the existence of antecedent-focused and response-focused regulatory strategies. On the one hand, antecedent-focused strategies are supposed to affect emotion generation in response to a given situation and include processes of situation selection (i.e., the ability to anticipate the emotional impact of an environmental stimulus in order to approach or avoid it), situation modification (i.e., the active modification of environmental stimuli), attention deployment (i.e., the ability to allocate attentive resources to more or less emotionally cues), and reappraisal (i.e., the cognitive reevaluation of the mental model triggered by the environmental stimulus). On the other hand, response-focused strategies are thought to be critical for the subsequent modification of a previously generated emotion through processes of emotion intensification, suppression, and temporal modulation (prolonging or shortening).

3.1.4 Cognitive reappraisal

Cognitive reappraisal is an antecedent-focused regulatory strategy that is aimed at regulating feelings, particularly when they have negative valence. Several studies have shown that reappraisal of emotionally connoted stimuli can lead to reduction of the subjective experience of negative emotions (Gross, 1998; Hajcak & Nieuwenhuis, 2006; McRae et al., 2010; Ochsner et al., 2004; Ochsner, Bunge, Gross, & Gabrieli, 2002a; Phan et al., 2005). Furthermore, cognitive reappraisal makes people feel less negative emotions while looking at pictures that have been previously reappraised in comparison with those who had not (Vanderhasselt, Kühn, & De Raedt, 2012) and decreases the evaluation of the pictures' negative valence and arousal (Schulze et al., 2011). Interestingly, Jackson et al. (2000) showed that reappraisal was the strategy spontaneously selected by individuals who had been asked to decrease the negative experience of experimentally-triggered emotions. Moreover, in some studies it was associated to a decreased activity of the *corrugator supercilii*, a muscle usually activated while processing stimuli with negative valence (Kim & Hamann, 2012). Thus, cognitive reappraisal seems to moderate both subjective and physiological responses to negative stimuli.

3.1.5 Neural underpinnings of cognitive reappraisal

Reappraisal of negative stimuli has been shown to engage an articulated network of cortical and subcortical brain regions, which includes the amygdala (Ochsner, Bunge, Gross, & Gabrieli, 2002b; Phan et al., 2005), the dorsal anterior cingulate cortex (McRae et al., 2010; Ochsner et al., 2004; Phan et al., 2005), medial (McRae et al., 2010; Ochsner et al., 2004, 2002a, 2002b; Phan et al., 2005) and lateral prefrontal cortices (Ochsner et al., 2004, 2002a; Phan et al., 2005; Vanderhasselt et al., 2012; see also Kalisch, 2009 for a meta-analysis), left insula (Ochsner et al., 2002a), inferior parietal cortices (Vanderhasselt et al., 2012; Ochsner et al. 2002a), middle temporal and right medial occipital gyri (Ochsner et al., 2002a). Interestingly, many of these areas overlap with the neural networks associated with attentional control (fronto-parietal network; Ochsner and Gross 2005; Ochsner et al. 2010; Wessing et al. 2013), goal identification (temporo-parietal network; Van Overwalle 2009), and semantic control (fronto-temporo-parietal network; Badre and Wagner 2007; Jefferies 2012; Wagner et al. 2001), reflecting the different processes involved in the emotional reappraisal of environmental stimuli.

3.2 Developmental assessment of emotion regulation strategies in relation to impulsivity

The terms “impulsivity” and “impulsiveness” refer to a wide range of behaviors with the common characteristic of being performed without considering the outcomes (Evenden, 1999). However, not all of these behaviors are disadvantageous, as under optimal circumstances when a quick reaction with little reflection might be the only chance to take an advantage (Dickman, 1990). In a modern, biosocial approach to the concept of personality, defined as the “dynamic organization of the psychobiological systems that moderate adaptation to experience” (Cloninger, 2000), impulsivity is considered a non-unitary factor: indeed, multiple impulsivity related components have been associated with different personality factors, such as the tendency to forget to check for risks when enthusiasts about a new idea, waiting before taking decisions, getting involved in things too hastily, etc. Each impulsivity component in each domain may generally be conceived as the tendency to minimize the latency of response. Many studies associate impulsivity to other cognitive functions such as decision making (Vigil-Colet, 2007), inhibitory control (Logan, Schachar, & Tannock, 1997) and emotion regulation (Schreiber, Grant, & Odlaug, 2012) and with various clinical disorders such as drugs addiction (Dalley, Everitt, & Robbins, 2011), attention deficit, hyperactivity disorder, obsessive-compulsive disorder, trichotillomania (see Chamberlain & Sahakian, 2007 for a review), personality disorders (Moeller et al., 2001; Swann, Bjork, Moeller, & Dougherty, 2002) and generally with DSM-IV (American Psychiatric Association, 2000) Axis I and Axis II diagnosis (Swann et al., 2002). The association with emotion regulation seems to us to be of particular interest, since the use of emotion regulation strategies have been found to affect long-term well-being (Gros7s & John, 2003; John & Gross, 2004; McRae, Jacobs, Ray, John, & Gross, 2012). In this study, we assessed the use of emotion regulation strategies and different components of impulsivity in different ages in order to evaluate their development and possible association.

3.2.1 Methods

Participants

We tested 3 groups of subjects with different age and education. The first group (“pre-adolescents”) consisted of 87 students (44 girls and 43 boys) attending three public secondary education schools in the province of Udine, Italy. Their mean age was 12.05 years (SD = 1.03) for girls and 12.16 years (SD = 1.02) for boys. The second group (“adolescents”) consisted of 89 students (74 girls and 15 boys) attending four public high schools in the province of Bologna, Italy. Their mean age was 16.47 years (SD = 1.25) for girls and 16.26 years (SD = 1.28) for boys. The last group (“adults”) consisted of 43 adults, 24 females and 19 males with a mean age of 25.86 years (SD = 4.34) for females and 28.32 years (SD = 3.74) for males and with medium to high education (one subject had a secondary school certificate, while the rest had high schools certificates or a degree, or were studying to obtain a degree). Participation was voluntary, with the consent of both parents (when possible) in the case of minors (minor age in Italy is 18 years).

Procedure

Impulsivity components can be measured both with self-report questionnaires and with experimental computerized procedures. Both have advantages and disadvantages: the former suffer from self-image issues (Barker, Pistrang, & Elliott, 2005), while the outcome the latter, by definition, is the outcome of a series of processes that involve an execution which may be determined by other factors in addition to what the test is supposed to measure. As such, we developed a battery of neuropsychological tests encompassing self-assessment of trait impulsiveness, computerized measure of executive inhibitory skills and self-report emotion regulation strategies use.

Trait impulsiveness. Trait impulsiveness was measured using the Italian adaptation of the Barratt Impulsiveness Scale (BIS) (Fossati, Di Ceglie, Acquarini, & Barratt, 2001). The BIS consists of 30 sentences: the subjects have to rate each sentence on a 4-point scale ranging from “Never/Rarely” to “Almost Always/Always” on the basis on how often they engage in the behavior described in the sentence. Items score range from 1 to 4 and the total BIS score is the sum of each item score. We considered as variables both the six first-order subscales, each one defining a different aspect of impulsiveness: the first-order subscales include attentional impulsiveness ("Attention"), motor impulsiveness ("Motor"), self-control ("Self-Control"), cognitive complexity ("Cognitive Complexity"), persistence in the cognitive patterns ("Perseverance") and disordered thought ("Cognitive Instability").

Executive inhibitory skills. The ability to inhibit a pre-associated response was measured with a Go-No Go task in which subjects had to press a key as quickly as possible every time a letter appeared in the center of the screen, while they had to inhibit this response (and thus not press the key) when the letter "X" appeared. The Inhibition Subtest of the NEPSY-II battery (Brooks, Sherman, & Strauss, 2010) was used for measuring inhibition in different contests. In the first block ("nepsy-baseline"), participants are shown white or black arrows pointing upward or downward, and they have to press the key "UP" for the upward arrows and the key "DOWN" for the downward arrows. In the second block ("nepsy-inhibiting"), they have to press the opposite keys, i.e. "DOWN" for upward arrows and viceversa. In the last block ("nepsy-switching"), they have to press the correct key as in the baseline block when black arrows were presented, but had to press the opposite block as in the inhibiting block when white arrows were presented. The accuracy (percentage of correct responses) in these tests was used.

Emotion Regulation. Emotion regulation was measured using our Italian translation of the Emotion Regulation Questionnaire (ERQ) (REF). The ERQ is constituted of 10 sentences-items: the subjects have to rate them on a 7-point Likert scale ranging from "Completely Agree" to "Completely Disagree". Two subscales constitute the scores to the ERQ, the "Reappraisal" and the "Suppression" subscales, the scores of which are calculated by the sum of, respectively, 6 and 4 items. The Reappraisal subscale is considered a measure of the frequency of use of the reappraisal strategy, while the Suppression subscale is considered a measure of the frequency of use of the suppression strategy.

3.2.2 Results

In order to assess the developmental changes within the considered domains, we compared the three groups on each variable. Moreover, since the Adolescent group was mainly constituted of females, we wanted to check for the independence of gender and group. While group differences are expected, if sex differences determine different scores independently from the group, we should find a main effect of gender but no interaction with group. We tested the interaction by entering all the variables in a 2*3 factorial ANOVA, with gender (male *vs.* female) and group (pre-adolescent *vs.* adolescent *vs.* adult) as between subjects independent variables and the remaining variables as dependent within subjects variables. Post-hoc multiple, pairwise comparisons were performed using the Duncan test.

The ANOVA shows a main effect of group ($F_{(2,402)} = 4.333$; $p < 0.001$; $\eta^2_p = 0.2055$) but no main effect of gender ($F_{(1,201)} = 1.32$; $p = 0.209$; $\eta^2_p = 0.073$). *Post-hoc* univariate ANOVA showed no difference in emotion regulation strategy use (both Fs < 2.191; $p > 0.114$); however, in the trait impulsiveness scales, the Self-Control ($F_{(2,201)} = 8.987$; $p < 0.001$) and Perseverance ($F_{(2,201)} = 15.737$; $p < 0.001$) values both reached significance, while others scales didn't (all Fs < 2.622; $p > 0.075$); moreover, accuracy in the nepsy-baseline ($F_{(2,201)} = 3.64$; $p < 0.027$), nepsy-inhibiting ($F_{(2,201)} = 4.473$; $p < 0.012$), nepsy-switching ($F_{(2,201)} = 3.068$; $p < 0.049$) and go-nogo ($F_{(2,201)} = 18.071$; $p < 0.001$) conditions were found to reach significance. *Post-hoc* Duncan test showed that adults reported lower levels of impulsivity related to self-control (12.42 ± 0.41) in comparison to both adolescents (14.04 ± 0.37; $p < 0.001$) and pre-adolescents (14.51 ± 0.28; $p < 0.001$), which in turn didn't report significantly different levels ($p > 0.3$), as shown in Fig.1. Adults reported higher levels of impulsivity related to perseverance (6.94 ± 0.21) than adolescents (6.19 ± 0.19; $p < 0.009$) but lower levels than pre-adolescents (7.52 ± 0.14; $p < 0.006$), which in turn reported higher levels than adolescents ($p < 0.001$), as shown in Fig.2. As for executive inhibitory skills, adolescents were less accurate in the nepsy-baseline condition (0.935 ± 0.012 %) than both adults (0.977 ± 0.013 %; $p < 0.006$) and pre-adolescents (0.97 ± 0.009 %; $p < 0.021$), which in turn didn't significantly differ ($p = 0.595$), as shown in Fig.3. Pre-adolescents were less accurate in nepsy-inhibiting (0.868 ± 0.018 %) than adults (0.93 ± 0.025 %; $p < 0.036$) but not significantly different then adolescents (0.949 ± 0.023 %; $p = 0.202$), which in turn didn't differ from adults ($p = 0.169$), as shown in Fig.4.

3.2 Developmental assessment of emotion regulation strategies in relation to impulsivity

Adults were more accurate in the nepsy-switching condition (0.9 ± 0.029 %) than pre-adolescents (0.814 ± 0.02 %; $p < 0.011$), but not significantly different from adolescents (0.855 ± 0.027 %; $p = 0.169$), which in turn weren't significantly different than pre-adolescents ($p = 0.202$), as shown in Fig.5. Finally, adults were more accurate in the go-nogo task (0.665 ± 0.028 %) than both adolescents (0.573 ± 0.026 %; $p < 0.044$) and pre-adolescents (0.461 ± 0.02; $p < 0.001$), which in turn were less accurate than adolescents ($p < 0.001$), as shown in Fig.6.

We calculated a Pearson correlation matrix of the variables in order to better explore their relations (Tab.1.).

	Reappraisal	Suppression	Attention	Motor	Self-Control	Cognitive Complexity	Perseverance	Cognitive	nepsy-baseline	nepsy-	nepsy- switching	go-nogo
Reappraisal	1											
Suppression	-,0221	1										
Attention	-,1518*	,0192	1									
Motor	-,0731	-,0628	,3606***	1								
Self-Control	-,2039**	-,0863	,4462***	,3556***	1							
Cognitive Complexity	-,0347	,0361	,1765**	,2072**	,3008***	1						
Perseverance	,1095	-,0000	,1142˜	-,0030	,1003	,1172˜	1					
Cognitive Instability	,0345	-,0512	,1754**	,3682***	,0872	-,1163˜	-,0532	1				
nepsy-baseline	,0824	-,0273	,0054	-,1794**	-,1223˜	-,1778**	,0425	,0261	1			
nepsy-inhibiting	,0346	,0519	,0089	-,0166	,0509	,0881	,0506	,0221	,0328	1		
nepsy-switching	-,1170˜	-,0860	,0219	-,0644	-,0532	-,0667	-,0253	,0360	,1983**	,0554	1	
go-nogo	-,0688	-,0180	-,1868**	-,1044	-,2168**	-,1730*	-,1812**	-,0710	,1168˜	,0480	,2618***	1

Table 1. Pearson correlation matrix of the variables of the study. * indicates correlations with $0.05 < p < 0.01$, ** indicates correlations with $0.01 < p < 0.001$, *** indicates correlations with $p < 0.001$, ˜ indicates borderline significant correlations with $0.1 < p < 0.05$.

Reappraisal showed a significant correlation with Attention (r = -0.1522; p < 0.025), Self-Control (r = -0.2061; p < 0.002) and with nepsy-inhibiting (r = -0.1594; p < 0.018), suggesting that lower attentional impulsivity and lower impulsivity related with self-control are associated with higher frequency of reappraisal use and this, in turn, correlates with accuracy in task requiring inhibition of pre-associated responses. Conversely, suppression use didn’t correlate with any variable. Attention also correlated with Motor (r = 0.3608; p < 0.001), Self-Control (r = 0.4463; p < 0.001), Cognitive Complexity (r = 0.1794; p < 0.009), Cognitive Instability (r = 0.1753; p < 0.01) and with accuracy in the go-nogo task (r = -0.1875; p < 0.005), suggesting that higher levels of attentional impulsiveness are associated with higher levels of motor-related impulsiveness, impulsiveness related with cognitive complexity and disordered thought and lower levels of success in inhibitory tasks. Motor impulsiveness showed a significant correlation also with Self-Control (r = 0.357; p < 0.001), Cognitive Complexity (r = 0.2095; p < 0.002), Cognitive Instability (r = 0.3687; p < 0.001) and nepsy-baseline (r = -0.1789; p < 0.008), suggesting that higher motor impulsiveness is also associated with impulsiveness related to cognitive complexity and disordered thought and with lower accuracy when following simple instructions under time constraints. Self-Control also correlated with Cognitive Complexity (r = 0.2979; p < 0.001) and with the accuracy in the go-nogo task (r = -0.2198; p < 0.001), suggesting that higher impulsivity related to self-control is associated with impulsiveness related to cognitive complexity and with lower accuracy in tasks that require inhibition. Cognitive Complexity was also correlated with accuracy in the nepsy-baseline (r = -0.1815; p < 0.007) and in the go-nogo task (r = -0.1781; p < 0.008), suggesting that higher impulsiveness levels related to cognitive complexity are associated also with lower accuracy in tasks requiring simple execution and inhibition. Perseverance was correlated with the accuracy in the go-nogo task as well (r = -0.184; p < 0.006), suggesting another inverse association between a factor of impulsiveness and inhibitory abilities. Nepsy-switching was correlated with both nepsy-baseline (r = 0.1969; p < 0.004) and nepsy-inhibiting (r = 0.199; p < 0.005) and accuracy in the go-nogo task (r = 0.2599; p < 0.001), which in turn also correlated with nepsy-inhibiting ($r = 0.1885$; $p < 0.005$), suggesting that the performances in these tasks are associated.

It is noteworthy that most of the Barratt Impulsiveness Scale first-order scales, while describing different dimensions of impulsivity, were found to positively correlate between themselves and to inversely correlate with the executive inhibition tasks, which in turn positively correlated between themselves. Moreover, of most interest for this study, reappraisal use did correlate with come trait impulsiveness scale but not with accuracy in executive inhibition task.

SEM

Considering the correlation matrix and the results described above, we explored how the variables related to one another by developing a structural equation model (SEM) of the relations between them. In first place we built a model by following our hypothesis. Then, we planned on pruning the model of the weaker correlations, except for those linking reappraisal to other variables. Finally, we planned on comparing the different models resulting from the possible (hypothesis driven) relations of reappraisal. All the models were tested using the SPSS plugin AMOS (version 18.0.0). We estimated the models through the maximum likelihood technique and evaluated them through multiple fit indices: the χ^2 statistic, root mean square error of approximation (RMSEA) and Akaike's Information Criterion

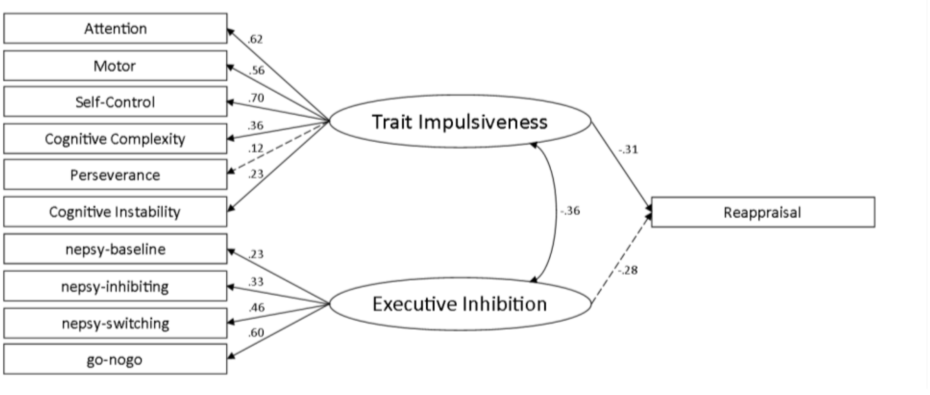


Figure 7. Full-path model of emotion regulation and impulsivity. Numbers on straight arrows indicate standard regression weights. The number on the curved arrow indicate correlation between latent variables. Dotted lines indicate paths that don't reach statistical significance. Correlation between Trait Impulsiveness and Executive Inhibition is borderline significant (p = 0.056).

(AIC).

Hypothesis. As specified above, we thought that a latent variable approach separating the trait impulsivity and the executive inhibition factors would be ideally suited to describe the correlations that emerged from the matrix. As such, we hypothesized two latent variables, one (Trait Impulsiveness) as a predictor for BIS subscales and one (Executive Inhibition) as a predictor for the computerized tasks. Our hypothesis regarding the relationship between these variables was as follows:

H0 – no relation between these variables

H1 - Trait Impulsiveness predicts Executive Inhibition or viceversa

Following H0, Trait Impulsiveness and Executive Inhibition are two different constructs, meanwhile by following H1 we hypothesize that either Executive Inhibition is explained by Trait Impulsiveness, or viceversa: indeed, H1 leaves open the possibility for a causal relationship (but doesn't explain it), or the existence of a common of cause, alongside the ubiquitous possibility of the correlation being just a coincidence.

Test of hypothetical model. We built a candidate model by starting from our conceptualization of the relationship between the functions we measured. We built the first model as a full-path model between Reappraisal and the latent variables Trait Impulsiveness and Executive Inhibition.

The full-path model, depicted in Fig.7., showed adequate fit indices ($\chi^{2 =}$ 93,096; $p < 0.001$; RMSEA = 0.74; AIC = 163.096), with only two paths that didn't reach significance, the one between Trait Impulsiveness and Perseverance and the one between Executive Inhibition and Reappraisal (both $p > 0.74$), while the covariance between the two latent variables showed a trend towards significance ($p = 0.056$).

Test of Reappraisal relation with latent impulsiveness variables. From the first full-path model, we excluded the Perseverance for its weak correlation with the Trait Impulsiveness latent variable. From the remaining model, we derived 3 different models:

-SEM1, in which Reappraisal was only predicted by Trait Impulsiveness

-SEM2, in which Reappraisal was only predicted by Executive Inhibition

-SEM0, in which Reappraisal was totally independent from latent variables

The fit indices of these alternative models were compared. The results are shown in Tab.2.

model	χ^2	*p*	RMSEA	AIC	Estimated %
full-path	93,096	***	0.074	163.096	11.2
SEM1	85.032	***	0.082	147.032	3.7*
SEM2	89.523	***	0.086	151.523	1.2
SEM0	90.653	***	0.084	150.653	-

Table 2. Fit indices for all models.

By comparison, the model that better fits our data is SEM1, depicted in Fig.8. All paths reached statistical significance (all $p < 0.037$), including the covariance between Trait Impulsiveness and Executive Inhibition ($p = 0.050$).

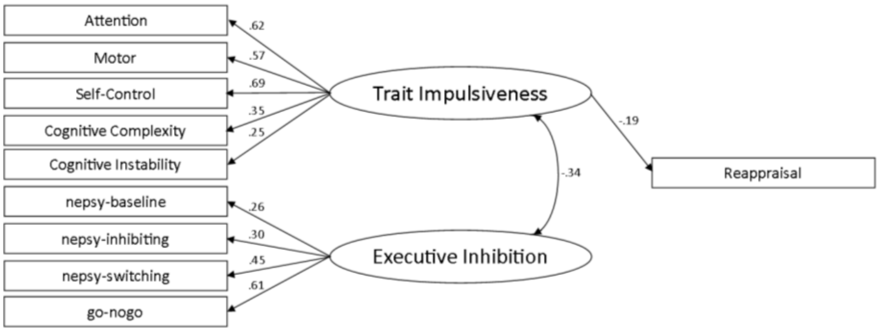


Figure 8. Best fitting model of emotion regulation and impulsivity. Numbers on straight arrows indicate standard regression weights. The number on the curved arrow indicate correlation between latent variables. All paths reach statistical significance (all $p < 0.037$).

3.2.3 Discussion

In this study we provided evidence for developmental changes in some trait impulsivity facets and in the performance in tasks requiring inhibition, but we find no difference in the frequency in the use of emotion regulation strategies.

Furthermore, we showed evidence that impulsivity is associated with the use of emotion regulation strategies. In particular, the trait impulsiveness more than executive inhibitory skills are associated with the frequency in use of reappraisal. These results will be briefly discussed.

Developmental changes. We showed a decrease in the impulsivity related to self-control in adult age. While this was expected, it is noteworthy that no significant change was found between pre-adolescence and adolescence. The absence of changes seems interesting in contributing to the theories about adolescent impulsivity-related disorders, such as drugs addiction (Dalley et al., 2011).

The other developmental change in trait impulsiveness factors we found was related to the persistence in cognitive patterns. Interestingly, by analysing perseverance scores as a function of group age, a u-shaped pattern emerges, with low scores in adolescence, and overall higher scores in pre-adolescence. While this result seems intuitive when focusing on the decrease between pre-adolescence and adolescence that seems to reflect an increased maturity of cognitive patterns, it is puzzling why in adults these patterns seem less mature than during adolescence. However, it has to be noted that adult participants may have more variance in lifestyle and background than adolescent participants do. This argument is furthered by the fact that adolescent participants come from four public high schools, an environment that may very well be more standardizing than life at university or at work.

A u-shaped pattern also emerges from the developmental analysis of the first task of the NEPSY-II Inhibition Subtest. This task is used to associate stimuli and responses that will be inhibited in the following task. By analysing the accuracy in this task we are able to assess the stimulus-response association strength. As such, it is puzzling why adolescents performed worse than both pre-adolescents and adults. It is possible, however, that adolescents traded accuracy for reaction speed, while other groups were more conservative or slower. However, all the remaining inhibitory tasks show an increase in accuracy from pre-adolescence to adulthood, with the pure inhibitory NEPSY-II task showing a plateau from adolescence to adulthood and with the switching task showing a significant difference only in the comparison between pre-adolescents and adults. All these results suggest that executive inhibitory skills undergo a process of development and are in line with previous literature (e.g., Jonkman, Lansbergen, & Stauder, 2003).

Impulsivity and emotion regulation. Our main goal with this study was to assess the relation of impulsivity with emotion regulation. From the linear correlation matrix, the frequency of reappraisal use appeared to be associated with both trait impulsiveness, particularly attentive and self-control- related, and executive inhibition. However, when all the variables were considered together in a SEM, reappraisal use was better predicted by trait impulsiveness than by executive inhibition. As such, with this study we confirmed the previously found association between impulsivity and emotion regulation (Schreiber, Grant, & Odlaug, 2012) and propose that trait impulsivity is a better predictor of emotion regulation strategies than executive impulsiveness.

3.3 A brain stimulation study of the role of Inferior Frontal Gyrus in emotion regulation during storytelling

In structured experimental contexts, subjects are usually asked to decrease the intensity of an emotion, either by providing general instructions to feel less or more emotion (Jackson et al., 2000) or by pre-specifying a given context to interpret the upcoming stimulus (Wessing et al. 2013; Macnamaraet al. 2009) . For example, Wessing et al. (2013) provided instructions to guide reappraisal strategies (e.g., “imagine that what you are about to see is staged/performed by actors rather than real”), while Macnamara et al. (2009) furnished predefined descriptions of the stimulus (e.g., “the person you are about to see is a terrorist”). However, these experimental models of emotional regulation only consider situations in which people explicitly receive from others prior information on the nature of the incoming stimuli and this allows them to process emotional content using a pre-appraisal strategy. This however does not reflect many everyday life situations, where emotion regulation is elicited spontaneously in response to environmental stimuli and is often embedded in a situational context. Therefore, explicit reappraisal and pre-appraisal studies seem to be useful for understanding how single components of emotion regulation do act; however, more ecological experimental manipulations are needed in order to understand how emotion regulation is spontaneously used in real-life situations.

In this study we explored the neural underpinnings of emotional regulation by studying the subjective and physiological responses to emotionally connoted stimuli during two storytelling production tasks that might or might not require regulation of the emotional content of the narratives. Both tasks were designed to resemble as much as possible real-life situation context. Indeed, the narrative production task employed in this study has been shown to have high ecological validity in the assessment of narrative skills of both healthy individuals (Marini, Boewe, Caltagirone, & Carlomagno, 2005) and brain damaged patients (e.g. Galetto et al. 2013). Crucially, instead of manipulating the instructions by telling participants how to regulate the emotion, we manipulated the social context within which participants were asked to produce the storytelling, thus leading to spontaneous use of regulatory processes. Participants were asked to describe what was going on in a series of pictures with negative and neutral emotional content: in the non-regulatory condition they were asked to describe the image as if they were talking to a peer; in the reappraisal condition they were asked to describe the image as if they were talking to a child. Therefore, in the critical condition (narration to a child) the participants were required to appraise the emotional valence of the stimulus, modulate their emotional reaction and eventually produce a regulated description of the events portrayed in the stimulus by implementing a reappraisal strategy. Furthermore, the causative involvement of the left inferior frontal gyrus (LIFG) in reappraisal of negative stimuli was investigated by using continuous theta burst stimulation (cTBS), which is expected to inhibit the areas underlying the coil (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Since LIFG is known to be involved in the cognitive control of the selection of semantic contents (Jefferies, 2012), we hypothesized that cTBS over this brain region would interfere with the creation of a mental model of the presented situation, thus affecting the cognitive reappraisal process. Former brain stimulation studies have shown that LIFG is implicated in the selection of contextually appropriate lexical items during storytelling (Marini & Urgesi, 2012), but also in other context-relevant conditions such as during synonym judgment (Gough, Nobre, & Devlin, 2005) or other semantic control tasks (Jefferies 2012; Whitney et al. 2011; see Badre and Wagner 2007 for a review). In the current study we explored the hypothesis that interference with LIFG as a region subserving context-driven semantic control would affect cognitive reappraisal of negative stimuli.

We expected that manipulation of the emotional regulation context of the narration would modulate the storytelling content, as well as the associated physiological and expressive behaviors, and this would occur in particular during narration of pictures with negative valence. Crucially, we hypothesized that interference with neural activity of LIFG using inhibitory cTBS would hamper the process of cognitive reappraisal and the modulation of the regulatory requirement and emotional valence of the narrations on one or more of the response systems (linguistic and emotional content of narratives, physiological orienting or emotional expression) affected by emotional regulation.

3.3.1 Methods

Participants

Fourteen volunteers (9 females, 5 males; age M = 22.71, SD = 5.25) participated in the study. They were graduate students with at least 14 years of formal education (Mean = 14.6; SD = 1.9). All participants were right-handed according to a standard handedness inventory (Briggs & Nebes, 1975) and reported normal or corrected-to-normal visual acuity in both eyes and no hearing loss. None of the participants had neurological, psychiatric, or other medical problems or any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). All participants released their written informed consent to participate to the study after all procedures had been fully explained. Participants were offered course credits for their participation. Approval for the study had previously been obtained from the ethics committee of the Scientific Institute (IRCCS) “E. Medea” (Bosisio Parini, Como; Italy) and the procedures were in accordance with the ethical standards of the 1964 Declaration of Helsinki. No adverse effects during TMS were reported or noticed and no participants asked to interrupt the stimulation protocol for any major discomfort induced by the facial muscular twitches evoked by TMS.

Stimuli and apparatus

Sixteen pictures were selected from the International Affective Picture System (IAPS; Lang et al. 2005) in two stages. The initial stage selection criteria were: i) having negative or neutral emotional valence; ii) depicting scenes from a first-person rather than third-person perspective; iii) having no unambiguous meaning (i.e., alternative narratives for the same picture could be elicited, e.g. a description of a preyed-upon dead animal scene as tragic and sad or, alternatively, as natural circle of life). After the initial selection, the second stage involved creating two groups of pictures, one with negative valence and the other with neutral valence, matched for level of arousal and topic (e.g., animals or children as subjects). As a result, 16 pictures were selected, half (2205, 3500, 6570, 6838, 9075, 9186, 9220 and 9417) with negative valence (M = 2.39, SD = 0.61) and half (1675, 2309, 2635, 5455, 7640, 8160, 8192 and 8211) with neutral valence (M = 5.31, SD = 0.34; two-tailed T test: t = 11.85, df 14, $p < 0.001$). The two groups had comparable levels of arousal (negative M = 5.41, SD = 1.01; neutral M = 5.26, SD = 1; two-tailed T test: t = 0.31, df 14, $p = 0.762$). The pictures were presented on a 17 inches LCD monitor with resolution of 1280x1024 (pictures occupied 75% of the height and 75% of the width of the screen) with participants sitting at a distance of approximately 60 cm from the screen.

Procedure and task

Figure 1 displays the organization of the experimental tasks. A trial started with the presentation of a fixation cross (5 sec), followed by the presentation of a picture (10 sec). Participants were instructed to look at the stimuli until they heard a sound (“attending phase”), which warned them to begin to describe the content of the picture (“storytelling phase”). The picture remained on the screen until the participant completed his/her storytelling. In line with previous studies (e.g., Lang et al. 1993), this sequence of stimulus presentation timing was chosen in order to allow us to record the physiological activity before and after the presentation of the picture, and to avoid any possible interference of producing a vocal response on physiologic measures (Fridlund & Cacioppo, 1986). Each experimental trial lasted about 1 minute.

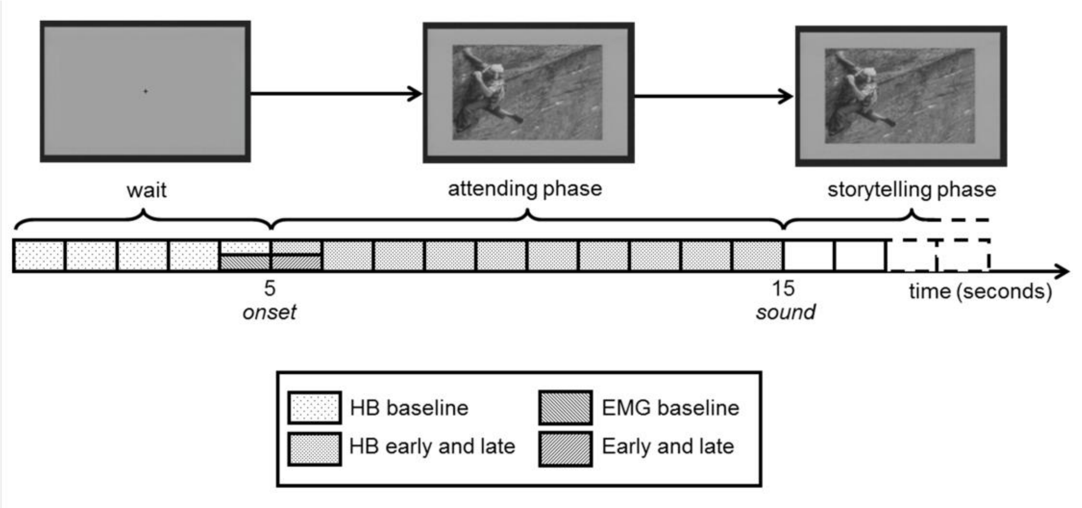


Figure 9. Trial structure.

The storytelling task was presented in two experimental conditions: in one (requiring the production of an unregulated narration), participants were instructed to narrate the content of the picture to a peer; in the other (requiring the production of a regulated narration), they were asked to tell the story as they were speaking to a child. Narrative conditions were administered in two separate blocks, each repeated for the two stimulation sites. Each block consisted of 8 consecutive trials of the same condition. The order of stimulation sites and narrative conditions was counterbalanced between participants.

Since the narration conditions were administered after both LIFG- and vertex-cTBS to the same participants, two subsets of 8 different pictures were used so to avoid participants repeating by heart the same narration in the two stimulation site conditions. The pictures' assignment to one subset or the other was pseudo-randomized for each subject so that for each block 4 negative pictures and 4 neutral pictures were presented. Thus, for each stimulation site 8 different pictures were shown twice, once for each of the two narration conditions. The same picture set was presented in the two narration conditions to increase the likelihood that participants were engaged in producing different narratives according to the regulation requirements and to improve the sensitivity of the within-subjects test of regulation efficacy independently of the subtle differences in the scenarios depicted in the pictures. Pseudo-random assigning the pictures to the two subsets and counterbalancing across participants the order of narration conditions controlled possible learning effects that might determine a systematic decrease in the emotional response to the scenario and a reduction of the difficulty of narration after repeated presentation of the same picture. In sum, the experimental design had repeated-measure variables, each with 2 levels: site (LIFG *vs.* vertex), narration (unregulated *vs.* regulated), and valence (negative *vs.* neutral).

TMS protocol

Offline repetitive TMS was delivered using a continuous theta-burst (cTBS) pattern (Huang et al., 2005) in which three pulses at 50 Hz are delivered every 200 ms for 40 seconds, for a total of 600 pulses. This protocol has been shown to inhibit neural activity in the underlying cortex for up to 30 minutes (Huang et al., 2005) and has been successfully used to interfere with neural activity of LIFG during several cognitive tasks (Acheson & Hagoort, 2013; Bohlhalter et al., 2011).

A 70 mm figure-eight stimulation coil (Magstim air-cooled coil) connected to a Magstim Rapid2 (The Magstim Company, Carmarthenshire, Wales, UK) and producing a maximum output of 0.93 T at coil surface (pulse duration: 250 µs, rise time: 60 µs) was used. The coil was placed tangentially on the scalp, with the handle pointing backward, in order to stimulate the sites with Talairach (Talairach & Tournoux, 1988) coordinates x = -54, y = 18, z = 20 for LIFG and x = 0, y = -42, z = 69 for the vertex. The stimulation sites were located for each participant with the SofTaxic Optic – neuronavigation system for TMS (Electro Medical Systems, Bologna, Italy; www.softaxis.com) using a Polaris Vicra optical tracking system (Northern Digital, Inc., Waterloo, Ontario, Canada) to digitize the participant’s scalp and estimate Talairach coordinates based on an MRI-constructed stereotaxic template. The coil was held on the scalp using a coil holder with an articulated arm; the coil handle was kept pointing backward and approximately parallel to the lateral sulcus. The intensity of cTBS was set at 80% of the active motor threshold (aMT), defined as the lowest TMS intensity able to evoke a visible twitch in the thumb muscle during a pinch grasp in 5 out of 10 stimulations over motor cortex. The aMT of the participants ranged from 47 to 66% of the maximum TMS intensity, with a mean of 58.21% and a standard deviation of 6.35%. The same intensity was used for LIFG and vertex stimulation, with an interval between the two stimulation site sessions of about 2 hours.

Physiological measure recording

Electrocardiographic (ECG) and electromyographic (EMG) signals were recorded using surface Ag/AgCl pregelled disposable electrodes (1 cm diameter) and a Biopac MP-36 system (BIOPAC Systems, Inc., Goleta, CA, USA) for amplification (gain: 1000), digitization (sampling rate: 1,000 Hz) and filtering of the signal. The ECG signal was recorded with band-pass filter of 0.5-35 Hz, while the EMG signal was recorded with a band-pass filter of 5-500 Hz. Facial EMG was recorded from the corrugator supercilii muscle, since it has been often proved to correlate with increases in self-reported experience of negative emotions (e.g., Larsen et al. 2003).

Data handling

Transcription and Analysis of the Picture Descriptions

Each storytelling was tape-recorded and subsequently transcribed verbatim by two of the authors (AM, TB); the transcription included phonological fillers, pauses, false starts and extraneous utterances. These transcriptions underwent quantitative analysis of the emotional content as well as in-depth linguistic and textual analysis focusing on three main aspects of linguistic processing: productivity, textual organization and lexical informativeness (Marini, Andreetta, del Tin, & Carlomagno, 2011). Furthermore, the emotional valence of the content of the storytelling was also estimated.

The linguistic analysis focused on the number of Words produced during each storytelling (a measure of productivity), the Percentage of Errors of Cohesion produced in each speech sample (a measure of text-level structuring) and the Percentage of Lexical Informativeness (a pragmatic measure). The Words' count included every well-formed recognizable word that had been produced with the exclusion of false starts, phonological paraphasias and neologisms. The Percentage of Errors of Cohesion measured the extent to which each utterance of the picture description was structurally related to the preceding one. Cohesion errors included misuse of cohesive ties like anaphoric pronouns, errors in number and gender agreement between pronouns or noun phrases across utterances, misuse of either cohesive function words or semantically related content words, and abrupt interruptions of utterances. This percentage was calculated by dividing the total number of cohesive errors by the number of utterances produced and multiplying this value by 100. Finally, the Percentage of Lexical Informativeness was based on the identification of the appropriate lexical information units (LIUs), i.e. those content and function words that were not only phonologically well-formed but also appropriate from a grammatical and pragmatic point of view. Therefore, all those words that were classified as semantic or verbal paraphasias, fillers, paragrammatic errors or forming tangential or extraneous utterances (i.e., utterances that were somehow deviating from the gist of the story) were excluded from the LIUs' count. The Percentage of Lexical Informativeness was then obtained by dividing the number of LIUs by the number of words and multiplying this value by 100.

As for the assessment of the emotional content of the storytelling, a transcription of each word or set of words that appeared in the storytellings was ordered randomly in a list; an independent group of 12 students (5 females, 7 males; age M = 21.33, SD = 0.98) evaluated the emotional valence of each item on a 7-point Likert scale with "very negative" (-3) and "very positive" (+3) as extremes. The values of emotional valence of each storytelling were estimated by the sum of the emotional valence values of all emotional words produced.

Physiological activity

We measured heart rate variability (HRV) as a physiological measure of orienting to the stimulus. HRV is a well-known physiological index that reflects the complex interplay between sympathetic and parasympathetic regulatory systems (Thayer & Lane, 2000). The HRV was estimated during the 10-sec phase in which participants attended to the stimulus before starting the storytelling using two series of five consecutives interbeat intervals. The initial five interbeat intervals after stimulus onset served to evaluate the "early" orienting response, while the remaining five interbeat intervals served to account for the "late" orienting response. In line with previous literature, we expected both these measures to show a heart rate deceleration in comparison with the HRV before the stimulus (Bradley, Codispoti, Cuthbert, & Lang, 2001; Bradley, 2009). In order to calculate a pre-stimulus baseline, we recorded the heartbeat signal in the 5 seconds before stimulus onset (with only the fixation cross displayed on the screen), a procedure that allowed us to estimate baseline HRV values. The heartbeat signal was first filtered with a high-pass filter (5 Hz) to isolate the R-spike component in order to extract the interbeat intervals. The resulting data set was smoothed of artifacts, noise and partial intervals. The number of beats per minute (BPM) was estimated by dividing the time unit (one minute) by the average duration of five consecutive interbeat intervals for both the early and late heart responses, while all available interbeat intervals were used in estimating the baseline. For each trial, the early and the late BPM were subtracted to the baseline BPM, resulting in an early and a late HRV that express a change in BPM in comparison (difference) with the baseline. This procedure was adopted in order to avoid possible temporary fluctuations in the cardiovascular status that otherwise could be confounded with experimental effects. The corrugator supercilii EMG activity was high-pass filtered (20 Hz), rectified and root-mean-squared. The EMG signal amplitude was averaged in the first 500 ms after stimulus onset and from 501 to 1000 ms from stimulus onset, thus allowing to disentangle early and late phases of reaction to stimulus pictures (e.g. Dimberg and Thunberg 1998). The average EMG amplitude in the last second of artifact free signal before stimulus onset was computed as baseline and used to calculate, for each trial, a comparative index, by subtracting it from the mean amplitude of the two data bins after stimulus onset. Therefore, in line with the procedure adopted with the HRV, the data values used for the EMG analysis were expressed as differences of means in EMG amplitude between the stimulus presentation condition and the baseline, allowing us to avoid confounding temporary fluctuations with experimental effects.

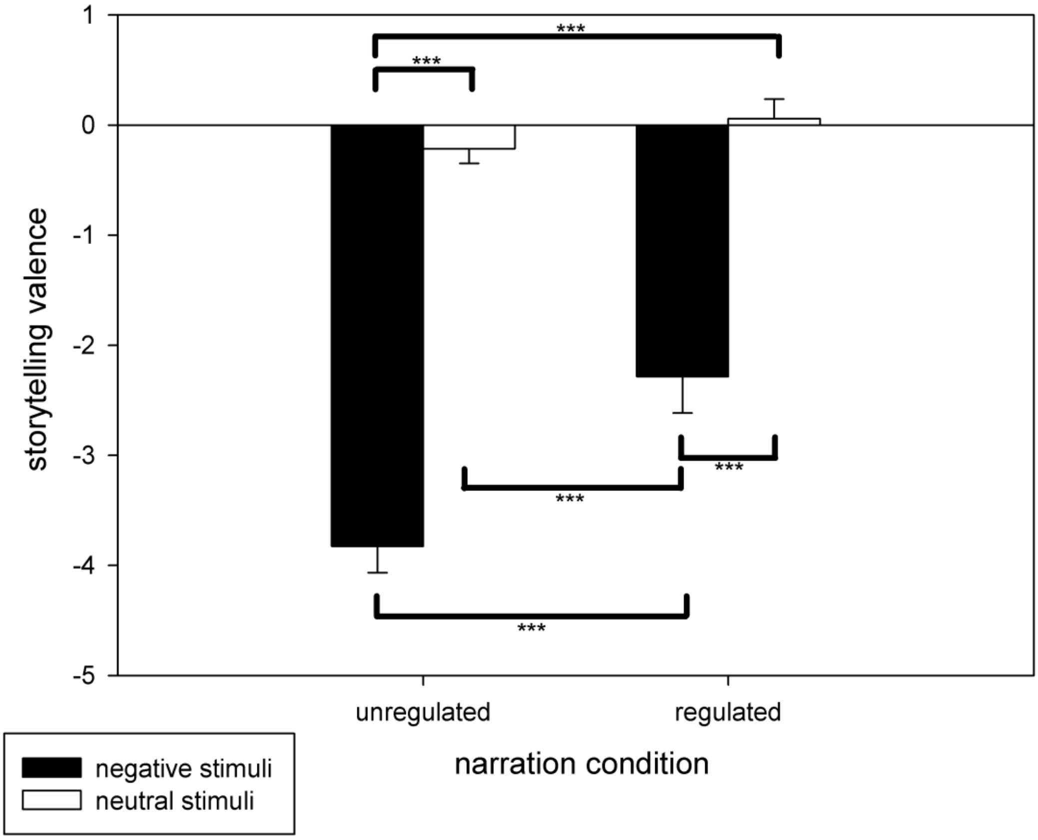
Statistical analyses

The individual mean values of the 6 dependent variables (Emotional Content, Word number, Lexical Informativeness, Cohesion errors, HRV, EMG) were calculated for each stimulation site, narration condition and picture valence. Two participants (one female) were excluded from the analyses for not complying with the storytelling instructions (i.e., they did not tell a story about the pictures but provided general comments about them). Data for the six variables were entered into separate 2 x 2 x 2 (x 2) repeated-measures ANOVAs, with site (LIFG *vs.* vertex), narration task (unregulated *vs.* regulated) and valence (negative *vs.* neutral) as common within-subjects variables, and with time-frame as a within-subjects variable (2 intervals after stimulus onset) for the two physiological measures. A Bonferroni correction was applied to the significance threshold of the effects of each one of the six ANOVAs (p < 0.008) to control for multiple testing. Post-hoc multiple, pairwise comparisons were performed using the Duncan correction for multiple comparisons. Effects sizes were estimated using the partial eta squared measure (ηp2).

3.3.2 Results

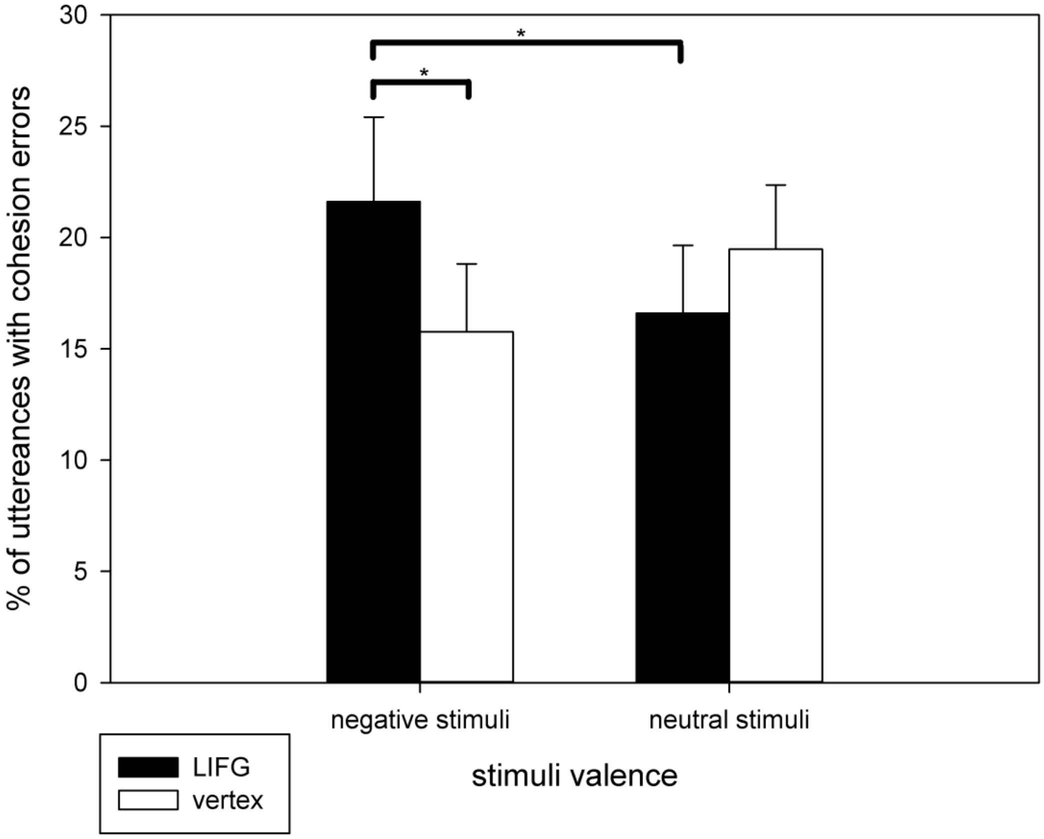
Storytelling content

The analysis of the valence of the emotional content of the storytellings revealed significant main effects of picture valence ($F_{(1,11)}$ = 119.2; *p* < 0.001; ηp2 = 0.915), showing that it was more negative for negative pictures (-3.054 ± 0.212) than for neutral ones (-0.077 ± 0.143), and task condition ($F_{(1,11)}$ = 13.794; *p* = 0.003; ηp2 = 0.556), showing that it was less negative during the regulated narration (-1.112 ± 0.2) than during the unregulated one (-2.020 ± 0.134). These main effects were further supported by the finding of a significant interaction between task and



picture valence (F(1,11) = 13.991; $p = 0.003$; ηp2 = 0.56; Fig. 2): while for neutral pictures storytelling valence content did not differ between regulated and unregulated narration (unregulated: -0.213 ± 0.135; regulated: 0.058 ± 0.179; $p = 0.283$), for negative pictures it was less negative during the regulated narration (-2.282 ± 0.334; $p < 0.001$) than during the unregulated one (-3.826 ± 0.241). These results point to successful manipulation of the valence of the storytelling and of the regulatory requirements of the task. No significant effect of stimulation site or its interaction with other variables was found (all Fs < 0.965; $p > 0.347$), showing that LIFG-cTBS did not affect either the emotional content of the storytelling or the ability to down-regulate it during narration to a child.

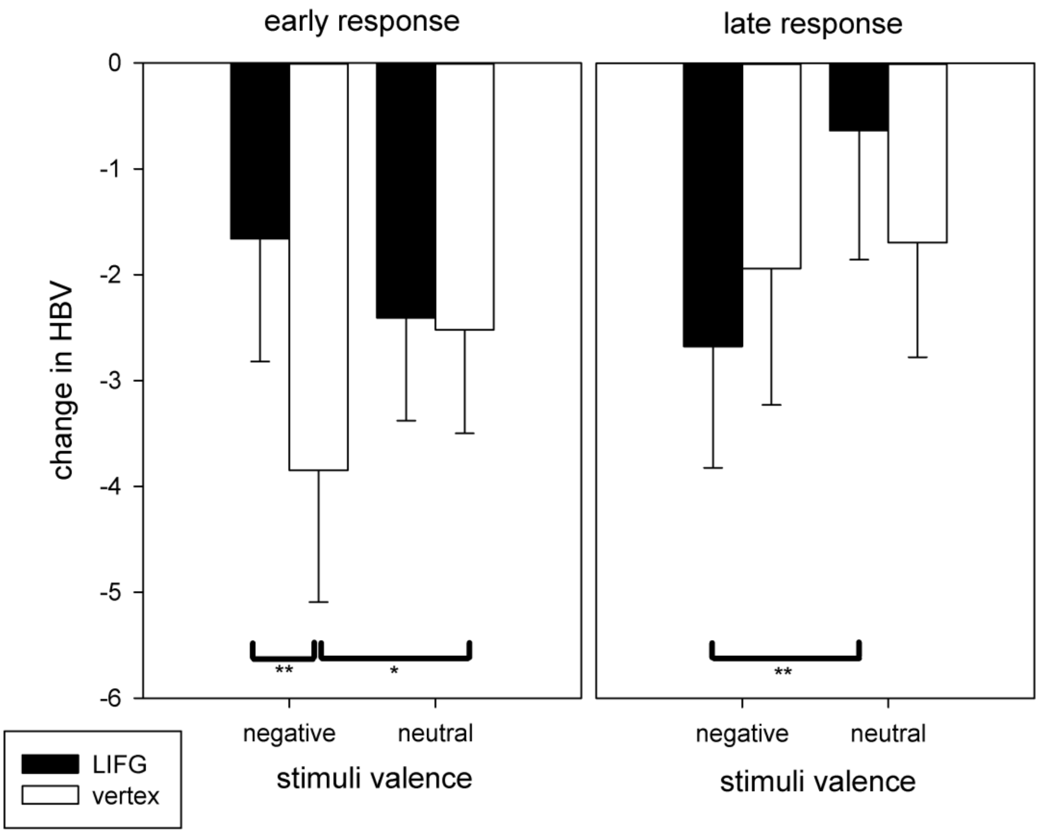
When the linguistic variables were considered, no significant effects were observed in the analyses of the number of words produced (all $p > 0.145$) and of the Percentage of Lexical Informativeness (all $p > 0.237$), suggesting that LIFG did not alter productivity and pragmatic aspects of storytelling. However, a significant two-way interaction between site and picture valence was found in the percentage of Cohesion Errors ($F_{(1,11)} = 11.386$; $p = 0.006$; $\eta p^2 = 0.509$; Fig. 3). Indeed, LIFG-cTBS increased cohesion errors as compared to vertex-cTBS during narration of negative pictures (21.61 ± 3.80% *vs.* 15.76 ± 3.06%, $p = 0.012$); conversely, no cTBS effect was obtained during narration of neutral pictures (16.61 ± 3.04% *vs.*



19.48 ± 2.88%, $p = 0.144$). Furthermore, while after vertex stimulation the difference between descriptions of neutral and negative pictures was not significant ($p = 0.078$), after LIFG stimulation it was higher for negative than for neutral pictures ($p = 0.024$). Thus, LIFG-cTBS disrupted the text-level structure of negative storytelling, both when they were directed to a peer and to a child.

Physiological response

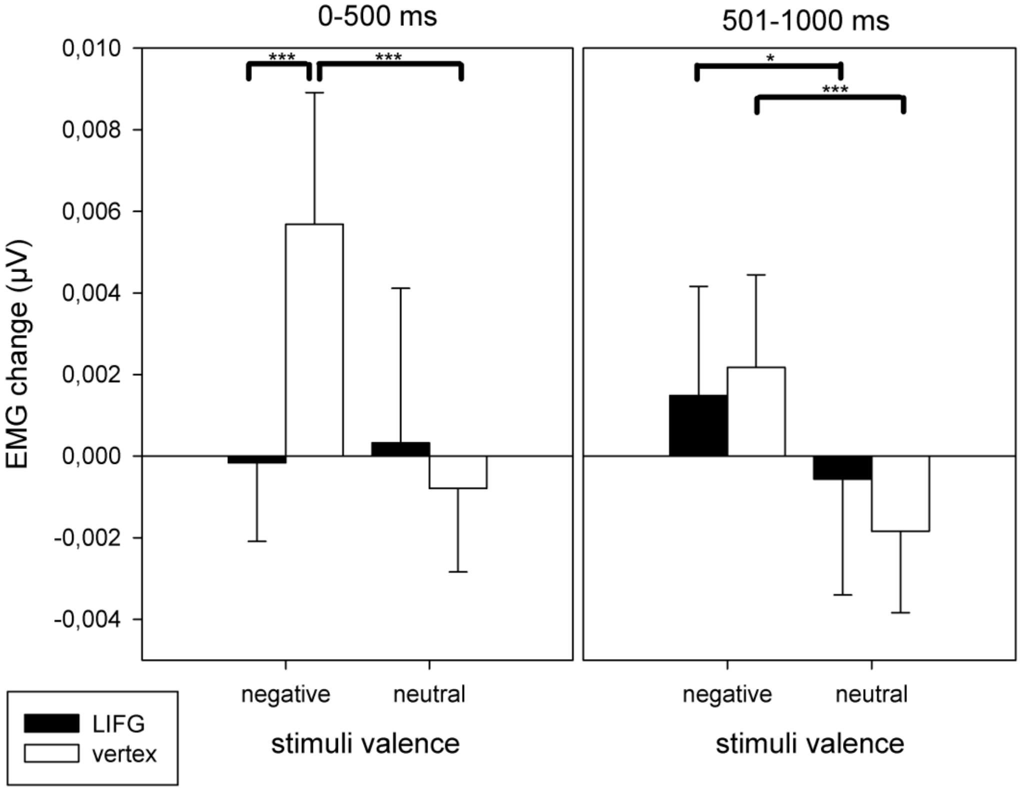
The analysis of the HRV did not reveal any main effect (all Fs < 2.202; $p > 0.166$; $\eta p^2 < 0.167$) or two-way interaction (all Fs < 4.6; $p > 0.055$; $\eta p^2 < 0.294$), but a significant tree-way interaction was found between time-frame, site of stimulation and picture valence ($F_{(1,11)} = 11.883$; $p = 0.005$; $\eta p^2 = 0.519$; Fig. 4). Post-hoc analysis showed that LIFG-cTBS attenuated the early reduction of HRV in response to negative pictures as compared to vertex-cTBS (-1.66 ± 1.16 bpm *vs.* -3.85 ± 1.24 bpm, $p = 0.005$), while no difference was obtained between LIFG- and vertex-cTBS for the early HRV response to neutral pictures (-2.41 ± 0.97 *vs.* -2.52 ± 0.98 bpm; $p = 0.845$). Furthermore, after vertex stimulation, the early HRV in response to negative pictures decreased more than in response to neutral pictures ($p < 0.045$), while after LIFG stimulation the early response was not modulated by picture valence ($p = 0.241$). No direct cTBS effect was obtained for the late HRV response for either negative ($p = 0.248$) or neutral pictures ($p = 0.099$). However, after LIFG stimulation the late HRV was modulated by picture valence, as HRV decreased more for negative pictures (-2.68 ± 1.15 bpm) than for neutral pictures (-0.64 ± 1.22 bpm; $p = 0.008$), while no difference was found after vertex cTBS ($p = 0.673$). Thus, LIFG-cTBS reduced the early HRV response to negative pictures, so that it was comparable to the response to neutral pictures. A greater HRV response to negative than neutral pictures was found, however, in the later phase after LIFG-cTBS, while a comparable late HRV response was obtained to negative and neutral pictures after vertex-cTBS. This suggests that LIFG-cTBS induced a delay rather than a suppression of the HRV orienting response to negative pictures.



EMG activity

The analysis of the corrugator supercilii early response revealed no main effect (all $F_{(1,11)}$s < 1.27; $p > 0.285$; $\eta p^2 < 0.11$) or two-way interaction (all $Fs_{(1,11)} < 5.21$; $p > 0.04$; $\eta p^2 < 0.322$). A significant three-way interaction between picture valence, site, and time ($F_{(1,11)} = 10.48$; $p = 0.0079$; $\eta p^2 = 0.488$; Fig. 5) was found, while the remaining three-way interactions and the four-way interaction did not reach the Bonferroni-corrected threshold (all $Fs_{(1,11)} < 8.8$; $p > 0.012$; $\eta p^2 < 0.445$). Post-hoc analysis revealed that the EMG activity was significantly lower after LIFG (-0.2 ± 1.92 µV) than after vertex stimulation (5.69 ± 3.22 µV, $p < 0.001$) for the initial 500 ms of presentation of negative pictures. Conversely, no between-site difference was found for the early response to neutral pictures (0.33 ± 3.79 µV, *vs.* -0.8 ± 2.05 µV, $p = 0.205$) or for the later response to both negative (1.48 ± 2.68 µV, *vs.* 2.18 ±

2.27 µV, *p* = 0.386) and neutral pictures (-0.6 ± 2.84 µV, *vs.* -1.8 ± 2 µV, *p* = 0.144). Comparing the modulation of EMG activity according to picture valence revealed higher early activation for negative than neutral pictures after vertex-cTBS (p < 0.001), but not after LIFG-cTBS (*p* = 0.538). The late activity of the corrugator supercilii was, conversely, higher for negative than for neutral pictures after both vertex- (p < 0.001) and LIFG-cTBS (*p* = 0.031). Thus, interfering with LIFG activity disrupted the immediate EMG response to negative pictures, whereas the later response was maintained.



3.3.3 Discussion

In the present study, we tested the role of LIFG as a cognitive control region in appraisal and reappraisal of emotional stimuli using a new task that triggers emotional regulation and, at the same time, simulates the everyday life situations in which reappraisal processes are spontaneously used. This was ultimately aimed at improving ecological validity as compared to previous studies on emotion regulation. To this aim, we asked participants to narrate the content of some images to an adult or a child. Results showed that the contextual manipulation of the storytelling task modulated the emotional valence of narrations, reducing the negative emotional content of narrations in response to negative pictures. No changes were, however, observed for the physiological and muscular responses to negative pictures, suggesting that emotional regulation affected the reappraisal rather than the appraisal of negative stimuli. Furthermore, the interference with neural activity of LIFG disrupted the text-level structuring of negative picture storytelling as well as the early cardiac and muscular response to viewing negative *vs.* neutral pictures. For no variables, did LIFG-cTBS effects interacted with the regulation task. These results are held to suggest that LIFG is involved in the initial appraisal, rather than reappraisal of emotional stimuli.

Effects of emotional regulation

The present study shows that emotion regulation affects socially contextualized narrative tasks, by adapting the emotional valence of the narrated content to the social audience. Indeed, the valence of the produced narrations was less negative when adult participants were required to produce a storytelling to a child than to a peer. This result, along with the modulation of the content according to stimulus valence, supports the claim that the task was sensible to both picture valence and reappraisal condition. Emotional regulation did not affect the paticipant's productivity (i.e., number of uttered words) and lexical informativeness while describing negatively connotated or neutral scenes., This suggests that they were able to generate appropriate mental models of the target scenes by pragmatically adapting the emotional content of the narrative to the audience. It is worth noting that the task employed here manipulated the context (i.e., the interlocutor) in which the storytelling was to be produced, but no explicit instructions to either down- or up-regulate the emotional content of the narrations had been previously provided. Thus, the direction of the regulatory strategy was spontaneously chosen by the participants on the basis of shared expectations regarding which emotions are socially unacceptable in specific contexts and how to reappraise the stimuli in order to trigger more socially acceptable emotions. The validation of ecological emotional regulatory tasks such as the one used in the present study may contribute to the comprehension of how different contextual cues might modulate those emotional regulatory processes that occur spontaneously in daily-life communicative interactions.

The manipulation of the emotional regulation requirements of the task affected the valence of the produced narratives. However, it did not exert any effect on the physiological orientation to the stimuli nor on the emotional expressive behavior assessed by measuring facial muscular activity. Considering the pattern of results obtained after control vertex stimulation as a model of what happens in similar everyday situations with a full-functioning neurocognitive system, this study replicated findings of behavioral studies that investigated how emotional regulation affects the physiological responses (Bradley et al., 2001; Thayer & Lane, 2000) and expressive behaviors to emotionally connotated stimuli. Indeed, the early HRV deceleration was more pronounced when participants looked at negative than neutral stimuli, suggesting that a greater orienting response is needed for stimuli with high affective content (Bradley et al., 2001; Bradley, 2009). Similarly, the results showed higher early response for negative than for neutral pictures in the EMG activity of the corrugator supercilii muscle, which is known to correlate with negative experiences (Larsen et al., 2003). Therefore, these results confirmed the hypothesis according to which the valence of the stimuli used in this study would successfully modulate the central autonomic system activation by decelerating the HRV and the automatic facial expressive behavior by activating the corrugator supercilii muscle. In contrast to our hypotheses, however, these autonomic and motor responses to negative stimuli were not modulated by the emotional regulation requirement of the task, as similar responses were obtained when producing narratives regardless of the interlocutor (i.e, an adult or a child).

The lack of significant physiological modulation of the contextual instructions after reappraisal is coherent with previous findings (Gross, 1998) showing that participants who received reappraisal instructions while watching a disgusting movie (i.e., limb amputation) mitigated their negative subjective feelings and expressive behavior as compared to participants receiving neutral instructions, but failed to show any sign of mitigated physiological responses, including HRV. On the other hand, the lack of modulation of corrugator supercilii muscular activity seems in contrast with previous studies (Jackson et al., 2000; Kim & Hamann, 2012; Urry, 2010) showing that reappraisal instructions decreased the EMG response of the corrugator supercilii muscle as compared to that expressed under neutral instructions. It is worth noting, however, that the modulation of the activity of the corrugator supercilii by reappraisal instructions was found only in later phases of stimulus processing (> than 5 seconds, Urry 2010), while no modulation was obtained on fast muscular responses to stimulus presentation, which reflects the early stages of emotion generation (Gross, 1998, 1999). All in all, the pattern of behavioral, physiological and muscular responses during vertex-cTBS suggests that contextual instructions to regulate emotions affected the later reappraisal of negative stimuli, when the regulated narratives had to be produced, but not the early phases of stimulus appraisal, which was reflected by early cardiac and EMG responses.

Role of LIFG in emotional regulation

In order to investigate the relation between cognitive control and emotion regulation, we applied cTBS to LIFG, a region known to be involved in attentional control (Ochsner & Gross, 2005; Ochsner et al., 2010; Wessing et al., 2013), goal identification (Van Overwalle, 2009) and semantic control (Jefferies, 2012). Furthermore, it has been suggested that this area might significantly contribute to the process of lexical selection during storytelling (Marini & Urgesi, 2012). By interfering with the activity in this region, the present study aimed at assessing its role in the process of emotional reappraisal during the generation of a story.

Crucially, no effect of LIFG-cTBS on the valence of the produced narrations, independently from whether they were directed to an adult or to a child, was found. This may suggest that LIFG is not significantly involved in processing the appropriate emotional content of narratives or in the regulation of the emotional content of storytelling according to the context. However, during the production of story tellings, LIFG cTBS increased the number of errors of cohesion for negative picture narration, while no difference was found for neutral stimuli. Interestingly, such errors were mostly due to abrupt interruptions of ongoing utterances that did not determine any conceptual shift among adjacent utterances. Rather, these difficulties triggered the reformulation of the interrupted utterances. Indeed, no effects of LIFG-cTBS were observed on language productivity or lexical informativeness of negative picture storytelling, suggesting that, contrary to our hypotheses, LIFG did not affect the capability to form an appropriate mental model of the picture scene with either regulated or non regulated emotional content. Therefore, LIFG-cTBS selectively disrupted the text-level structure of emotionally connoted storytelling, pointing to interference in the process involved in establishing the cohesive links between the planned utterances.

The analysis of the physiological and EMG measures after LIFG-cTBS also suggested that interference with neural activity in LIFG altered the initial response to negative stimuli as compared to what happened after vertex stimulation. Indeed, the early HRV response to negative pictures was attenuated by interference with LIFG activity, as a lower deceleration of HRV was obtained after LIFG-cTBS than after vertex-cTBS. Importantly, comparable early HRV responses were obtained for negative and neutral pictures after LIFG-TBS, showing that the initial orientation response was not modulated by picture valence. Importantly, however, such modulation of the HRV response according to picture valence was reestablished in the late phase, when a greater HRV deceleration was found for negative than neutral stimuli. This may suggest that LIFG-cTBS did not suppress the orientation to the emotional content of the pictures. Rather, it likely delayed it. Similarly, the early expressive behavior measured by EMG activity of corrugator supercilii was modulated by picture valence after vertex stimulation but not after LIFG stimulation. In contrast, the late valence modulation of muscular activity found after stimulation of the vertex was maintained also after LIFG stimulation. Overall, these results support the potential role of the LIFG in the initial appraisal of the stimulus preceding the emotion-formation phase, which seems to have occurred appropriately after LIFG-cTBS as reflected by the lack of cTBS effects on the valence of produced narratives. Crucially, however, the delayed initial orientation to the stimulus and the altered appraisal of its emotional content may have affected the quality of later storytelling. Indeed, it may be hypothesized that nonappropriate initial evaluation of the emotional valence of the stimuli may have triggered frequent re-evaluations during the process of storytelling and induced frequent interruptions of ongoing utterances leading to an increase of errors of cohesion.

The possibility that LIFG is involved in the initial orientation of the cognitive and physiological systems to the stimulus, but is not directly involved in the modulation of the processes inducing emotional regulation is in line with a recent neurocognitive model of emotion regulation proposed by Kohn and colleagues (2014). Indeed, following a large meta-analysis of neuroimaging studies investigating the different components of Gross' cognitive model of emotional regulation, these authors proposed a three-stage model, which involves: i) a first stage of affective arousal relayed by the amygdala to the ventrolateral prefrontal cortex (VLPFC), insula, supplementary motor area, angular and superior temporal gyri; ii) a second stage of appraisal subtended by VLPFC, which signals the need to regulate the emotion to the dorsolateral prefrontal cortex (DLPFC); iii) and a third stage in which DLPFC regulates emotional expression modulating the activity in angular gyrus, supplementary motor area, superior temporal gyrus and the amygdala, resulting in the generation of a regulated emotional state. Thus, in keeping with our findings, VLPFC, including IFG, is seen in this model as the source of stimulus appraisal, which may involve not only affective but also pre-affective dimensions, such as novelty, uncertainty, urgency and relevance (for a review see Ellsworth and Scherer 2003). This role of LIFG in emotional regulation would also keep with cognitive models that attribute to LIFG a role in attentional control (Ochsner & Gross, 2005; Ochsner et al., 2010; Wessing et al., 2013), goal identification (Van Overwalle, 2009), and semantic control (Jefferies, 2012).

3.3.4 Conclusion

In conclusion, in the present study we developed and validated a new ecological task to elicit spontaneous use of emotional regulation processes during storytelling. This task simulates everyday life situations in which adults need to reappraise the emotional content of scenes (for example, frightening TV news) to mitigate their emotional impact on exposed children. According to our hypotheses, the context of storytelling successfully modulated the valence of the produced narratives, reducing their negative valence when they were directed to a child as compared to when they were directed to an adult. However, it did not affect the early expressive behavior nor the physiologic orienting response to the picture. This suggests that the knowledge of the kind of audience (adult *vs.* child) triggers the reappraisal of stimuli but does not modulate their initial appraisal. It is noteworthy, however, that the nature, temporal dynamics and relation of different stages of emotional regulation processes is far from being understood (Kalisch, 2009). Indeed, it is possible that the task employed in this study triggered the suppression of behavioral response in addition to reappraisal, mitigating how negative pictures were described more than how the pictures were evaluated. These different processes are difficult to separate when considering only the final results of emotional regulation (i.e., the emotional content of storytelling) as we did in the present study. Crucially, however, LIFG seems to participate in the initial appraisal and modulation of the orienting response to emotional stimuli rather than in reappraisal (or suppression) of their emotional content. Although this role of LIFG in emotional regulation processes is in keeping with previous findings (Kohn et al., 2014), further studies are needed to better understand its role in specific components of emotion regulation and test the temporal dynamics of its involvement.

4

Automatic and controlled mechanisms in videogames

4.1 Definition of videogame

Videogames are a form of entertainment the origins of which date back to the early 1950s. While in 2008 videogames industry surpassed movies industry (Chatfield, 2009), surprisingly little academic research has been devote to study these products. Three approaches tried to define what is a videogame, listed below alongside main focus and main failures.

Narratological approach

Narratologists (e.g., Murray, 1997) argue that videogames are defined as interactive stories and, as such, can be included in the same category as literature and movies. However, many videogames do not include a narrative that is necessary, or even useful, to the gameplay itself. Some even lack a narrative altogether. Thus, narrative elements as a necessary condition fails at defining of videogames (Tavinor, 2008).

Ludological approach

Ludologists (e.g., Aarseth, 1997) focus on the game components that are inherent to the videogames. These elements include the presence of rules, quantifiable outcomes, goals and the non-trivial effort that is required for introducing new, multiple or even possible meaning to the narrative to unfold. However, being a game is not sufficient to be included in the videogame category (Tavinor, 2008).

Interactive fiction approach

Moreover, some videogames offer simulation *tout court*, with no other elements of gameplay. The third approach that tried to define videogames focus on the simulation that occurs during gameplay. However, while some games are explicitly simulators of some real life activity, the gameplay of others include only the manipulation of objects that are only weakly related to their meaning, thus limiting the activity of the player to physically moving colored areas on the screen (especially with the advent of thouchscreens) (Tavinor, 2008).

A disjunctive definition have been proposed by Tavinor (2008), with the condition of being an artefact in a digital visual medium, a condition that seems necessary but not sufficient *per se* (as it includes other products such as movies or web-pages). The definition is:

> X is a videogame if it is an artefact in a digital visual medium, is intended primarily as an object of entertainment, and is intended to provide such entertainment through the employment of one or both of the following modes of engagement: rule-bound gameplay or interactive fiction.

This definition will be used in this thesis. However, it is noteworthy that educational videogames exist as well as those intended for entertainment, but use entertainment as a mean towards education.

4.2 Game mechanics, motivation and learning

Videogames can communicate powerful ideas and teach in powerful ways. In playing videogames, gamers live designed experiences in which some elements of the world may be simulated and some others are definitively left out. (Squire, 2008). The tools by which the game is played are the game mechanics (Fabricatore, 2007). The interactive nature of game mechanics in videogames require the player to perform actions, as such rendering the act of gaming a performative act (Squire, 2008). The structure of the game system and the game mechanics lead to different kinds of performative acts that strongly rely on the motivation that the player finds in playing: emotional link to the content, involvement, immersion, free of choice, curiosity, perceived control, challenge (see Inchamnan & Wyeth, 2013 for a review). However, motivation can be intrinsic or extrinsic that is, motivation can be generated by the activity itself or by the external circumstance that the activity is a means towards (Ryan & Deci, 2000). In competitive environments, intrinsically motivated players engaged in optimally challenging situations in comparison with players with extrinsically motivated players (Abuhamdeh & Csikszentmihalyi, 2009). At the optimal level of challenge, the optimal level of learning occurs (Vygotsky, 1978). For their features, videogames are ideally suited to modulate the challenge, the intrinsic motivation and, as such, the learning processes.

4.3 Endogenous and exogenous videogames

Videogames are semiotic systems in which players need to learn to read the symbols and their meaning as the first step in the learning process: as such, the way in which the videogame is designed influences the conveyed message, the way in which the learning process occurs and, obviously, the gameplay[1]. Therefore, by

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[1] Here, I’m using the term “gameplay” as an umbrella term to refer generically to what concerns the usage of a videogame by a player, being it focused on the player (the actions done by the player, the meanings that the player attribute to the parts of the game, the mental model of the goals and sub-goals of the game, etc) or on the game (the set of actions that the game allows, the game-relevant knowledge that the game delivers or hides, the in-game goals and sub-goals, etc). However, while definitions of gameplay exist (e.g., “the structures of player interaction with the game system and interaction with other players”, in Björk & Holopainen, 2005), breaking down the gameplay experience in all of its components is a task that is out of the purpose of this thesis.

impacting the way in which the experience is decoded, game design allows for a manipulation of both the message and the learning process.

Squire (Squire, 2006) proposed a classification of videogames based on the relationship between game mechanics and meanings. Videogames with strong links between meanings and mechanics offer environments and narratives that are non-irrelevant to the gameplay. As such, the engaged player sticks to the intended meanings (eventually adding new or alternative meaning) and acts accordingly; often, the motivation is intrinsic to the acting on the game meanings. Conversely, videogames with a weak relationship between meaning and mechanics don't offer such non-irrelevant narratives (i.e., they offer gameplay-irrelevant narratives or no narratives at all). As such, the engaged player can't be motivated by the meanings of the game, and acts only on the perceptual features; often, the motivation is extrinsic. The videogames of the first kind have been named endogenous videogames, those of the second kind have been named exogenous videogames.

4.4 Learning processes in videogames

Gamers are considered active constructors of meanings and motivations. Many young gamers experience in videogames topics such as history, physics, economy, geography, urban planning (Squire, 2006) and expand their understandings of such topics by finding intrinsic motivation for reflecting and conceptualizing the gameplay (Squire, 2004). Squire (2006) argues for a superiority of videogames as new educational media in comparison with traditional media: indeed, in videogames, the player is put inside the game system that drives the learning process, while in traditional media the learning process is driven exclusively by exposure to content. As such, a good videogame design may allow players to go beyond mere exposure and actively reflect, conceptualize and understand the experience.

As already written above, in videogames knowledge becomes embodied in performance. The four proposed learning process phases are (Squire, 2008):

1. Learning how to read the game as a semiotic system
2. Understanding the effects of the allowed actions

3. Understanding the higher order interactions and emergent rules of the game system
4. Continuously monitoring and reflecting in a goal-oriented manner

Conversely, traditional educational media focus declarative knowledge. In videogames, declarative knowledge comes from the later conceptualization of the performance in which it is embodied (Squire, 2008).

Content in videogames is conceptualized and proposed in form of challenges, goals and practices (Squire et al., 2003). By conceptualizing social perception and social adaptation in terms of challenges, goals and practices, it may be possible to use manipulate the performative acts with the goal of boosting automatic or controlled mechanisms of action perception as well as social adaptation.

4.5 A proposal for action perception applications in videogames

Videogames allow for the possibility of teaching - and often require the learning of - complex gestures and motor patterns. A designed experience in which the goal or the mean towards one is to learn a complex motor pattern, by following the reasoning described above, may allow players to engage into the optimal learning experience. As seen in chapter 2, action understanding involves automatic and controlled processes, such as motor resonance and mentalized action understanding. However, traditional *in situ* teaching methods have limits in the control of automatic and controlled mechanisms modulation, while videogames can be designed in order to demolish such limits. This general proposal may have applications in high level motor skills teaching, such as sports, music and surgery. Human-computer interfaces that allow the player to communicate by using gestures are already available and commercialized. As such, gestures can be tracked by the computer and the current challenge level can be adapted to the skill level, enhancing the learning process (Vygotsky, 1978). Most importantly, the training process can be programmed in order to boost specifically automatic or controlled processes. Indeed, in a framework like the one proposed, automatic processes such as motor resonance can be used to enhance motor learning at first, for example by showing an avatar performing the required action. At higher challenge levels, the same automatic processes can be used to challenge gesture performance by inhibiting motor resonance, for example showing avatars performing different incongruent actions. This may increase the intrinsic motivation to memorize the gesture and to recall the motor pattern even in the absence of social cues such as motor resonance, or even in the presence of actively inhibiting interference, such as the presence of incongruent actions, thus recruiting controlled mentalized processes of motor pattern recall. The complex interplay between automatic and controlled mechanisms is interesting and particularly suited to be used in videogames with, ultimately, an educational goal.

4.6 A proposal for social adaptation applications in videogames

Contrary to gesture interfaces, affective interfaces exist only as experimental interfaces or for niche applications. However, there seems to be some new interest in developing affective interfaces (e.g., Gilleade, Dix, & Allanson, 2005; Nakasone, Prendinger, & Ishizuka, 2005). Traditionally, interaction with videogames is done purely on conscious levels, but player's emotional responses are likely to occur as well (and are explicitly intended in some franchising). An affective interface would require the measure of physiological responses such as heartbeat (Gilleade et al., 2005; Thayer & Lane, 2000), skin conductance and changes in facial expression (Nakasone et al., 2005) to be used as input to the game. Once affective state is inferred, it may be used in order to adapt the game contents to the emotional responses. This proposal may be useful, for example, in modulating the emotional impact of videogames on children. However, challenge level can be adapted to the affective state in order to keep an optimal challenge level, in line with what I wrote about learning in videogames above.

More interestingly, and maybe somehow a stretch, the affective state may be part of the conscious input that the player gives during the gameplay. Emotion regulation may be a part of the programmed set of required responses in order to advance in the game. Videogames may ask for an higher level of arousal or a lower heartbeat frequency in order to unlock the next level. As such, players would be faced with a challenge they need to win and a consequent learning, thus training in emotion regulation.

Three points are noteworthy. First, emotion regulation may be used as an exogenous or endogenous component that is, just as a required action in order to advance in the game or as a part of the gameplay, for example in a game in which social interactions are simulated. As discussed, in the endogenous case, players might find intrinsic motivation in using emotion regulation strategies, alongside the related advantages (K. Squire, 2006). The second point that is worth noting is that this proposal might need further ethical considerations, since by asking players to use emotion regulation strategies they might engage in regulatory acts that are correlated with lesser long-term wellbeing than those that are correlated with higher long-term wellbeing (such as suppression instead of reappraisal, e.g., Gross & John, 2003), and thus receiving a training in the former rather than in the latter. The third point is related to our results in the social adaptation chapter: indeed, we didn’t find any physiological effect of emotion regulation. However, while our results are in line with some studies (Gross, 1998), other authors found emotion regulation effects on at least some physiological variable (Jackson et al., 2000; Kim & Hamann, 2012; Urry, 2010). As such, while in principle this proposal holds some ground, further research is needed in order to assess its feasibility.

5

Conclusions

5.1 Conclusions and future directions.

This thesis purpose was to explore controlled and automatic processes in social cognition with a neuroscientific approach, and to discuss the results in light of potential applications for educational videogames. I showed how automatic processes depend upon different dynamics than controlled ones, both in social action perception (chapter 2) and in adapting one's own behaviour to the social environment (chapter 3). I've discussed how automatic and controlled processes may be used in videogames in order to create the optimal learning environment (chapter 4). The neuroscientific approach allowed the exploration of psychological and physiological facets of these processes (chapter 2 and 3). However, further research is needed in order to both assess the feasibility of this proposal and to evaluate which automatic and controlled processes can be used as means to this goal. Particularly, further research should target action perception with neuroscientific tools in order to better understand the neural substrates of social action perception, since we proposed a tentative interpretation of our results that needs support. Furthermore, visual human-computer interface may greatly benefeit from these studies. On the other hand, affective interfaces are at their beginning, so further research in psychological and neural aspects of social affective responses and adaptation should be targeted in first place, with an eye toward this application. As discussed (chapter 4), videogames can create the optimal learning environment, and thus may be the optimal area of convergence for implementation of social cognitive neuroscience in the educational domain.

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