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Electrophysiological exploration of semantic processing: the roles of expertise and sensory modality

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Abstract

Semantic memory consists of stored information about features and attributes that define concepts and the processes (Martin & Chao, 2001). The N400, an event-related brain potential (ERP) waveform, reflects process through which the meaning of an incoming stimulus is mapped onto the corresponding field in semantic memory (Sitnikova et al., 2003). In other terms, the amplitude of this component might index the difficulty to integrate the incoming information with previous information (Proverbio et al., 2010). Several previous studies revealed the sensitivity of the N400 to semantic violations related to a wide range of stimulus types across modality. However, it is still not clear how and when different types of semantic information are integrated in the brain. Therefore, this work aimed at investigating electrophysiological processing to semantic violations in different kinds of context.

More specifically, we focused on the processing of knowledge that requires the integration of automatic, rapid processing of emotional facial expressions into contexts of everyday life and the effects of experiences shaped by a specific artistic/motor training. In particular, we investigated the effects of semantic violations on the amplitude and the morphology of the N400 component. In addition, we verified if the difficulty (or the ease) to integrate the incoming information into the semantic memory is also affected by the sensory modality of the information.

To this aim, we carried out four studies in order to analyze these aspects. The results of the first study revealed that the N400 amplitude is modulated by the congruency of peculiar stimuli (faces) depicted in specific complex situations. The second study showed that the N400 response is sensitive to semantic violations in visual processing of actions related to a sport training. In particular, we observed that the N400 amplitude to violations was a function of the observers' expertise. The results of the third study demonstrated that the semantic processing related to a long lasting musical training affected the N400 amplitude even when stimuli are presented using a multisensory modality. Indeed, we showed that incongruent action-sound presentations elicited a greater N400 amplitude in musicians compared to naïve participants. Finally, in the last work we showed that incongruent words that evoked specific sounds in comics modulated the N400 response in a group of University students with experience in reading comics.

The results of this work revealed a cross-modal nature of the N400 showing that semantic violations to information characterized by differences in sensory modality elicited slightly different ERP scalp distributions. This evidence might suggest that the semantic processing of different knowledge might be affected by perceptual factors.

In addition, the data showed that the N400 amplitude is affected by the type of expertise related to a specific knowledge. Indeed, we observed that the proficiency in a specific context modulated the brain response to semantic anomalies. Overall, these data revealed that the semantic system might be affected by both experience-dependent knowledge and automatic, not experience-mediated processing.

Introduction

The meaning of things lies not in the things themselves, but in our attitude towards them.
Antoine de Saint-Exupery

What is semantic memory?

In 1976, Anderson proposed a distinction between declarative and procedural memory. The author defined declarative memories as knowledge of facts about the world and procedural memories as knowledge about how to do something. According to Ullman (2004), the declarative memory system is involved in the learning, representation, and use of knowledge about facts ("semantic knowledge") and events ("episodic knowledge"). Moreover, the content of this system can be consciously recollected (at least in part). On the other hand, Ullman defined the procedural memory as a system that subserves the learning of new, and the control of established, sensorimotor and cognitive habits, skills, and other procedures, such as riding a bicycle and skilled game playing. In addition, since the knowledge contained in this system is generally not available to conscious access, the procedural memory is named "implicit memory system".

Within declarative memory, Tulving (1972) suggested a distinction between episodic memory, characterized by contextual information about specific events, and semantic memory, composed of context-free, encyclopedic information. Semantic and episodic memory are typically considered distinct, even if, according to an interesting point of view, episodic memory might be considered the "gateway" to semantic memory (Squire & Zola, 1998). However, as Tulving (1990) pointed out, for sensorimotor aspects of semantic knowledge

(knowledge about the shape, size or smell of things), “new information enters semantic memory through our perceptual systems, not through episodic memory”.

Interesting evidences in favor of the dissociation between semantic and episodic memory come from clinical studies. For example, results provided by neuropsychological studies indicated that children who developed amnesia in early childhood (consequent to bilateral hippocampal damage) showed episodic memory impairments, but their semantic knowledge appeared relatively intact (Bindschaedler et al., 2011; Gardiner et al., 2008; Vargha-Khadem et al., 1997). Furthermore, studies on the famous amnesic patient H.M. have revealed that he acquired some semantic knowledge after the surgery that led to his amnesia (Gabrieli et al., 1988; O’Kane et al., 2004). Thus, these evidences suggest that semantic knowledge can be acquired independently of the episodic memory system.

Nevertheless, the fact that the semantic knowledge in these amnesic patients is not normal, suggested that the acquisition of semantic memory normally depends on the episodic system, but other points of entry can be used when the episodic system is damaged (Yee et al. 2013). According to another point of view, these patients may have enough remaining episodic memory to allow the acquisition of semantic knowledge (Squire & Zola, 1998). However, it is also important to underline that other theories support an opposite idea according to which the semantic memory might support episodic memory acquisition (Kan et al., 2009) and retrieval (Greve et al., 2007; Graham et al., 2000).

Today, we use the term semantic memory to refer to all kinds of stored information about the features and attributes that define concepts and the processes that allow us to efficiently retrieve, act upon and produce this information in the service of thought and language (Martin & Chao, 2001).

Elizabeth Warrington (1975) described the selective impairment of semantic memory in three patients with diffuse cerebral lesions. She reported that knowledge of pictorial representations of objects and words was impaired in these patients. This neurodegenerative disease causes gradual and selective atrophy of the anterior temporal cortex (Mesulam et al., 2003; Garrard & Hodges, 1999). The syndrome that has been called *semantic dementia*, is characterized by difficulties in word retrieving and marked deficits in identifying objects, concepts, and people (Snowden et al., 1989) regardless of the stimulus modality (e.g., pictures or written or spoken words; Bozeat et al., 2000; Hodges et al., 1992; Patterson et al., 2006, 2007; Rogers & Patterson, 2007). In addition, observations from neuropsychological patients have suggested knowledge subdivisions within semantic memory (Buxbaum & Saffran, 2002; Saffran & Schwartz, 1994; Thompson-Schill, 2003).

Therefore, the observations of different kinds of impairments in patients with brain injuries, led psychologists to ask questions about how the knowledge about the world is organized (Yee, 2013).

Theories of semantic memory organization

In this section, we describe different cognitive theories about the organization of semantic knowledge.

The first models about semantic memory, described the organization of knowledge in terms of a hierarchy that is structured according to abstract relations between concepts (Pylyshyn, 1973). Other psychologists hypothesized that semantic knowledge may be acquired and stored in a multiple semantic systems. This model suggests that words and pictures access different specialized, semantic systems (Kosslyn & Pomerantz, 1977; Paivio, 1971, 1983, 1986). For example, according to Paivio's (1986) dual coding theory, there exist two structurally and functionally distinct subsystems: a system of *logogens* for processing words and a system of *imagens* for processing nonverbal material. The author posits that even though these two systems are independent, they can communicate with each other.

A more recent popular model, the *domain-specific theory* (Caramazza & Shelton, 1998), theorize that the representation of categories that are particularly relevant for survival or reproduction (i.e., animals, plant life, conspecifics, and possibly tools) are contained in distinct neural mechanisms. In addition, this model suggests that representations of conceptual knowledge may be distributed over different sensory modalities in which, however, the representations of different categories remain distinct (Yee et al., 2013). This theory is based on evidences coming from several clinical studies: some of them revealed that patients with brain injuries may exhibit different semantic impairments. For example, some patients had more difficulty identifying living than non-living things (Warrington & McCarthy, 1983; Warrington & Shallice, 1984; Warrington & McCarthy, 1994). Therefore, these evidences suggested the existence of distinct neural regions dedicated to processing different categories of objects. However, it has been noticed that some patients' recognition deficits cannot be included in category boundaries (Yee et al., 2013).

Another model, the *sensory-functional theory*, stated that conceptual knowledge is divided into anatomically distinct sensory and functional stores (Yee et al., 2013). According to this model, the conceptual knowledge is organized in the brain by modality (visual, olfactory, motor/functional, etc.) and sensory and functional properties are differentially important in identifying members of the living and nonliving categories, respectively (Caramazza & Shelton, 1998). This model specified that the category-specific deficits emerge because the representations of different concepts tend to rely on sensory and functional information to different amounts (Farah & McClelland, 1991; Warrington & McCarthy, 1987). In the frame of this theory, Allport (1985) pointed out that sensory information should not be considered a unitary entity, but rather should be divided into multiple attributes (e.g., color, sound, form, touch). Hence, according to Allport's model, representations are sensorimotor-based, and consequently, the divisions of labor that exist in sensorimotor processing should be reflected in conceptual representations (Yee et al., 2013).

However, Caramazza and Shelton (1998) criticized the *sensory-functional theory* underlining that some semantic deficits cannot be captured through a binary sensory-functional division. In other words, they affirmed that a simple two-way segregating of semantic features is too simplistic (Yee et al., 2013).Therefore, Caramazza and colleagues (Caramazza et al., 1990; Hillis et al., 1995; Rapp et al., 1993) proposed a new unitary, amodal system of conceptual organization. This model, called *Organized-Unitary Content hypothesis* (OUCHT), is based on two fundamental characteristics of natural kind objects and artifacts: i) the properties that define an object are highly intercorrelated; ii) members of a superordinate category share many common features (Gelman & Coley, 1990; Keil et al., 1989; Markman et al., 1989; Rosch et al., 1973, 1975; Rosch et al., 1976). However, Caramazza and Shelton (1998) specified that these intercorrelated properties are differentially distributed in the categories of living and nonliving things (Caramazza & Mahon, 2003). In addition, according to this point of view, multidimensional space of semantic properties is not homogeneously occupied but there are regions that are densely packed and others that are only sparsely occupied (Caramazza & Mahon, 2003).

The final class of models is defined as *Conceptual-Structure account* (Gonnerman et al., 1997; McRae et al., 1997; Tyler & Moss, 2001). According to Caramazza and Mahon (2003), this model is based on three assumptions: i) living things have more shared features than non-living things; ii) for living things, biological function information is highly correlated with shared perceptual properties (e.g. can see/has eyes), and for artifacts, function information is highly correlated with distinctive perceptual properties (e.g. used for spearing/ has tines); iii) features that are highly correlated with other features will be more resistant to damage than features that are not highly correlated.

As Caramazza and Mahon (2003) pointed out, each of the hypotheses discussed above makes assumptions at a different level in a hierarchy of questions about the organization of conceptual knowledge. However, a still unclear question is whether conceptual knowledge is represented in modality-specific semantic stores specialized for processing/storing a specific type of information, or in an amodal, unitary system.

Where is the semantic memory?

In the past, many attempts have been made to identify the neural bases of the semantic memory. In 2009, Binder and colleagues analyzed 120 functional neuroimaging studies focusing on semantic processing. The aim of this work was to identify the brain regions specifically involved in semantic processing.

The authors included in their work the previous studies in which tasks involved a difference in either the degree to which stored knowledge was accessed or the specific type of knowledge accessed. In addition, they excluded studies in which the semantic processing were strongly influenced by low-level sensory, orthographic, phonological, syntactic, working memory, attentional, response selection, or motor processes.

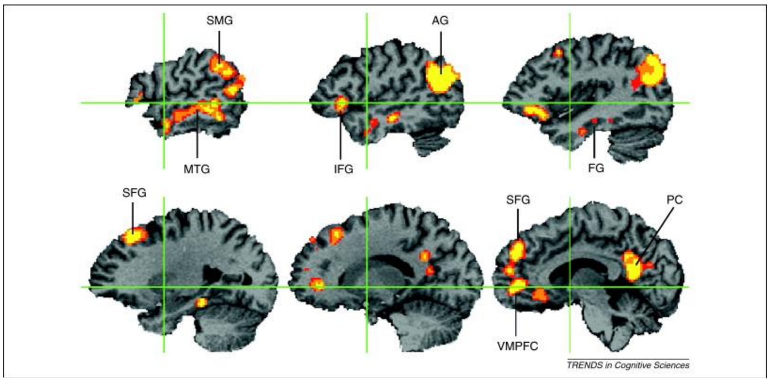

Fig.1. Meta-analysis of functional imaging studies of semantic processing by Binder and colleagues (2009).

The results of the meta-analysis revealed that seven brain regions are clearly involved in semantic processes (Fig. 1.). One of them is the posterior inferior parietal lobe (angular gyrus and portions of the supramarginal gyrus), that could play a role in complex information integration and knowledge retrieval. According to

Geschwind (1965), the angular gyrus may be considered the best candidate for a high-level, supramodal integration area in the human brain because of its anatomical location (closed to visual, spatial, auditory, and somatosensory association areas). In addition, functional imaging evidences showed the activation of this area in response to semantically anomalous words embedded in sentences, suggesting that it plays a role in integrating individual concepts into a larger whole (Ni et al., 2000; Friederici et al., 2003; Newman et al., 2003). Other areas that are involved in semantic processing are the lateral temporal cortex and the ventral temporal cortex (mid-fusiform and adjacent parahippocampal gyrus). Several functional imaging studies have revealed the activation of these regions by auditory stimuli, particularly during language tasks (Démonet et al., 1992; Binder et al., 1997; Wise et al., 2000; Noppeney et al., 2003; Rissman et al., 2003; von Kriegstein et al., 2003; Xiao et al., 2005; Humphries et al. 2006; Orfanidou et al., 2006; Spitsyna et al., 2006; Baumgaertner et al., 2007). Furthermore, other evidences revealed the activation of the temporal lobe by perceptual information about objects and their attributes (Martin et al., 1995, 1996; Cappa et al., 1998; Chao et al., 1999, 2002; Moore & Price 1999a; Perani et al., 1999; Grossman et al. 2002a; Kable et al., 2002; Phillips et al., 2002; Noppeney et al., 2003; Tyler, et al., 2003; Davis et al., 2004; Kable et al., 2005; Noppeney et al., 2005; Wallentin et al., 2005). In light of these evidences, the authors stated that these regions are likely amodal cortex involved in supramodal integration and concept retrieval.

In addition, the results of this meta-analysis revealed that the dorsomedial prefrontal cortex (DMPFC) is involved in semantic processing. In particular, the authors hypothesized that, given its position (i.e. adjacent to motivation and sustained attention networks in the anterior cingulate gyrus and just anterior to premotor cortex), might be involved in a semantic retrieval role.

Moreover, another region that turned out to be active during semantic processing is the inferior frontal gyrus (IFG). This region is implicated in working memory and syntactic processes

(Démonet et al., 1992; Zatorre et al., 1992; Paulesu et al., 1993; Buckner et al., 1995; Fiez, 1997; Smith et al., 1998; Fiez et al., 1999; Poldrack et al., 1999; Burton et al., 2000; Embick et al., 2000; Poldrack et al., 2001; Gold & Buckner 2002; Friederici et al., 2003; Nyberg et al., 2003; Davis et al., 2004; Indefrey & Levelt 2004; Fiebach et al., 2005; Owen et al., 2005; Tan et al., 2005; Grodzinsky & Friederici, 2006). Thus, according to the authors, despite the attempt to avoid considering studies that used tasks in which semantic processing was confounded with phonological processing, it is possible that this activation reflects residual phonological or working memory confounds.

Another active region during semantic task is the ventromedial prefrontal cortex (VMPFC). Previous studies have demonstrated that this region is involved in motivation, emotion, and reward processing and probably plays a central role in processing the affective significance of concepts (Damasio, 1994; Drevets et al., 1997; Mayberg et al., 1999; Bechara et al., 2000; Phillips et al., 2003). Therefore, its activation during semantic tasks may be due to incidental processing of the emotional attributes of words (Kuchinke et al., 2005).

Finally, the posterior cingulate gyrus was found to be involved in semantic processing. This general region has been linked with episodic and visuospatial memory functions (Valenstein et al., 1987; Rudge & Warrington, 1991; Gainotti et al., 1998; Aggleton & Pearce, 2001; Vincent et al., 2006; Epstein et al., 2007), emotion processing (Maddock, 1999), spatial attention (Mesulam, 1990; Small et al., 2003), visual imagery (Hassabis et al., 2007; Johnson et al., 2007; Burgess, 2008), and other processes (Vogt et al., 2006). The authors proposed that the posterior cingulate gyrus, because of its strong connections with the hippocampus, acts as an interface between the semantic retrieval and episodic encoding systems.

The authors pointed out that all these regions described so far are involved in high-level integrative processes. In particular, they refer to these areas as “heteromodal”, indicating that they receive multimodal and supramodal input. In conclusion, the authors indicated that the human semantic system corresponds to the network of parietal, temporal, and prefrontal heteromodal association areas, which are greatly expanded in the human relative to the nonhuman primate brain (von Bonin, 1962; Geschwind, 1965; Brodmann, 1994/1909). Moreover, in a more recent review, the authors underlined that the same locations are consistent with the areas that are subjected to pathological changes in semantic dementia, as well as with the regions involved in vascular lesions causing semantic impairments (Binder et al., 2011; Damasio et al., 1989; Hart & Gordon, 1980).

Are pictures and words stored in different semantic systems?

In this section, we describe some evidences about the processing and the storage of particular classes of stimuli (words and pictures) that are of particular interest for this dissertation.

Some clinical studies have suggested dissociations in performance between tasks that investigated semantic knowledge using pictorial or verbal stimuli (Chainay & Humphreys, 2002; Rumiati & Humphreys, 1998; Saffran et al., 2003b). For example, some evidences revealed that patients with optic aphasia are unable to identify objects presented visually, but their performance with lexical/verbal stimuli is preserved (Hillis & Caramazza, 1995; Riddoch & Humphreys, 1987). Conversely, Saffran and colleagues (2003b) described a patient whose object recognition performance was enhanced when the stimuli were pictures but not words. Neuroimaging studies on healthy participants revealed both similarity and differences in brain activation when accessing the same concept from pictures and words (Gates & Yoon, 2005; Vandenberghe et al., 1996). For example, some of them pointed out a common semantic system for pictures and words in left inferior frontal gyrus and left temporal lobe, and evidence for modality-specific activations for words in both temporal poles and in both occipitotemporal cortices for pictures (Bright et al., 2004).

Prior electrophysiological works suggested the existence of a single semantic store shared by pictures and words (Nigam et al., 1992). Indeed, it has been observed that integrating both types of stimulus with a related prime (Barrett & Rugg, 1990; Bentin et al., 1985; Holcomb & McPherson, 1994) or a congruent sentence context (Ganis et al., 1996; Kutas & Hillyard, 1980, 1984; Nigam et al., 1992) reduces the negativity between 250 and 500 ms after stimulus onset (N400). On the other hand, it has been observed that the electrophysiological responses to words and pictures differed in scalp distribution, implicating nonidentical neural generators (Ganis et al., 1996; Holcomb & McPherson, 1994). In addition, Federmeier and Kutas (2001) found different response patterns to pictures than to words, some of these related to perceptual predictability differences, whereas others seemed to reflect modality-based differences in semantic feature activation. The authors concluded that semantic processing of words and pictures is not amodal.

An electrophysiological instrument to explore semantic memory: the N400

The N400 is a component of the human scalp-recorded event-related brain potentials (ERPs). Its name derives from the fact that the N400 is a negative-going potential, which peaks around 400 ms post-stimulus (and is observed between about 250 and 550 ms).

The existence of the N400 was first reported by Marta Kutas and Steven Hillyard in a study published in *Science* in 1980. At the time, electrophysiological studies concerned almost exclusively perceptual processes. Marta Kutas performed studies using the P300 (P3b) component, an endogenous, mostly modality-independent response whose amplitude is inversely correlated with the item’s probability of occurrence (reviewed in Kutas & Hillyard, 1983; Kutas & Federmeier, 2011).

Marta Kutas wondered whether or not this component would also be sensitive to oddballs of language. Therefore, Kutas and Hillyard designed a series of experiments in which undergraduates university students read seven-word sentences presented one word per second; 75% were congruent control sentences (e.g., I shaved off my mustache and beard), while a random 25% ended oddly, with an improbable word (case 1: He planted string beans in his car) or a wholly anomalous one (case 2: I take coffee with cream and dog). In all cases, sentences were presented one word at a time, approximately 1 per second. The results of this study showed that all unexpected endings elicited a large negativity with a broad (parietally maximal) scalp distribution, peaking around 400 ms (largest for semantic anomalies, but also present for improbable but sensible endings); it was therefore called the "N400" (Kutas & Hillyard, 1980 a,b,c) (see Fig. 2).

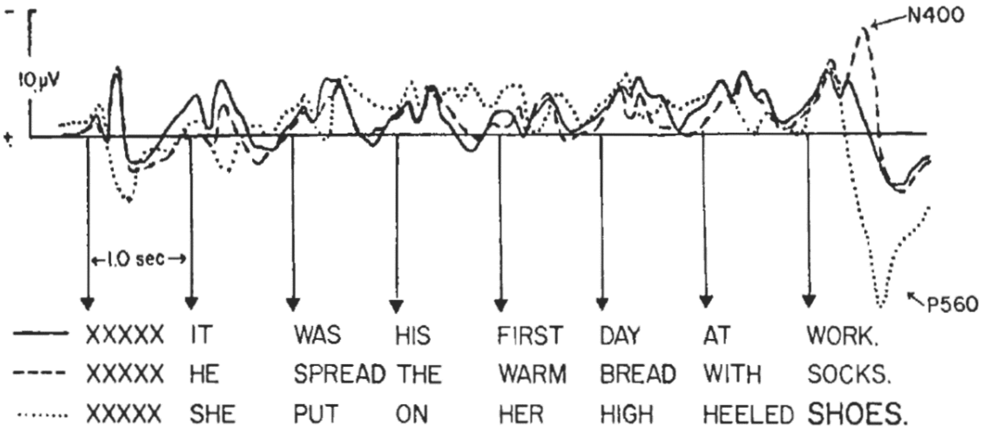

Fig. 2. The discovery of the N400 (Kutas and Hillyard, 1980)

The N400 reflects process through which the meaning of an incoming stimulus is mapped onto the corresponding field in semantic memory (Sitnikova et al., 2003). The N400 is sensitive to semantic violations related to a wide array of meaningful and potentially meaningful stimuli, including visual and auditory words (and word-like strings of letters), acronyms, sign language, pictures, environmental sounds, and gestures.

The amplitude of this component is greater to critical words that are semantically unrelated (vs. related) to previous single words in semantic priming paradigms (Bentin et al., 1985). Evidences also revealed a greater N400 response to words that were incongruent (vs. congruent) with their preceding sentence contexts (Kutas & Hillyard, 1980, 1984) or global discourse contexts (Camblin, et al., 2007; van Berkum, et al., 2003; van Berkum, et al., 1999). In addition, the N400 is sensitive to semantic information that are incongruent with real-world knowledges, both in a verbal (Kutas & Hillyard, 1980; Hagoort et al., 2004) and in nonverbal modality (Proverbio & Riva, 2009; Sitnikova et al., 2008).

The idea that arises from these evidences, is that semantic memory may contain representations of individual concepts that have connections characterized by different strength (Hutchison, 2003; Zacks & Tversky, 2001; Fischler & Bloom, 1985; Bower et al., 1979). Under this view, the N400 component seems to reflect the process through which the meaning of an incoming stimulus is mapped onto the corresponding field in semantic memory (Sitnikova et al., 2008). Indeed, the N400 negativity to potentially meaningful stimuli is reduced as a function of associative, semantic, and repetition priming and fit to context, whether the context is in the same or a different modality (Kutas & Federmeier, 2000).

The N400 in language domain

After the discovery of the N400, several ERP studies of word, sentence, and discourse comprehension have been carried out. Indeed, several investigations showed that the N400 is not just related to manipulation of meaning in sentences, but is also found for manipulations of discourse contexts (van Berkum et al., 1999) and semantic or repetition priming manipulations where only one word represents the context (Bentin et al., 1985). For example, in studies of semantic priming, the amplitude of the N400 is reduced to words that are associatively or semantically related to the preceding context word relative to when they are not (Bentin, 1985; Brown and Hogoort, 1993; Holcomb, 1993).

Other studies have shown that the N400 is sensitive to lexical proprieties of words. For example, real words elicit smaller N400 amplitudes than pseudowords, but random letter strings do not produce an N400 component (Laszlo & Federmeier, 2010). In addition, high-frequency words show smaller amplitude of the N400 than low-frequency words (Barber et al., 2004), but this effect is modulated by the context, such that words later in the sentence no longer show lexical frequency effects (Van Petten & Kutas, 1991). Other studies too showed that words with a small orthographic neighborhood showed reduced N400s relative to words with large orthographic neighborhoods (Holcomb et al., 2002). In addition, some studies manipulated the concreteness or imageability of words observing an increased negativity to high-imageable/concrete words than low-imageable/abstract words. The results showed that the topographic distribution of this N400 effect was anterior, instead of the typical centro-parietal scalp distribution of the N400 (Holcomb et al., 1999; Swaab et al., 2002).

In addition, a relevant line of work concerns the N400 response associated with the processing of the meaning of words embedded in sentence contexts. These kind of studies are very important because they analyze the influence of the meaning of the sentence context on lexical processing. The first studies in this field revealed that the amplitude of the N400 was influenced by the cloze probability (Kutas, 1984). According to the definition of Kutas, the cloze probability is *the proportion of respondents supplying that particular word as a continuation given the preceding context in an offline norming task, ranging from 0 to 1 in value* (Kutas and Federmeier, 2011). In addition, some evidences revealed that the N400 response is also influenced by sentential constraints (Kutas, 1984): *the degree to which the context establishes an expectation for a particular upcoming word, generally empirically defined as the cloze probability of the highest probability continuation, ranging from 0 to 1* (Kutas and Federmeier, 2011). Some studies revealed that low-cloze words that are related in meaning to the best sentence completion are processed more easily in high than in low-constraint sentences (Federmeier and Kutas, 1999; Kutas et al. 1984). According to Federmeier and colleagues (2007) the high contextual constraint can influence the processing of upcoming words at different stages. In other terms, high sentential constraint can facilitate processing of words that are unexpected but related in meaning to the best completions because the context has activated a set of semantic features that matches the meaning of words.

Finally, other studies in the linguistic area, analyzed the N400 effect in the nonliteral language comprehension, such as metaphorical language. They found that literal endings elicited the smallest N400, metaphors the largest N400, whereas literal mappings elicited an N400 of intermediate amplitude. In addition, some studies indicated a special role of the right hemisphere in nonliteral language and joke comprehension (Coulson & Van Petten, 2007; Coulson & Lovett, 2004; Coulson & Williams, 2005).

The N400 in “nonlanguage” domain

The N400 component has been observed also in nonlinguistic meaningful contexts such as paradigms using line drawings (Ganis et al., 1996), stories that are formed by a series of cartoon-like pictures (West & Holcomb, 2002), short movies (Sitnikova et al., 2003), faces (Olivares, 1999), environmental sounds (Van Petten & Rheinfelder 1995), actions (Proverbio & Riva 2009; Bach et al., 2009; Giglio et al., 2013). These evidences suggested that the comprehension of both language and the visual real world might rely on similar mechanisms that access graded semantic memory networks (Sitnkova, 2008). However, the different stimulus modality elicited differences also in the N400 modulation. For example, in some picture studies an early negative component, N300, has been found (McPherson & Holcomb, 1999). In addition, the N300/N400 complex elicited by pictures revealed a more anterior scalp distribution compared to the N400 response found in language studies (McPherson & Holcomb, 1999). These distributional differences may reflect a neuroanatomical distinction between semantic memory networks accessed by different stimuli (Sitnikova et al., 2006; McPherson & Holcomb, 1999).

In the next section, we will discuss the results of some electrophysiological studies related to the processing of the semantic information learned through a specific training and based on world-knowledge.

Semantic knowledge processing in different contexts: the role of experience

In this section, we report some evidences about the semantic processing of knowledge whose acquisition is modulated by experience.

First, we consider the semantic processing of the so-called "world knowledge" in which we include faces, body language, human actions and everyday events processing.

In the previous sections, we showed that the N400 component is sensitive to how well verbal and nonverbal stimuli fit the previous pragmatic context. However, strong evidences suggested that the N400 is also modulated by violations of world-knowledge learned during every-day life (Proverbio et al. 2009). Hagoort and colleagues (2004), presented electrophysiological data that demonstrated the rapid parallel integration of both semantic and world knowledge during the interpretation of a sentence. Their idea was that if a distinction can be made between linguistic meaning and world knowledge, different processing during the interpretation of a sentence should be observed. To verify this hypothesis they presented three versions of sentences such as "the Dutch trains are yellow/white/sour and very crowded". Given that Dutch trains are typically yellow, only the first condition (the Dutch trains are yellow) was correct. However, despite the linguistic meaning of the alternative term "white" was not semantically incongruent with the context, it elicited an N400 response similar to that observed in response to "sour" that contained an explicit violation of semantic constraints. This amplitude similarity, in addition to similarity in topography, onset, and peak latency of the

N400 for the two violation types, suggested that both world knowledge and lexical semantic knowledge influence online meaning processing in a similar way (Metusalem et al., 2012).

Therefore, in the context of “world-knowledge”, a modulation of the N400 amplitude as a function of the semantic access has been observed also during the observation of scene/action representations. West and Holcomb (2002) found a larger N400 to visual scenes that were incongruous (vs. congruous) with sequentially presented static pictures conveying stories. Proverbio and Riva (2009) found an N400 effect during the visual presentation of comprehensible vs. incomprehensible actions, revealing a greater amplitude of the component to the second compared to the first ones. The incomprehensible actions used in this study were purposeless, socially inappropriate or impossible to understand (in terms of the agent’s intentions). In other terms, they violated the so-called “world knowledge” about typical human actions in ecological environments (Proverbio & Riva, 2009). Sitnikova and colleagues (2003) conducted an ERP study in which they investigated short, silent video vignettes. In this study, movie clips of common goal-directed, real-world activities ended either with a congruous or incongruous final event. In the congruent final event, an appropriate object was introduced, while in the incongruent one an inappropriate object was used. The results showed that the incongruent scenes evoked an anteriorly distributed N400 effect relative to the congruent ones where the context-appropriate object was used. Recently, Giglio and colleagues (2013) conducted an ERP study to verify if the N400 effect found in previous studies might reflect a response to macroscopic inconsistency rather than subtle violations of known actions/scenes. Therefore, they presented a sequence of physically feasible actions with congruent and incongruent endings. The results of this study did not reveal any larger N400 response to incongruent endings compared to congruent ones. However, in line with other studies that used nonverbal material (Sitnikova, 2003; Proverbio, 2012; Cohn et al., 2014) a late positivity response was found for unexpected endings.

Proverbio and colleagues (2013) performed a study to investigate the neural mechanisms underlying the human ability to understand emotional body language (EBL). To this aim whole-figure photographs of female and male actors portraying 40 typical emotional or mental states were presented to a group of University students. Pictures were preceded by a short verbal description of a feeling that could be consistent or not with the following picture. ERP data an increased anterior N400 response to incongruent body language compared to congruent ones.

Overall, these studies revealed that the N400 response could be modulated by the familiarity and the appropriateness of information learned during everyday life experience and included in the so-called “world knowledge”.

In the following second section, we will describe some evidence about how semantic knowledge that have been learned through a specific artistic/motor or linguistic long-lasting training are processed. Specifically, we consider the effects of semantic violations on the amplitude and the morphology of the N400 component.

In the domain of language, some studies revealed that the amplitude or the latency of the N400 response is sensitive to an individual’s proficiency with a given language. According to Kutas and Federmeier (2011) this effect could reflect the competence in adult second language acquisition. In 1996, Weber-Fox and Neville investigated the influence of bilingual proficiency on hemispheric lateralization of linguistic brain areas, testing a large sample of Chinese/English bilinguals who had been exposed to English at different stages of their development. The authors found a delay in N400 latency to semantic anomalies for bilinguals exposed to English after the age of 10, but no differences in the amplitude or topography of N400 on comparing bi- and monolinguals. Proverbio and colleagues (2002) investigated the semantic processing in monolinguals and bilinguals during a task that involved silent reading. The results showed that the congruity effect did not distinguish between bilingual and monolingual’s first language. The authors attributed this result to the fact that bilingual speakers were highly fluent and had acquired both languages in early infancy. In addition, in the bilinguals, semantic incongruence resulted in greater response over the left hemisphere than over the right. The authors concluded that this brain activation pattern did not depend on the age of acquisition or the fluency level but on the functional organization of the bilinguals’ brain due to polyglotism (Proverbio et al., 2002).

Other ERPs studies found a differential pattern of bilingual brain activation in semantic violation studies on the N400 component. For example, Meuter and colleagues (1987) found that N400 was greater over the left parietal sites than over the right for the second language, while it was bilaterally symmetrical for their first language. Other findings suggested that the N400 was greater over the right parietal side in monolinguals and over the left side in bilinguals (Ardal et al., 1990). Neville et al. (1992) investigated N400s in response to semantic incongruities in American Sign Language (ASL) finding that some of the hearing/deaf differences in language processing experiments reflect the difference between a first and second language (Kutas et al., 2007).

So far, we have described some studies that investigated the effects of semantic anomalies using linguistic material. However, there are evidences that suggest that the semantic incongruences, related to a specific knowledge, can modulate the amplitude of the N400 response also in the nonlinguistic domain. This is the case of music.

Indeed, evidence revealed that music can activate brain mechanisms related to the processing of semantic meaning (Koelsch et al., 2004). For example, previous works compared processing of semantic meaning in language and music, investigating the semantic priming effect as indexed by the N400 component (Koelsch et al., 2004; Daltrozzo & Schön, 2008). The results of this studies showed that the N400 priming effect did not differ between language and music with respect to time course, strength or neural generators (Koelsch et al., 2004). More in general, these findings make clear that music may convey concepts (Daltrozzo & Schön, 2008).

In addition, the results of recent investigations pointed out different patterns of brain response between musicians vs. nonmusicians during the detection of musical incongruities. In particular, these studies indicated that, only in musicians, the presentation of inconsistent musical stimuli elicited a greater N400 response compared to consistent ones (Besson et al., 1994; Proverbio et al., 2014).

These findings draw attention to the effects of a long-lasting training on the ability to access semantic knowledge that belongs to a specific repertory. In chapter 4 we will deeply describe and discuss this evidence. Overall, the results of the studies revealed that the processing of semantic violations might be modulated by the level of experience in specific contexts. However, scarce knowledge is available about the effects of not experienced-mediated information on the semantic system.

Aim of the present work

The brief overview of some studies described so far, revealed the sensitivity of the N400 to semantic violations related to a wide range of stimulus types across modality. However, it is still not clear how and when different types of semantic information are integrated in the brain.

Therefore, this dissertation is aimed at investigating electrophysiological processing to semantic violations in different kinds of context. In particular, we focused on the semantic processing of information that does not require learning or training and on the effects of experiences shaped by a specific artistic/motor training. To this aim, we investigated the effects of semantic violations related to the acquired and not-acquired knowledge on the amplitude and morphology of the N400 component.

In addition, we explored if and how the processing of the semantic information, and therefore the amplitude and/or the morphology of the N400 component, changes across different sensory modalities presentation. In other words, we verified if the difficulty (or the ease) to integrate the incoming information into the semantic memory is also affected by the sensory modality of the information.

To this aim, we carried out four studies in order to analyze these aspects. In the first chapter, we will describe an experiment in which we investigated the semantic processing related to knowledge that is not learned through an explicit training, but that requires the integration of automatic and fast processing of emotional expressions into situations of everyday life. In particular, we analyzed the N400 response to the congruency of peculiar stimuli (faces) depicted in specific complex situations (misfortune). In this study we used a unisensory modality presentation (the stimuli were only visually presented).

In the experiment presented in the second chapter, we will focus our attention on the neural mechanisms underlying the semantic violations of actions related to a long-lasting sport training. To this aim, we compared the N400 modulation to correct and incorrect basketball actions in professional basketball players and naïve viewers. As in the first study, the scenes were visually presented to the participants.

In the third experiment, we still explore the semantic processing related to a specific skill learned by imitation and exercise. In particular, we investigated how a long-lasting musical training affected the N400 amplitude to semantic violation even when stimuli are presented using a multisensory modality. Indeed, in this study, we focused on the effects of the integration of auditory and visual stimuli on the N400 response.

Finally, in the last study we explored the understanding of language embedded in a type of visual narrative, namely comics (Cohn et al., 2013) In particular, we analyzed the N400 response to incongruent words that evoked specific sounds in comics in a group of University students with experience in reading comics. The novelty of this study is that we investigated the multimodal processing when stimuli are presented in the same sensory modality, avoiding the effect of a multisensory presentation on the semantic processing.

All in all, the studies carried out will provide useful data about the temporal dynamics and the brain topography related to semantic processing of a specific information associated with different types of learning and experience and the interactions with the sensory modality in which the information is presented.

In addition, the results of this work could shed some light on the cross-modal nature of the N400 showing if semantic violations to information characterized by differences in sensory modality could elicit different ERP responses. In other terms, the data provided by these experiments might help to clarify if the semantic processing related to different kinds of experience is also affected by perceptual factors.

1. Which faces make you laugh? An electrophysiological exploration of semantic processing in misfortunate situations.

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1.1 Introduction

In this chapter, we'll report an experiment in which we investigated the semantic processing related to complex scenes. In particular, we focused on the semantic processing of different types of facial expressions showed by the people involved in a humorous (or not) misfortunate situation.

Humor is the tendency of particular cognitive experiences to provoke laughter and provide amusement. According to Dennett (2011), Humor is an evolved adaptation used by humans to "debug" incongruities and mistakes within mental representations. Since our brain has limited resources, humor acts as a self-correcting mechanism that filters-out information that impedes its function or leads the individual to commit potentially costly errors from erroneous conclusions leading our resources to endeavors that are more fruitful.

Previous works investigated kinds of humor (e.g., comics, strips, cartoons) that require high level cognitive functions, such as theory of mind, breaking up the phenomenon into cognitive and affective elements (Gardner et al., 1975). The cognitive element (humor detection) would refer to ‘‘getting the joke’’, the moments in which the perceiver attempts to comprehend disparities between punch lines and prior experience (Brownell et al., 1984). The affective element would refer to ‘‘enjoying the joke’, the moments during which the perceiver experiences visceral, emotional responses dependent upon the hilarity of the experience (Moran et al. 2004). According to the Incongruity-Resolution theory (Suls, 1972) the ability to comprehend humor is crucially dependent upon the capacity to resolve the incongruity between the punch line and the expectations shaped by the storyline (Bartolo et al., 2006). This theory separates humor into two distinct states: surprise and coherence (Brownell et al., 1984). Surprise is a feeling generated by an unexpected situation. According to this theory, to comprehend a joke one must go beyond the state of surprise and formulate a new coherent interpretation of the information (Bartolo et al., 2006).

The first studies examined humor comprehension and appreciation in patients with different brain lesion localizations. In 1986, Bihrle and colleagues (1986) tested right hemisphere damaged patients (RHD) and left hemisphere aphasic patients (LHD) on a non-verbal cartoon completion task that included a humorous and non-humorous condition. They found that, in both conditions, RHD patients performed worse than LHD patients. Moreover, differences emerged between the two groups of patients as regards to the errors committed. In particular, they found that RHD patients were less able to recognize coherence but preserved the sensitivity to the surprise element of humor. On the other hand, the LHD patients presented an impaired sensitivity to the surprise element of humor, but conserved the ability to integrate contents across parts of a narrative. In 1999, Shammi and Stuss (1999) investigated the humor appreciation by using verbal (jokes) and non-verbal (cartoon) tests in patients who had focal damage in various brain areas. The results showed that the patients with damage in the right frontal lobe were impaired in the ability to appreciate humor. They also revealed diminished physical or emotional responses (laughter, smiling). Since this brain region is crucial in novel problem-solving, the authors interpreted their pattern of data in the view of the incongruity-resolution model that considers humor appreciation as a problem-solving task in which the punch-line, incongruent with the body of the text, must be identified and then reconciled with the lead.

Recently, several neuroimaging studies investigated the humor processing also in healthy adults. In an fMRI study Goel and Dolan (2001) tested subjects who listened to semantic and phonological jokes (puns) and indicated whether or not they found the items amusing; Mobbs and colleagues (2003) used event-related fMRI (efMRI) to seek hemodynamic increases in regions associated with cartoons considered to be funny. The results of both studies found the activation cluster centred in the left temporo-occipital junction, IFG, and temporal pole that would presumably be needed to comprehend and find the cartoon jokes funny (get the joke). According to the authors, these regions are of particular theoretical interest as they fit well with Suls' incongruity-resolution theory (1972): the temporo-occipital junction detects visual incongruence as suggested in previous studies of humor and laughter (Goel and Dolan, 2001; Iwase et al., 2002), while more anterior regions, including Broca's area and the temporal pole, ascertain linguistic coherence. In addition, they revealed that humor detection engages a subcortical network, including the nucleus accumbens, which plays a key role in reward mechanisms (Schultz, 2002) and the medial ventral prefrontal cortex, a region involved in ''higher order'' reward processing (Mobbs et al. 2003).

Coulson and Kutas (2001) recorded event-related brain potentials (ERPs) from adults reading one-line jokes or non-joke controls with equally unexpected endings. The authors found a pattern of effects that did not fit with the incongruity-resolution two-stage model of joke comprehension. In particular, their results revealed that joke and non-joke related ERPs differed in several aspects depending on participants' ability to get the joke and contextual constraint: in good joke comprehenders, all jokes elicited a left-lateralized sustained negativity (500–900 ms), indexing frame-shifting. In addition, low constraint jokes elicited a frontal positivity (500–900 ms), and high constraint jokes elicited a N400 and a later posterior positivity. By contrast, poor joke comprehenders showed only a right frontal negativity (300–700 ms) to jokes. Therefore, the authors concluded that while the positivities might reflect a surprise component of joke processing, and the sustained negativity index frame-shifting needed to re-establish coherence, all these effects occurred within the same time window. For this reason, they claimed that joke processing cannot be explained in terms of a simple two-stage model with surprise and coherence engaged in sequence.

Although several studies investigated different elements of the humor experience using verbal and non-verbal tasks, few works explored differences or similarities in brain activity induced by two kinds of humor: visual humor (sight gags) and language-based humor. Watson and colleagues (2007) performed an fMRI study trying to differentiate the brain activity induced by the hedonic similarities and cognitive differences inherent in visual and language-based humor. Their findings indicated that high-level visual areas were activated during visual humor while classic language areas were involved during the language-dependent humor processing. They also found a common network activated by both types of humor that included the amygdala and midbrain regions. According to the authors, these regions reflected the euphoric component of humor.

While much is known about a sort of cognitively-based humor described so far, scarce knowledge is available about the semantic processing related to a source of humor that involves misfortunate situations and comes from a particular kind of comedy, called slapstick, characterized by a type of broad, physical comedy. Dennett (2011) refers to this kind of humor also as real-world humor.

We noticed that a misfortunate situation might trigger different reactions in the observers, as laughing or empathy. We hypothesized that the element that triggers a different reaction in the observers during the perception of other people’s misfortune is the facial expression of the victim. Therefore, the aim of this study was to investigate if the semantic processing of a misfortunate scene may vary as a function of different facial expressions showed by the victims. Indeed, according to our hypothesis, the perceptive element that let us to categorize a misfortunate situation as comic or unhappy is the facial expression of the victims: if they show a funny bewilderment face, the observer’s reaction will usually be laughing, while if they express pain or anger, it is unlikely that the observer’s reaction will be laughing, but he might empathize with the victims instead. Consequently, we hypothesized that hiding the facial expression of the victim would make this kind of situation ambiguous. In other terms, we thought that if a person involved in a misfortune does not show the facial expression, the observer could not be able to categorize the situation displayed as amusing or unhappy.

In this study several hundreds of ecological pictures representing persons of various number, age and sex, involved in different misfortunes were presented to 30 Italian healthy volunteers, while their EEG was recorded. We compared the perception of people showing a bewilderment expression and, so, a comic look, with pictures in which people exhibited a painful or angry expression and pictures in which the facial expression of the victims was not visible.

Since according to our hypothesis, the element that allows distinguishing a comic misfortunate situation from an unhappy one is the expression of the victim, we expected to observe an electrophysiological modulation reflecting the perception of the three facial expressions at an early stage of processing.

Finally, since we assumed that the facial expression of the victim affects the semantic processing of a misfortune, we expected to observe a modulation of the N400 response to the different stimuli. In particular, we expected a greater N400 response to “no face pictures” compared to the others, maybe reflecting the difficulty of comprehending the nature (funny or not) of the scenes presented.

1.2 Methods

1.2.1 Participants

Thirty healthy right-handed University students (16 women, 14 men; mean age = 22.9 years, SE = 3.7) participated in this study. They earned academic credits for their participation. All had normal or corrected-to-normal vision, and reported no history of neurological illness or drug abuse. Their handedness was assessed by means of the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985), a laterality preference questionnaire reporting right-handedness and right ocular dominance for all participants.

Experiments were conducted with the understanding and the written consent of each participant. Two women and two men were excluded from statistical analyses because of EEG artefacts. The experimental protocol was approved by the ethical committee of the University of Milano-Bicocca.

1.2.2 Stimuli

The images were all copyrights free and comprised several color photos depicting males and females of various ages and numbers involved in different misfortunate situations. We selected stimuli from a wider sample of 243 photos. We considered three different types of photos: in the “Affective” type people involved in misfortunate situations showed a painful or an angry facial expression; in the “Comic” ones people showed a bewilderment expression and, so, a comic look; in the category named “No face” people depicted were still involved in a misfortune but their facial expression was not visible (Fig. 1.1).

Fig 1.1 Exemplars of pictures used as stimuli in the Comic, Affective and No Face categories.

In order to be validated, images were randomly ordered in a PowerPoint file, one per page, and presented to a group of 20 different judges of similar age and educational level as the experimental subjects. The task of the examiners consisted in judging the pictures for two elements: hilarity level and arousal. To test the hilarity, the experimenter showed the pictures (one by one) to the judges through a self-paced task and asked them to evaluate if the situation presented seemed amusing to them by means of a 3-point scale [2= very much amusing; 1= amusing; 0= not at all amusing]. To test the arousal, the judges rated each picture along a 3-point scale scale [2= very much exciting; 1= exciting; 0= relaxing]. As the judge gave his/her opinion on the pictures, the experiment recorded the results for each photograph.

To provide a clear distinction between the amusing and non-amusing stimuli, we placed pictures scoring above 0.6 in the Comic category, whereas pictures scoring below 0.1 were included in the Affective category. Images where the victims missed the facial expression were scored with a value between 0.1–1.45. We excluded 33 comic pictures because of an insufficient average score. An ANOVA applied to the values attributed to the 3 group stimulus classes (F 2, 38= 115.92; p< 0.01) showed that their hilarity level was significantly different (Comic=1.01, SE=.06; Affective=0.25, SE=.03; No face=0.51, SE=.04). Stimuli in the 3 classes were also matched for their arousal value. An ANOVA analysis (F 2, 38=1.61; p=0.21) showed that their arousal values were not significantly different (Comic=0.79, SE=.08; Affective=0.70, SE=.06; No face=0.71, SE=.06). At the end of this process, we selected 210 pictures (70 for each category) that were balanced for gender, age, number of persons and the body parts involved.

In order to have subjects performing a secondary task, we also included 20 further photos depicting common natural or urban landscapes without visible persons (including offices, shops, the countryside, a seascape, a mountain landscape, etc.). These images had the same average luminance and size as the others.

We presented 70 Comic, 70 Affective and 70 No face photos randomly mixed with 20 neutral infrequent targets. The stimulus size was 12 X 12.5 cm subtending a visual angle of 6º X 6º15’. The mean luminance was measured by means of a Minolta luminance meter, and luminance values were compared across classes by a one-way ANOVA (F 2, 207=0.205; p=0.81) that proofed stimulus equiluminance between groups of pictures. Stimuli were presented randomly mixed for 1500 ms at the centre of a PC screen with an ISI ranging from 1200 to 1300 ms. The outer background was dark grey.

1.2.3 Procedure

The task consisted of responding as accurately and quickly as possible to the presence of landscapes or interior (scenarios without visible persons) by pressing a response key with the index finger of the left or right hand. The two hands were used alternately during the recording session. We counterbalanced the order of the hand and task conditions across subjects. Participants were comfortably seated in a darkened, acoustically and electrically shielded test area. They faced a high-resolution VGA computer screen located 114 cm from their eyes. They were instructed to gaze at the centre of the screen, where a small circle served as the fixation point, and to avoid any eye or body movements during the recording session. Stimuli were presented at the centre of the screen and were randomly mixed in 4 different short runs of 45–55 trials that lasted about 3 minutes each. For each experimental run, the target stimuli varied between 4 and 6 runs. The order of presentation differed across the subjects.

After the EEG experiment, we asked participants to rate the funniness of comic stimuli seen during the EEG recording in order to obtain a measure of the subjective funniness perception associated to the comic stimuli. Similarly to the validating process performed by the 10 judges, the EEG participants estimated the hilarity level of the stimuli by means of a 3-point scale (2= very much amusing; 1= amusing; 0= not at all amusing).

1.2.4 Electroencephalographic recording

The EEG was continuously recorded from 128 scalp sites at a sampling rate of 512 Hz by means of ANT-EEprobe 3.1. system. Horizontal and vertical eye movements were also recorded. Linked ears served as the reference lead. The EEG and electro-oculogram (EOG) were amplified with a half-amplitude band pass of 0.016–100 Hz. Electrode impedance was kept below 5 kΩ (Fig.1.2).

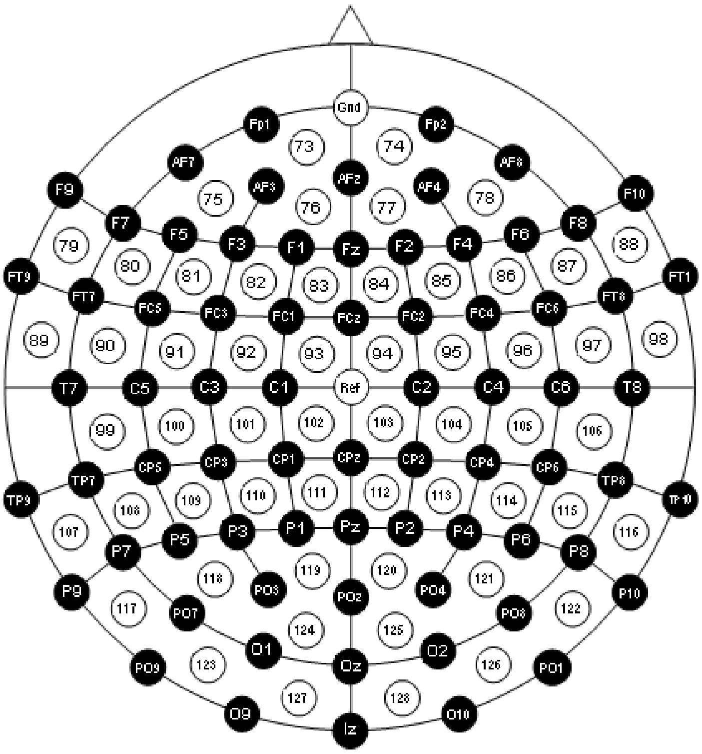

Fig.1.2. EEG recording layout, with 128 electrodes distributed over the whole surface.

1.2.5 Statistical analysis of ERPs

Computerized artefact rejection was performed before averaging to discard epochs in which eye movements, blinks, excessive muscle potentials or amplifier blocking occurred. The artefact rejection criterion was peak-to- peak amplitude exceeding 40μV, and the rejection rate was 5%. EEG epochs were synchronized with the onset of stimuli presentation. Evoked-response potentials (ERPs) were averaged off-line from 100 ms before through 1200 ms after stimulus onset. ERP components were identified and measured with respect to the baseline voltage, which was averaged over the pre-stimulus interval from -100 ms to 0 ms. The mean amplitude of the occipito-temporal N170 component was measured at P9, P10, PO9, PO10 sites in the 150–180 ms time window. The mean amplitude voltage of anterior N220 response was measured at the AF3, AF4, AFF1, AFF2, AFF5h, AFF6h, F7, F8 electrode sites in the 190–260 ms time window. The mean amplitude of the P300 response was measured at P7, P8, PO7, PO8 sites in the 250–400 ms time window. The N400 mean amplitude was quantified at prefrontal and anterior frontal electrode sites (AF7, AF8, AFP3h, AFP4h, FP1, FP2) in the 370–520 ms time window. Finally, the mean amplitude voltage of the late positive response was measured at centro-parietal sites (CP1, CP2, CPP1h, CPP2h, P1, P2, PPO1, PPO2) in the 500-700 ms (Table 1.1).

Different repeated-measures ANOVAs were carried out on ERP amplitude values relative to occipito-temporal N170, anterior N220, P300, N400 and late positive responses and included three within-subjects factors: Stimulus content (Comic, Affective, No face), Electrode (dependent on the ERP component of interest) and Hemisphere (left, right). Multiple comparisons of means were performed by means of the post- hoc Fisher's tests. In addition, quantitative correlations analyses were performed to provide a direct evidence for the link between subjective funniness ratings and the brain responses. Therefore, a series of correlations (Pearson's Rho) was performed between the individual funniness ratings to comic stimuli (provided by the subjects after the EEG experiment) and the comic effect size (obtained by subtracting comic–affective electrophysiological responses) of N170, N220 and P300 components in individual average ERPs. We were able to calculate the correlation analysis on 23 participants from the total sample (n=26) because 3 participants decided to not participate to the post-test.

ERP COMPONENT	TIME WINDOW	ELECTRODES
N170	**150–180 ms**	P9, P10, PO9, PO10
N220	**190–260 ms**	AF3, AF4, AFF1, AFF2, AFF5h, AFF6h, F7, F8
P300	**250–400 ms**	P7, P8, PO7, PO8
N400	**370–520 ms**	AF7, AF8, AFP3h, AFP4h, FP1, FP2
LPP	**500-700 ms**	CP1, CP2, CPP1h, CPP2h, P1, P2, PPO1, PPO2

Tab. 1.1. ERP components of interest for the present study

1.3 Results

1.3.1 Electrophysiological results

Occipito-temporal N170 (150-180 ms)

The ANOVA computed on the mean amplitude of the posterior N170 component showed a significant main effect of Stimulus content (F 2, 50= 4.63, $p<0.05$), revealing a much greater amplitude responses to Comic than Affective ($p < 0.05$; Comic = 0.52 μV, SE= 0.45; Affective = 0.86 μV, SE= 0.50) and No Face pictures ($p < 0.05$; No Face = 1.02 μV, SE= 0.48) (Fig.1.3).

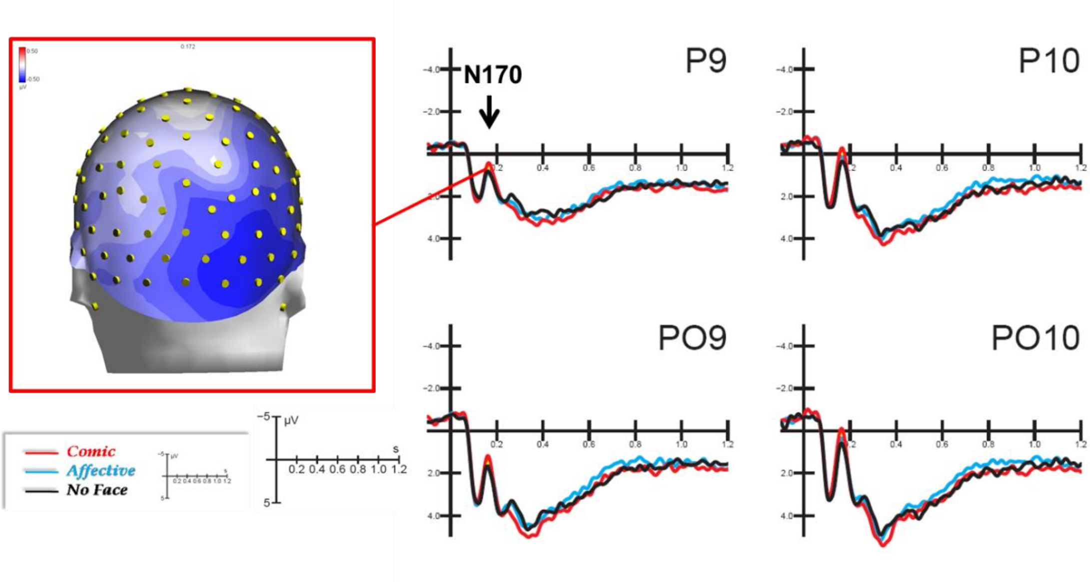

Figure 1.3. On the left: back view of the scalp voltage distribution of the occipito-temporal N170 in response to Comic pictures (170 ms). On the right: grand-average ERPs recorded at occipito-temporal sites in response to Comic (red) Affective (blue) and No Face (black) stimuli.

Post hoc analysis of mean values showed no difference in the N170 response to Affective vs. No Face stimuli. The further significance of Electrode (F 1, 25= 7.38, $p<0.05$) showed the presence of a larger N170 at occipito-temporal (P9-P10) (0.52 μV, SE= 0.38) than parieto-occipital (PO9-PO10) (1.08 μV, SE= 0.38) sites. The significance of the Hemisphere (F 1, 25 = 5.53, $p<0.05$) and Hemisphere × Electrode factors (F 1, 25 = 6.56; $p<.05$) indicated larger N170 potentials over the right (0.36 μV, SE = 0.54) than the left (1.24 μV, SE = 0.46) hemisphere, especially over the parieto-occipital area ($p < 0.05$; PO9 = 1.69 μV, SE= 0.57;

PO10 = 0.48 µV, SE = 0.61; P9 = 0.80 µV, SE = 0.38; P10 = 0.23 µV, SE= 0.47) , as also indicated by post hoc comparisons.

Anterior N220 (190–260 ms)

Anterior N220 amplitude was strongly modulated by Stimulus content (F 2, 50 = 3.66, p < 0.05) with larger amplitude in response to Comic than Affective (p < 0.05; Comic = -7.30 µV, SE = 0.64; Affective = -6.83 µV, SE= 0.61) and No Face (*p* < 0.05; No Face = -6.79 µV, SE= 0.58) stimuli (Fig.1.4). Post-hoc analysis among means didn't reveal any difference in the anterior N220 response to Affective and No Face stimuli. ANOVA also revealed a significant main effect of Hemisphere (F 1, 25 = 4.99, p < 0.05) showing that, at this latency and in this regions, the N220 response was greater over the left (-7.21 µV, SE = 0.64) than the right hemisphere (-6.74 µV, SE= 0.58).

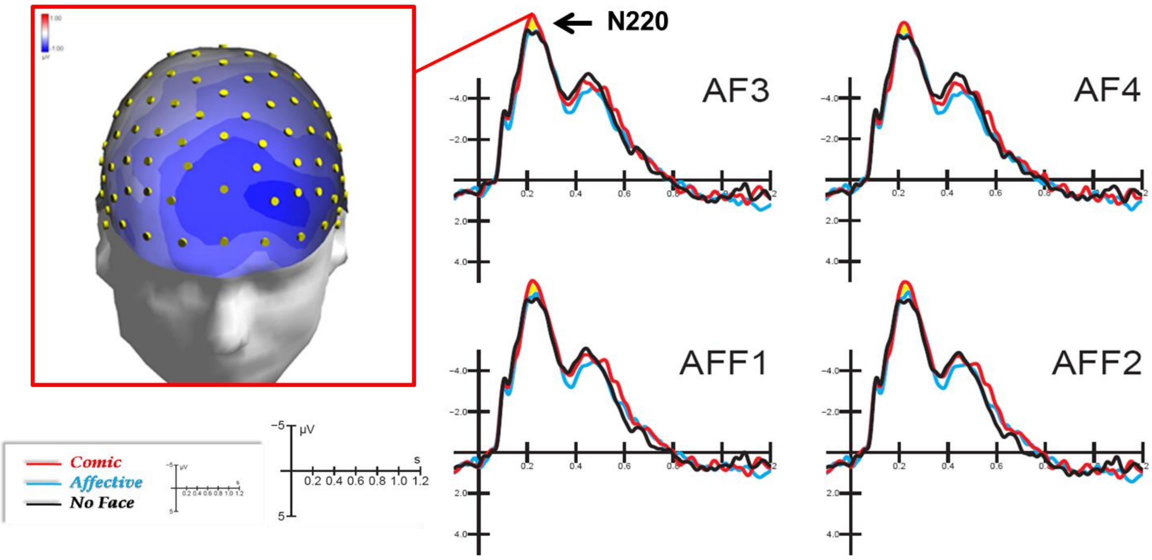

Figure 1.4. On the left: top view of the scalp voltage distribution of the anterior N220 in response to Comic pictures (220 ms). On the right: grand-average ERPs recorded at anterior sites in response to Comic (red) Affective (pale blue) and No Face (black) stimuli.

P300 (250-400 ms)

The mean amplitude of P300 component was measured at the lateral occipito-temporal sites during the 250–400 ms time window. The ANOVA analysis showed a significant main effect of Stimulus content (F 2, 50 = 3.52; $p < 0.05$). Post hoc comparisons among means indicated a greater amplitude to Comic scenes compared to Affective and No face ones ($p < 0.05$; Comic = 5.34 µV, SE = 0.72; Affective = 4.84 µV, SE = 0.70; No Face = 4.72 µV, SE = 0.67) and no differences in the P300 response to Affective and No Face stimuli (Fig.1.5). The further significance of Electrode (F 1, 25 = 17.88; $p < 0.01$) revealed a larger P300 potential at occipito-temporal (PO7-PO8) (5.45 µV, SE= 0.67) than parieto-temporal sites (P7-P8) (4.48 µV), especially on the left than the right sites ($p< 0.05$; PO7 = 5.86; PO8 = 5.05, SE = 0.67) as shown by the significance of the interaction Electrode x Hemisphere (F 1,25 = 6.10; $p < 0.05$).

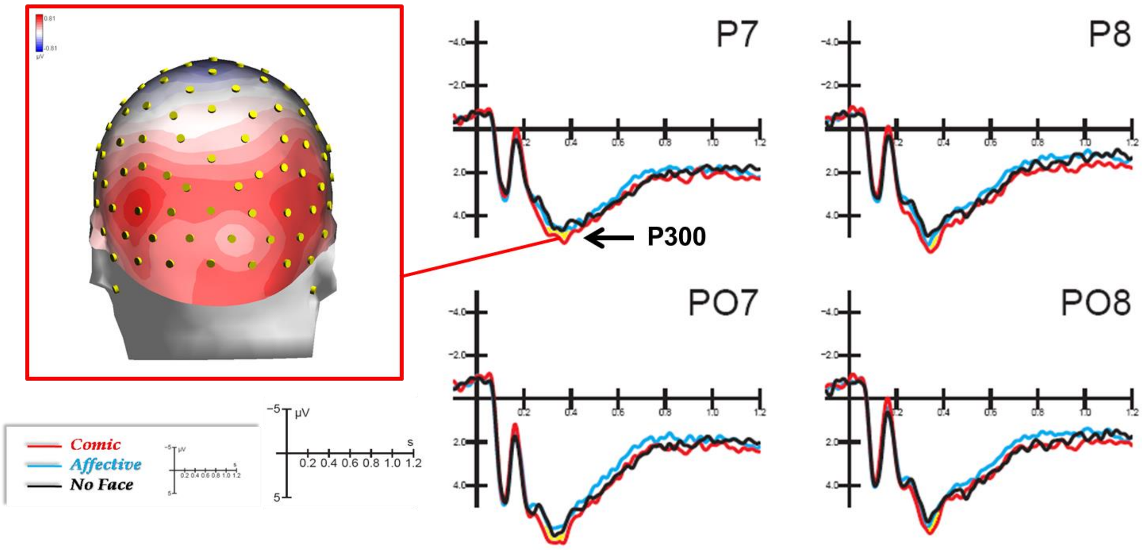

Figure 1.5. On the left: back view of the scalp voltage distribution of the occipito-temporal P300 in response to Comic stimuli at 350 ms. On the right: grand-average ERPs recorded at prefrontal sites in response to Comic (red) Affective (pale blue) and No Face (black) stimuli.

N400 (370-520 ms)

Statistical analysis computed on the mean amplitude of the N400 component recorded at prefrontal sites showed a main effect of Stimulus content (F 2, 50 = 8,00 $p < 0.01$) with much greater responses to No Face (-5.26 μV, SE = 0.58) than Comic ($p < 0.05$; Comic = -4.40, μV, SE= 0.58) and Affective ($p < 0.05$; Affective = -4.15 μV, SE= 0.56) pictures (Fig.1.6). Post hoc analysis of mean values didn't reveal any difference in the N400 response to Comic and No Face stimuli. The further interaction of Stimulus content x Electrode (F 4, 100=2.99; $p < 0.05$) indicated a much larger N400 response to No Face than Affective and Comic stimuli over all electrode sites ($p < 0.05$; AF7-AF8: No Face = -5.25 μV, SE= 0.5; Affective = -4.26 μV, SE = 0.50; Comic = -4.53 μV, SE = 0.53; AFP3h-AFP4h: No Face = -5.13 μV, SE = 0.70; Affective = -4.04 μV, SE= 0.70; Comic = -4.44 μV, SE= 0.70; FP1-FP2: No Face = -5.40 μV, SE= 0.67; Affective = -4.14 μV, SE= 0.60; Comic = -4.25 μV, SE = 0.61). Also, the ANOVA revealed, regardless of Stimulus content, a significant main effect of Hemisphere showing that the N400 amplitude was larger over the left (-4.83 μV, SE = 0.58) than the right (-4.37 μV, SE = 0.58) hemisphere (F 1, 25 = 8.13, $p < 0.01$).

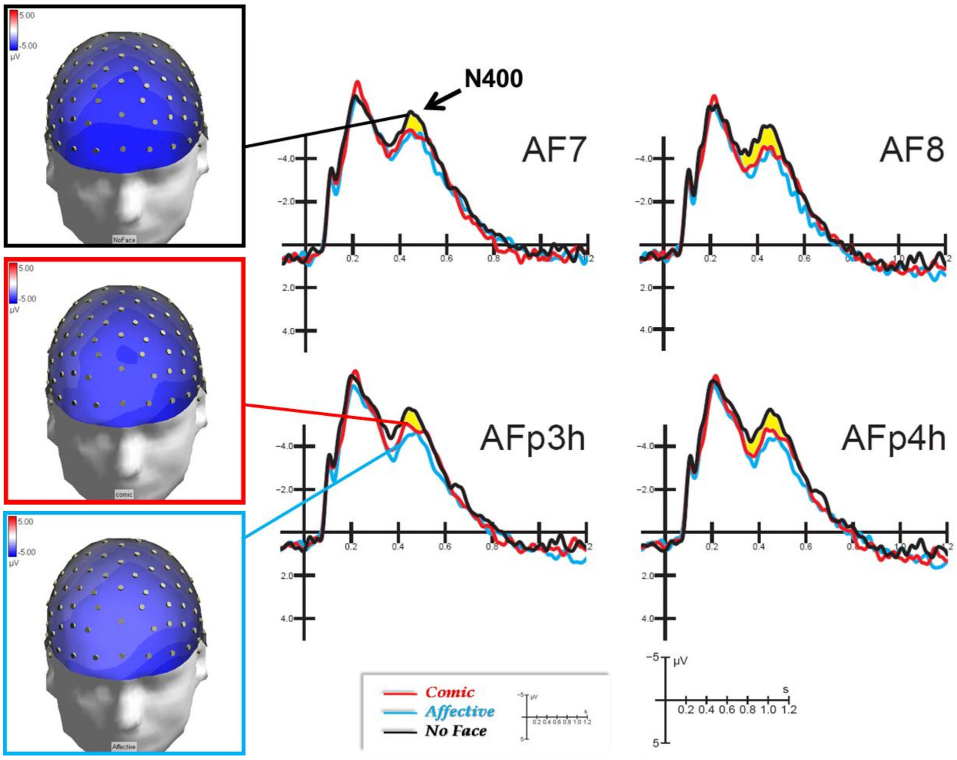

Figure 1.6. On the left: top view of the scalp voltage distribution of the anterior N400 in response to no Face (black border), Comic (red border), Affective (pale blue border)stimuli at 400 ms. On the right: grand-average ERPs recorded at prefrontal sites in response to Comic (red) Affective (pale blue) and No Face (black) stimuli.

Late positivity (500-700 ms)

A late positivity (LLP) was measured over the centro-parietal sites. This component was significantly affected by Stimulus content (F 2, 50 = 5.70; p < 0.01), with larger amplitudes to No Face stimuli than other stimuli categories (No Face = 3.14 μV, SE = 0.56; Affective = 2.14 μV, SE = 0.55; Comic = 2.40 μV, SE=0.49) (Fig.1.7). The effect of electrode (F 3, 75 = 9.72, p<0.01) indicated that the slow positive deflection reached its maximum amplitude over the parietal sites (P1, P2: 2.84 μV, SE = 0.3; PPO1, PPO2: 2.86 μV, SE = 0.53) than the centro-parietal area (CP1, CP2: 2.08 μV, SE = 0.51; CPP1h, CPP2h: 2.48 μV, SE = 0.51). Also, this component showed a hemispheric asymmetry (F 1, 25 = 5.27; p <0.05), with larger amplitudes over the right (2.67 μV, SE=0.53) than the left (2.42 μV, SE = 0.49) hemisphere.

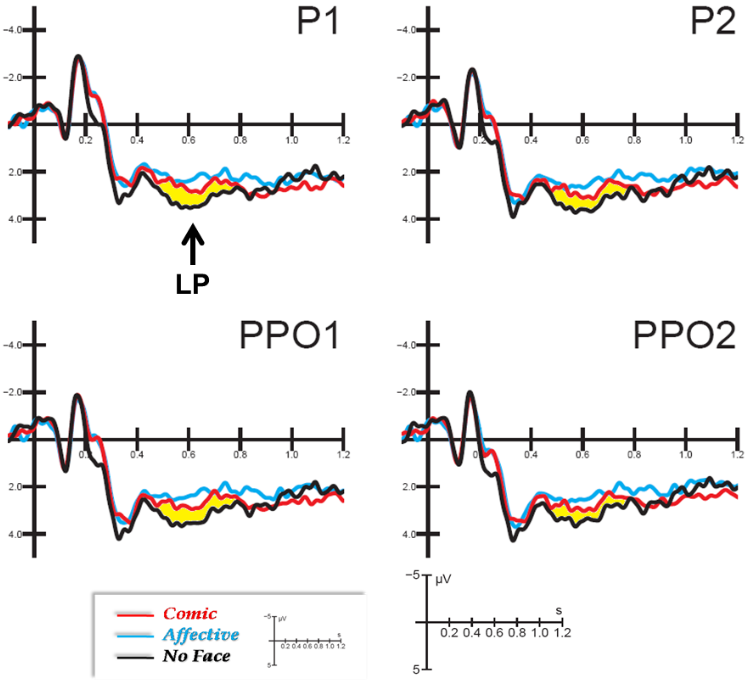

Figure 1.7. Grand-average ERPs recorded at posterior sites in response to Comic (red) Affective (pale blue) and No Face (black) stimuli.

1.3.2 Pearson's correlations

This analysis provided useful information for attesting the correlation between the comic effect size of the ERP components and subjective funniness ratings. The comic effect size was computed as the mean amplitude elicited by comic stimuli subtracted by the mean amplitude elicited by affective stimuli. Therefore, we verified if the greater amplitude difference of the N170, N220 and P300 components found in response to comic stimuli reflected the subjective funniness perception of the content depicted in the comic pictures.

The Pearson correlation test indicated that there was no significant correlation between the comic effect size of the N170 and subjective funniness ratings ($r = -0.40$; $df = 21$), however a statistical positive trend between the two variables ($p = .05$) was found (Fig.1.8). The comic effect size of the N220 was significantly correlated with the values of the subjective funniness ratings ($r = -0.52$; $df = 21$; $p < .05$) (Fig. 1.9). The negative correlations between the comic effect size of the N170 and N220 components and the subjective funniness ratings were due to the negative polarity that characterizes these electrophysiological components. Therefore, the correlations indicated that the higher the funniness ratings were, the greater amplitude the components displayed.

In contrast, no significant correlation was found between the comic effect size of the P300 and corresponding subjective funniness ratings ($r = -0.40$; $df = 21$; $p >.05$) (Fig. 1.10). Since the P300 is a positivity-polarity component, the (nonsignificant) negative correlation was not caused by the polarity of the P300. Indeed, this correlation exhibited a tendency toward a negative correlation that suggested a weak association between the amplitude of the P300 and the funniness ratings: the higher the funniness ratings were, the smaller amplitude the P300 exhibited.

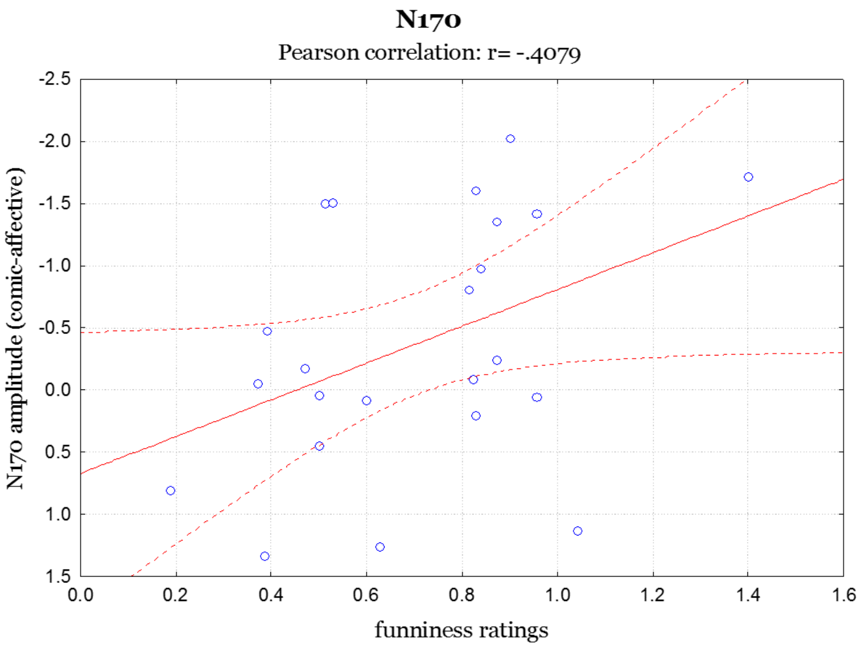

Figure 1.8. Spearman’s Rho correlation between the comic effect size of the N170 and the values of the subjective funniness ratings

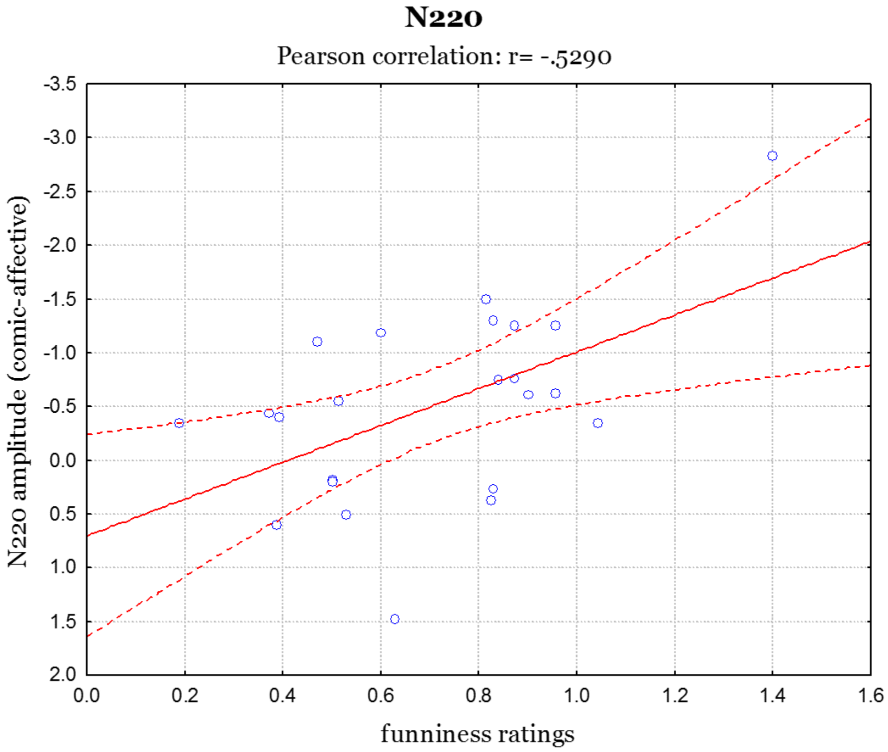

Figure 1.9. Spearman’s Rho correlation between the comic effect size of the N220 and the values of the subjective funniness ratings

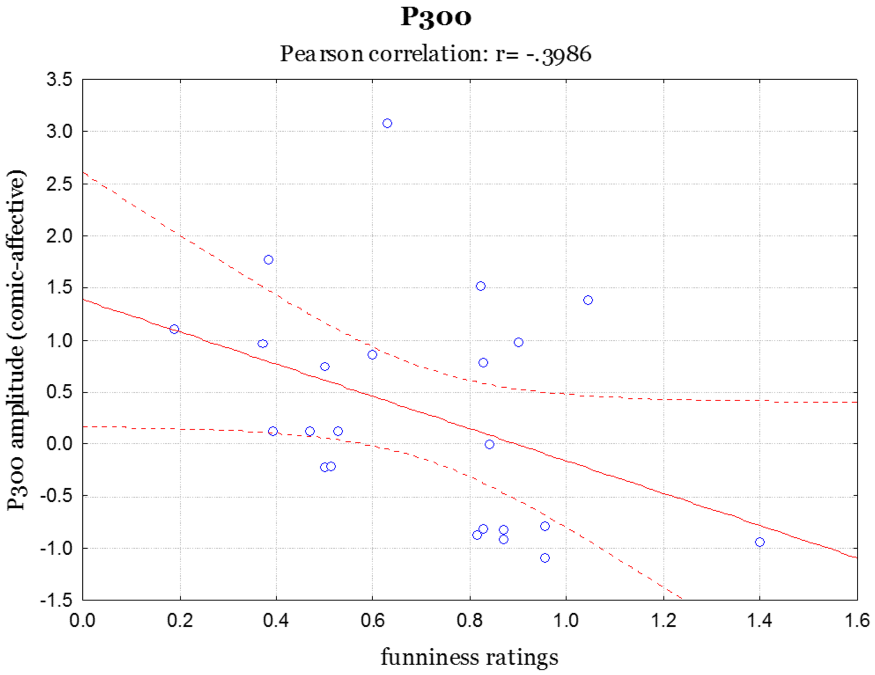

Figure 1.10. Spearman's Rho correlation between the comic effect size of the P300 and the values of the subjective funniness ratings

1.4 Discussion

In this first study, we investigated the semantic processing related to knowledge that are not learned through an explicit training, but that requires the integration of automatic, rapid processing of emotional expressions into a specific context.

We choose to examine the semantic processing related to different facial expressions showed in complex misfortunate situations. Indeed, since several evidences suggest an early automatic encoding of emotional facial expressions (Sergent, 1994; Batty & Taylor, 2003; Proverbio et al., 2006), we investigated how their processing might affect the meaning of a misfortunate situation. In particular, we examined how different types of facial expressions showed by people involved in this kind of situation may affect the comprehension of the nature of the situation displayed.

Our hypothesis was that the element that allows distinguishing a comic misfortunate situation from an unhappy one is the expression of the victim: a funny bewilderment facial expression usually triggers a laughing reaction, while a painful or angry facial expression could generate an empathic reaction in the observers. In addition, when the facial expression of the victim is not visible, understanding the affective valence of the presented situation might be difficult.

Consequently, the aim of this work was to investigate the semantic processing of the interaction between the facial expressions of the victims and the context in which they are presented. In this study the stimuli were only visually presented, thus we used a unisensory modality presentation.

Overall, we presented 210 ecological scenes depicting people of different ages and sexes involved in a misfortunate circumstance. Viewers were male and female University students attentively perceiving the pictures but engaged in a secondary perceptual task. We introduced the secondary task to avoid conscious awareness of the experimental manipulation of victim's facial expression. The three types of stimuli were matched for several perceptual characteristics except for the facial expression of the characters involved in the misfortunes (bewilderment in Comic, painful or anger in Affective, no face expression showed in No Face).

To categorize the stimuli as comic or unhappy, we presented pictures involving different misfortunate situations to a group of 10 judges. We asked to evaluate if the situation presented seemed amusing to them by testing the hilarity level by means of a 3-point scale [2= very amusing; 1= amusing; 0= not at all amusing]. In addition, in order to control the effects of the arousal on the hilarity level, we tested the arousal level using a 3-point scale [2= very exciting; 1= exciting; 0= relaxing]. The results of the test showed that the pictures differed only along the hilarity dimension. In particular, we found that similar misfortunate situations were interpreted as being funnier when the people depicted in the pictures showed bewildering facial expressions as opposed to pained or anger expressions and to those in which people missed the facial expression.

Regarding the electrophysiological results, the statistical analyses performed over the posterior scalp sites evidenced that the mean amplitude of the posterior N170 response was greater over the right than the left hemisphere. This result was in line with the previous literature revealing that the face-related (Bentin et al., 1996; Rossion et al., 2003) and body-related (Gliga & Dehaene-Lambertz, 2005) N170 electromagnetic response tends to have greater amplitude in the right hemisphere than the left one. Moreover, the results showed a larger response to Comic stimuli compared to Affective and No Face ones in the 150-180 ms time window. Previous studies revealed that the facial expression modulates the N170 amplitude (Batty and Taylor, 2003; Miyoshi et al., 2004; Caharel et al., 2005; Eimer and Holmes, 2007; Flaisch et al., 2008), noting larger amplitude for fearful faces in comparison to neutral faces (Batty and Taylor, 2003; Stekelenburg and de Gelder, 2004; Pourtois et al., 2005; Leppänen et al., 2007; Luo et al. 2010; Proverbio et al., 2006a, 2006b). The bewildered and disoriented expression depicted in the Comic stimuli of our study shares several facial features with the fearful expression, including eye widening. Thus, we can speculate that the N170 effect to Comic stimuli might reflect analogous fast and automatic processing.

However, the non-significant correlation between the comic effect size of the N170 amplitude and subjective funniness ratings suggested that, even if the N170 amplitude dissociated comic from affective expressions, it couldn’t be considered a specific index of the funniness perception of the Comic stimuli. However, the existence of a statistical positive trend might suggest that some individual funniness ratings did correlate with the corresponding N170 mean amplitude and others not. Future studies might clarify, perhaps by increasing the sample size, the functional meaning of this early component during tasks that involve humorous elements.

In our study, the N170 wave was followed by a greater, slightly lateralized to the left, anterior N220 response (170–270 ms) during the perception of Comic stimuli in comparison to the Affective and No face ones. Previous studies investigating attentional mechanisms within complex visual scenes found an anterior N2 effect in the flanker paradigm (Gehering et al.1992; Liu et al. 2013) and in the Stroop paradigm (West and Alain, 1999, 2000; Folstein and Van Petten, 2008). In other words, in these studies a larger N2 component was observed for stimuli containing conflicting features (e.g. incompatible trials) (Luck and Kappenman, 2012). In light of these previous evidences, we can assume that the content represented in the comic pictures, even if at a higher level of processing, contains conflicting elements that could trigger the amused reaction in the observers. Specifically, we can speculate that during the perception of the Comic stimuli, the processing of the non-life-threatening context and the like-fearful expression of the victims could cause a contrasting effect. This effect may draw a form of a paradoxical effect triggering the amused reaction in the observers. Therefore, we could argue that the other people amused response during a misfortunate situation would occur in a second stage of the process, when also the context has been processed. Moreover, Proverbio and colleagues (2009) indicated that the anterior N2 response could reflect the activity of the orbitofrontal pleasure circuit during perception of social information such as faces and persons: the authors found that the orbitofrontal N2 response to human beings was larger in a positive than negative emotional context. Other studies confirmed that the orbitofrontal pleasure circuit is active during the observation of many kind of positive and pleasant emotional social information (Bartles & Zeki, 2004; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Nitschke et al., 2004). In addition, Goel and Dolan in an fMRI study (2001) showed that the affective appreciation of humor involves access to a central reward system in the medial ventral prefrontal cortex (MVPFC). Therefore, we can hypothesize that the N220 response, as index of orbitofrontal pleasure circuit, was stronger to Comic than Affective and No Face stimuli, possibly also because of the salient and arousing nature of that kind of stimuli.

In addition, we found the existence of a significant correlation between the comic effect size of the N220 amplitude and subjective funniness ratings. This might reveal that the bewilderment expression depicted in the Comic stimuli, and judged funnier than the other class of stimuli, elicited a greater early response (220 ms post stimulus) that might be correlated to the subjective perceived funniness of the Comic stimuli.

Furthermore, a roughly bilateral occipito/temporal P300 exhibited a larger response to Comic than Affective and No Face stimuli. The lack of correlation between the comic effect size of the P300 amplitude and subjective funniness ratings found in this study suggested that the greater P300 amplitude observed in response to the Comic stimuli was not associated specifically to the perceived funniness of the Comic stimuli. In a previous ERP study, Liu and colleagues (2013) showed that affective incongruent trials induced a larger P300 activation than congruent trials, reflecting executive evaluation processing on facial expressions. Similarly, in our study the increase of the P300 amplitude might be interpreted as a sign of the increased allocation of attentional resource associated with the processing of the affective conflicting elements depicted in the Comic stimuli (the non-life-threatening context and the like-fearful expression of the victims).

Also, we observed a modulation of the N400 component in response to the three different kinds of facial expression. In particular, we found a greater anterior N400 to No Face compared to Comic and Affective stimuli, particularly over the left hemisphere. As we reported in the Introduction of this work, the N400 component, a large negative deflection peaking at about 400 ms, is sensitive to a wide array of meaningful and potentially meaningful stimuli, including pictures and faces.

Some evidences reported that the N400 response is sensitive to facial processing. In particular, some works focused on the effects of the familiarity of the face (Schweinberger and Burton, 2003; Olivares et al. 1999; Voss and Paller, 2006). For example, Olivares and colleagues (1999) carried out a study in which subjects had previously observed an incomplete familiar face, and then the same face completed by inserting either matching internal features or mismatching internal features from another face. The results of this study showed a greater N400 response for familiar faces completed by mismatching versus matching internal features in the occipital area. Other studies investigated the semantic processing related to the facial expressions. For example, Balconi and colleagues (2005) explored event-related potentials related to recognition of facial expressions and the effect of the semantic content of the stimulus. They presented faces with three prototypical emotional expressions (fear, happiness, and sadness) and with three morphed expressions. The data revealed that the emotional morphed faces elicited a negative peak at about 400 ms, over the posterior site. The authors concluded that this N400-like effect may reflect a specific cognitive process underlying decoding of facial expressions in case of semantic anomaly detection. Differently, Caldara and colleagues (2004) conducted an ERP study in which subjects performed incongruity detection on words, facial identities and facial expressions. The results of this work indicated that the N400 response was sensitive only to language and facial identities incongruities. Indeed, no N400 effect was found in response to facial expressions.

In addition, recent works indicated that the N400 response also reflects contextual comprehension process of incoming input with the world knowledge learned over the lifetime (Proverbio and Riva, 2009; Proverbio et al., 2010; Proverbio et al. 2012; Sitnikova et al., 2008; Giglio et al. 2013). These evidences showed that the N400 elicited by pictures has a more anterior scalp topography than the N400 observed in most language studies (McPherson & Holcomb, 1999).

In our study, we manipulated the facial expression of the victim in a misfortunate situation. Therefore, the N400 effect observed during the presentation of the three kinds of picture, characterized by different facial expressions, might reflect the semantic processing related to the facial expression-context interaction. The results showed no difference in N400 amplitude to Comic and Affective stimuli. This evidence might indicate that the meaning associated to both the Comic and the Affective scenes might be easy to understand. In other words, it is possible that the funny bewildered facial expression and the angry or painful ones facilitate the semantic access to the misfortunate situation presented.

In addition, the larger anterior N400 observed during the No Face stimuli processing could indicate the difficulty of retrieving the information related to the scene presented. In other words, this finding may reflect the difficult to comprehend the nature of the situation displayed without any affective facial information.

Finally, the results of this study revealed a larger roughly bilateral late positivity to No Face stimuli than the Comic and Affective ones. Previous evidences revealed that the late positivity (LLP) is sometimes elicited together with the N400 and has been related to a process of re-analysis of the incongruent situation produced by inconsistent meaning (Sitnikova et al., 2003; Ibanez et al., 2011). Recent studies have been reported of N400 and LPP components elicited by meaningful but non-linguistic stimuli such as faces (Hannula et al., 2006), objects (Ganis and Kutas, 2003), music (Daltrozzo et al., 2010), pictures (Barrett and Rugg, 1990; Ganis et al., 1996; McPherson and Holcomb, 1999; Federmeier and Kutas, 2001; West and Holcomb, 2002; Guerra et al., 2009), gestures (Proverbio and Riva, 2009), hand actions (Aravena et al, 2010), videos of incongruent gestures (Neville et al., 1997; Kelly et al., 2004; Wu and Coulson, 2005; Kelly et al., 2007; Özyüreck et al., 2007; Wu and Coulson, 2007). In our study this component could be related to the previous N400 component revealing a re-analysis processing of the ambiguous misfortunate situation (comic or unhappy) depicted in the No Face stimuli.

In this study, we investigated the semantic processing related to the facial expression-context interaction. The results revealed that the rapid, automatic encoding of emotional facial expressions influences the semantic processing related to a specific complex situation, such as a misfortune.

In conclusion, this study shed some light on the semantic processing of information that does not require learning or exercise to be comprehended and reveals that the semantic processing might be affected by early, automatic and not experience-mediated, processing.

2. An ERP investigation on semantic processing associated with basketball actions perception.

[This research has been published in: Proverbio AM, Crotti N, Manfredi M, Adorni R, Zani A (2012). Who needs a referee? How incorrect basketball actions are automatically detected by basketball players' brain, *Scientific Reports (Nature*), 2: 883]

2.1 Introduction

In this experiment, we investigated the neural mechanisms underlying the representation of complex actions related to a long-lasting sport training. In particular, we focused our attention on the neural mechanisms underlying the semantic violations of actions related to basketball scenes by comparing the N400 modulation to correct and incorrect basketball actions in professional basketball players and naïve viewers. As in the first study, the scenes were visually presented to the participants.

As we mentioned in the previous chapters, the N400 response is not only sensitive to semantic linguistic information but also to violations of world-knowledge in non-linguistic context (Hagoort et al. 2004). For example, a modulation of the N400 component has been observed in paradigms using line drawings (Ganis et al., 1996), stories that are formed by a series of cartoon-like pictures (West & Holcomb, 2002), short movies (Sitnikova et al., 2003), faces (Olivares, 1999), environmental sounds (Van Petten & Rheinfelder 1995), actions (Proverbio & Riva 2009; Bach et al., 2009; Giglio et al., 2013).

Regarding semantic processing of actions, Proverbio and colleagues (2009) showed that purposeless actions (e.g., a man splashing his face with nuggets, or a surgeon cutting up a book) elicited a greater anterior N400 response compared to correct and understandable actions (e.g., a person doing the laundry). In another ERP study, Bach and colleagues (2009) investigated if the understanding of actions of tool use depends on the motor act that is performed and/or on the function of the objects involved in the action. The inserting actions could mismatch in two ways: functional mismatches occurred when the function of the objects was not appropriate to achieve the given action outcome (e.g., credit card being applied to a ticket canceller). Orientation mismatches occurred when the orientations of insert and slot of the target object were not consistent with an inserting action being performed (different orientations of insert and slot). The results showed that both types of mismatch gave rise to a negative inflection in the latency range of the N400 component followed by a positive modulation. According to the authors, the results indicated that the motor act and the function of the objects are derived by two at least partially different subprocesses and become integrated into a common representation of the observed action.

In another ERP study, Gunter and Bach (2004) presented meaningful and meaningless hand postures to a group of University students. The participants had to judge whether a hand posture was meaningful or meaningless by pressing button. The data showed that meaningless hand postures elicited an anteriorly distributed N300 and a centro-posteriorly distributed N400 component. Several evidences suggested that the N300 component might be sensitive to picture-specific semantic processing (Barrett and Rugg, 1990; Federmeier and Kutas, 2001; McPherson and Holcomb, 1999). Therefore, the authors concluded that the N300 reflects picture-specific processes, whereas the N400 response probably indicated processing in an amodal semantic network. Interestingly, the scalp distribution of the N400 observed in this study was more posterior than usually reported in picture processing. According to the authors, this evidence might suggest that the semantic processing associated to the meaningful hand postures has similar properties to those of abstract words.

Most previous studies investigated the semantic processing associated to actions/gestures experienced in everyday life. In other terms, they investigated semantic knowledge acquired without a specific training. On the contrary, in the study that we will report in this chapter, we explored the processing of semantic violations related to knowledge that have been learned through a specific long-lasting training.

In this field of investigation, previous neuroimaging studies explored the neural mechanisms that support the acquired capability to recognize learned actions in sport games (Aglioti et al. 2008; Abreu et al. 2012; Kim et al., 2011; Shimada et al. 2009). In particular, some of them focused on the relation between the observer's motor experience of a given action and the fronto-parietal mirror neuron system (MNS), which includes the inferior frontal gyrus, the left inferior parietal lobule and the superior temporal sulcus (Hamilton et al., 2008; Rizzolatti et al. 1996; Iacoboni et al. 2005; Pelphrey et al. 2004; Saxe et al. 2004).

For example, Kim and colleagues (2011) carried out an fMRI study in which Western-style archery movements were presented to expert archers and non-archer control subjects while their brains were scanned. The results of this study revealed a stronger activation of the premotor and inferior parietal cortex in expert archers compared with non-archer control subjects.

In addition, Aglioti and colleagues (2008) investigated the ability to predict an error in a basketball game. In particular, they explored the neural correlates of the superior perceptual and motor abilities underlying action anticipation in elite basketball players. They used psychophysical and transcranial magnetic stimulation studies to investigate the dynamics of action anticipation and its underlying neural correlates in professional basketball players. The psychophysical evidence revealed that professional basketball players predict the outcome of free shots at a basket observed on a video earlier and more accurately than people with comparable visual experience (coaches or sports journalists) and naïve people. Moreover, the TMS study showed an increase of motor excitability only in athletes when they performed an observational task that employed the ability to predict the outcome of shots at a basket. According to the authors, this evidence may suggest that athletes are able to predict the basket shot's outcome by observing the body kinematics. Furthermore, despite all the experts (both visual and visuo-motor) showed an increased activation of the motor-evoked potentials during the observation of the basket shots, only the athletes were able to detect erroneous basket pitches.

As mentioned above, several electrophysiological evidences revealed that processing of purposeless, inappropriate actions/gestures in everyday life context elicit N400 effects. However, scarce knowledge is available about the semantic processing related to the effects of experiences shaped by a specific artistic/motor training. Therefore, in this study we explored the processing of semantic violations related to the representations of rules and gestures that constitute a specific motor repertoire learned through a prolonged exercise. In other words, the aim of this work consisted in investigating the temporal course and the neural mechanisms underlying the representation of complex actions related to a long-lasting training. In particular, we focused on the N400 response as index of the ability to recognize specific actions related to basketball game.

Thus, in this research we visually presented several pictures representing correct and incorrect basketball actions to professional basketball players and naïve viewers while their EEG was recorded. We then compared the brain activity related to the perception of correct and incorrect actions in both groups.

Several findings pointed out that a long-lasting sport or musical training might cause significant effects on brain neuroplasticity (see Aglioti et al. 2008; Abreu et al. 2012; Kim et al., 2011; Shimada et al. 2009; Pantev et al., 2008; Munte, 2002, Gaser&Schlaug, 2003; Lee & Chen, 2003; Strait & Kraus, 2011). Thus, we assumed that a basketball training might induce structural and functional cortical plasticity effects in basketball players. To test this hypothesis, we examined the different neural mechanisms underlying the semantic processing related to the observation of players in action by inexpert and naïve people. In particular, we expected to observe the electrophysiological manifestation of this cortical plasticity effect in the modulation of the N400 to semantic violations of basketball actions only in skilled brains.

2.2 Methods

2.2.1 Participants

Fifteen healthy, right-handed professional basketball players (mean age = 24.4; SE = 53) and 13 non-players (mean age = 24.3 years; SE = 54.8) participated in this study. Non-players had no familiarity with playing or watching basketball.

The basketball players played professional basketball (C1– C2 leagues) for 4–10 years and they trained for a mean of 4 h per week. All of the participants had normal or corrected-to-normal vision and no reported history of neurological illness. Their handedness was assessed by means of the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985), a laterality preference questionnaire reporting right-handedness and right ocular dominance for all participants.

Experiments were conducted with the understanding and the written consent of each participant. The experimental protocol was approved by the ethical committee of the University of Milano-Bicocca.

2.2.2 Stimuli

The stimulus set comprised 380 several color photos of real basketball actions placing indoors or outdoors. The basketball players portraying in the picture were seven different male players. They performed correct or incorrect body posture or gestures.

To obtain a clear distinction between correct and incorrect actions, all pictures were evaluated by a group of 10 judges. They were either professional basketball players, referees or coaches of C1 or C2 basketball teams. The judges evaluated the basketball actions using a 3 point Likert scale (2 = correct action; 1 = it is impossible to judge from the picture, I am unsure, 0 = incorrect action).

Based on the scores obtained for each photo, we obtained 107 correct pictures (1.5–2.5) and 169 incorrect pictures (0–0.45). We discarded 104 photos (0.5–1.4).

Each picture displaying a correct action was paired with a similar action displaying a violation. The pictures were balanced for: i) number of players involved; ii) location (indoor vs. outdoor) and position with regard to the hoop; iii) body district involved in the violation (hand, arm, leg, or torso); iv) presence or absence of ball; and v) camera distance from the players and angle (front, back, profile). At the end of this process, we selected 100 correct and 100 incorrect basketball actions (Fig.2.1).

Fig 2.1. Exemplars of pictures used as stimuli in the Correct (on the left) and Incorrect (on the right) categories

In order to have subjects performing a secondary task, we also included 50 photos showing empty basketball courts. The mean luminance was measured by means of a Minolta luminance meter, and luminance values were compared across classes by a one-way ANOVA (F 1, 99 = 1.8; $p > 0.05$) that proofed stimulus equiluminance among all pictures (Correct, Incorrect, Target). The stimulus size was 12 X 12.5 cm subtending a visual angle of 6º X 6º15’. Stimuli were presented for 1500 ms at the centre of a PC screen with an ISI ranging from 1000 to 1100 ms. The outer background was dark grey.

2.2.3 Procedure

The task consisted of responding to the target pictures showing empty basketball courts by pressing a response key with the index finger of the left or right hand. The left and right hands were used alternately during the recording session. We counterbalanced the order of the hand and task conditions across subjects. During the experiment, participants were comfortably seated in a darkened, acoustically and electrically shielded test area. They faced a high-resolution VGA computer screen located 114 cm from their eyes. The subjects were instructed to gaze at the center of the screen where a small circle served as a fixation point and to avoid any eye or body movement during the recording session. Stimuli were presented in random order at the center of the computer screen in 8 different, randomly mixed, short runs lasting approximately 2.5 minutes.

2.2.4 Electroencephalographic recording

The EEG was continuously recorded from 128 scalp sites at a sampling rate of 512 Hz by means of ANT-EEprobe 3.1. system. Horizontal and vertical eye movements were also recorded. Linked ears served as the reference lead. The EEG and electro-oculogram (EOG) were filtered with a half-amplitude band pass of 0.016–100 Hz. Electrode impedance was maintained below 5kΩ (Fig.2.2).

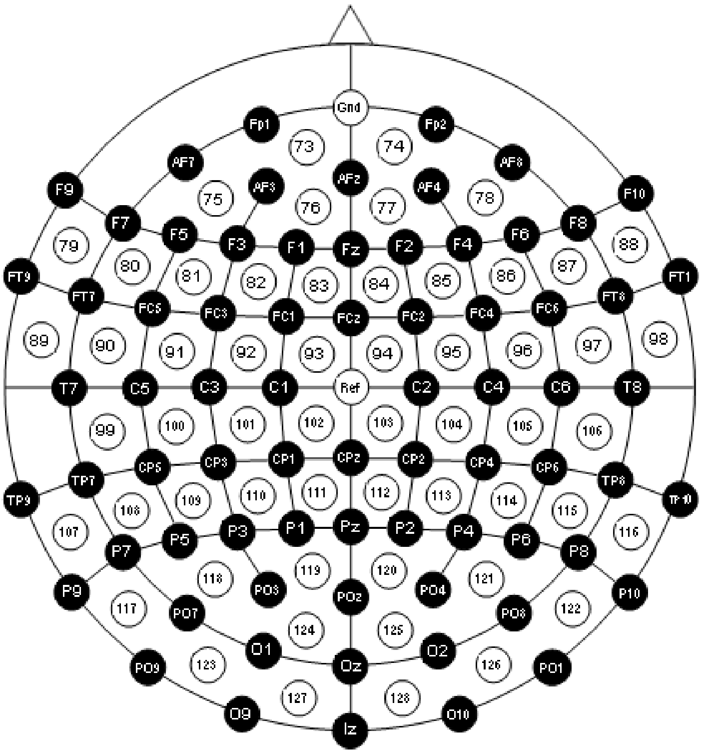

Fig.2.2. EEG recording layout, with 128 electrodes distributed over the whole surface.

2.2.5 Statistical analysis of ERPs

Trials contaminated by blinks, muscle tension (EMG), channel drift, and/or amplifier blocking were discarded before averaging. The artefact rejection criterion was peak-to- peak amplitude exceeding 40 μV, and the rejection rate was 5%. EEG epochs were synchronized with the onset of stimuli presentation. Evoked-response potentials (ERPs) were averaged off-line from 100 ms before through 1200 ms after stimulus onset. ERP components were identified and measured with respect to the baseline voltage, which was averaged over the pre-stimulus interval from -100 ms to 0 ms.

We selected the electrode sites and time windows for measuring and quantifying ERP components of interest on the base on the previous literature.

Two ERP components of interest were identified: a N400 and a Late Positivity Potential (LPP). The mean amplitude of the anterior N400 response was quantified at FP1 FP2, AF7 AF8, AFF5h, AFF6h sites in the 450– 530 ms time window. The mean amplitude of the Late Positivity Potential (LPP) was also measured over the same sites in the 900–1000 ms time window (Table 2.1). Mean amplitude of each component was analyzed by a repeated measures ANOVA that included 1 between-groups factor (Basketball players, Naïve) and three within-subjects factors: Action correctness (Correct, Incorrect), Electrode (dependent on the ERP component of interest) and Hemisphere (Left, Right). Multiple comparisons of means were performed by Fisher post-hoc test.

In this experiment source analysis was performed according to the swLORETA method (standardized and weighted Low Resolution brain Electromagnetic Tomography) with ASA software (ANT Software BV). SwLORETA is a recent update of the standardized low-resolution brain electromagnetic tomography (sLORETA) method introduced by Pascual-Marqui in 2002. sLORETA is a useful tool for modelling spatially distinct source activities in the absence of prior knowledge of the generators' anatomical location. The sLORETA method generates statistical parametric maps that reflect the reliability of the estimated current source density distribution. It shows exact topographic properties, with a zero-localization error for single dipoles in noiseless simulated data. swLORETA additionally incorporates a singular value decomposition-based lead field weighting that compensates for the sensors' differing sensitivity to current sources at different depths (Palmero-Soler, Dolan, Hadamschek, & Tass, 2007). This weighting enables accurate reconstruction of surface and deep current sources in simulated data - even in the presence of noise and when two dipoles are simultaneously active. The swLORETA solution was computed using a three-dimensional grid of points (or voxels) representing the possible sources of the signal. Furthermore, the solution was restricted to the grey matter by selecting only voxels in which the grey matter probability was not equal to zero (based on the probabilistic brain tissue maps available from the Montreal Neurological Institute (Collins et al. 1994; Evans et al. 1993). Lastly, the 1056 grid points (with a 5 mm grid spacing) and the recording array (128 electrodes) were registered against the Collins 27 MRI map (with a 1 mm spatial resolution) (Evans et al. 1993). The Boundary Model was used to compute the lead field matrix. The lead field matrix models the mechanism by which the original current sources are superimposed on each other to produce the measured voltage fields at each detector. This constitutes the first step in any attempt to compute an inverse solution (Geselowitz, 1967). The source space properties included a grid spacing (the distance between two calculation points) of 5 points and an estimated signal-to-noise ratio (SNR, which defines the regularization: a higher value indicates less regularization and therefore less blurred results) of 3. swLORETA was performed on the group data and identified statistically significant electromagnetic dipoles ($p < 0.05$) in which larger magnitudes correlated with more significant activation. In this experiment, swLORETA was performed on the ERP waveforms at the N400 latency stage (450–530 ms).

ERP COMPONENT	TIME WINDOW	ELECTRODES
N400	**450–530 ms**	FP1 FP2, AF7 AF8, AFF5h, AFF6h
LPP	**900–1000 ms**	FP1 FP2, AF7 AF8, AFF5h, AFF6h

Tab. 2.1. ERP components of interest for the present study

2.3 Results

2.3.1 Electrophysiological results

N400 (370-520 ms)

The ANOVA computed in the N400 time window revealed a significant interaction of Hemisphere x Group (F 1, 22 = 4.44, $p < 0.05$) that indicated a larger N400 amplitude over the left hemisphere in naïve people and bilateral in basketball players (Naïve: LH = -3 μV, SE 0.87; RH= -2.29, SE= 0.9. Players: LH= -2.55 μV, SE=0.87, RH= - 2.88, SE= 0.93). Moreover, the further significant interaction Group x Action correctness revealed that the N400 was strongly affected by Action correctness in the group of basketball players (F 1, 22= 5.96; p <0.05) (Fig. 2.3). In particular, post-hoc comparisons revealed that the N400 amplitude was greater in response to incorrect compared correct actions only in basketball players (Players: incorrect = - 3.47 μV, SE = 1.01 vs. correct = -1.97 μV, SE = 0.79, p<0.05; Naïve: incorrect= -2.66 μV, SE= 1; correct= 2.63 μV, SE= 0.8, n.s.) (Fig.2.4).

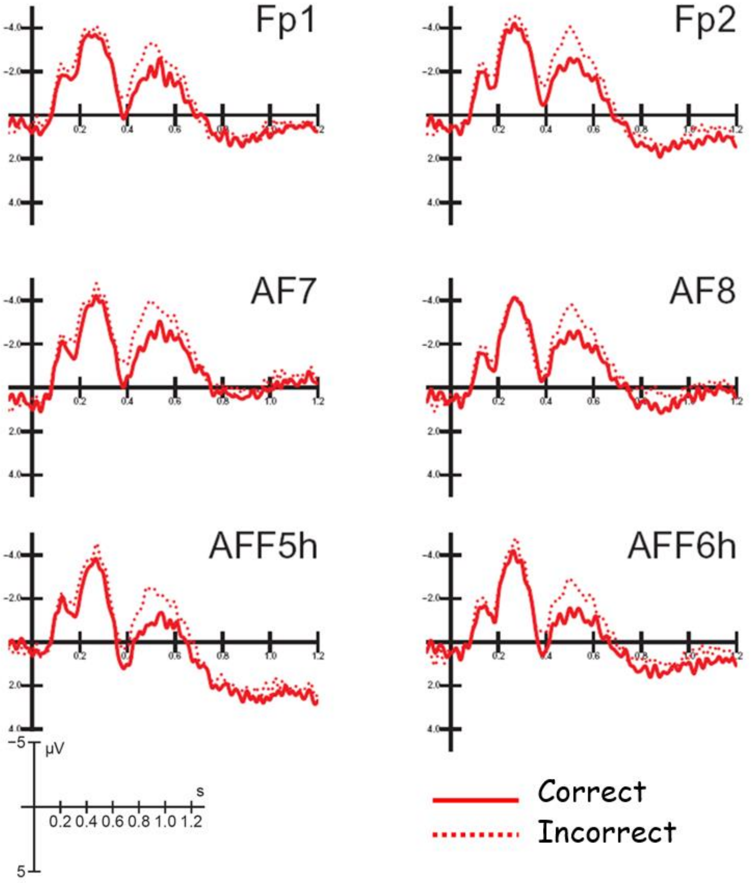

Fig. 2.3. Grand-average ERPs recorded at anterior sites in response to Correct (solid line) and Incorrect (dotted line) actions in basketball players

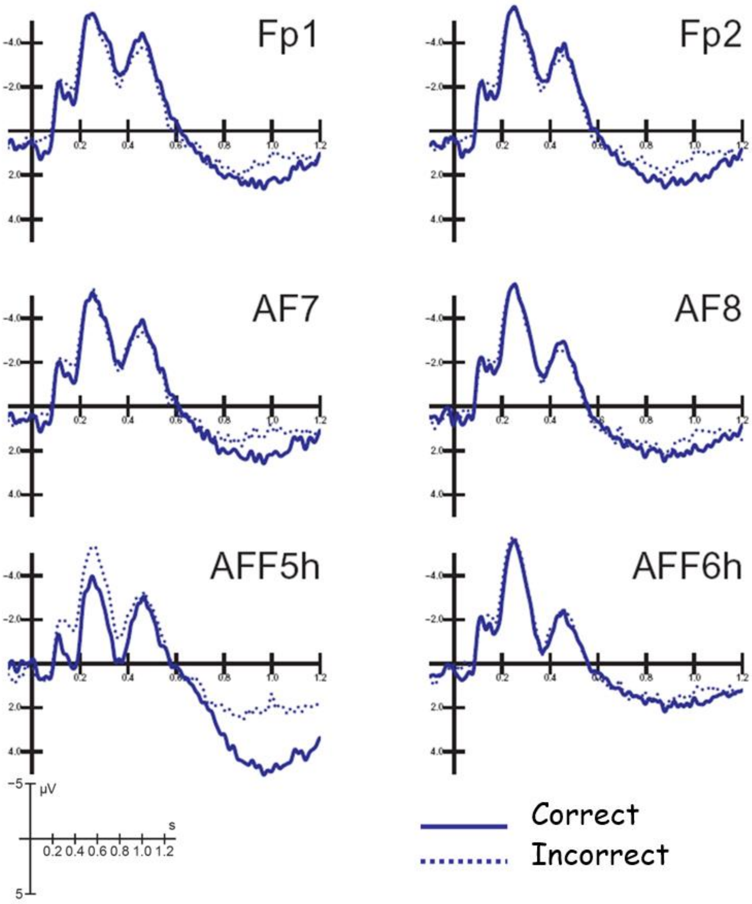

Fig. 2.4. Grand-average ERPs recorded at anterior sites in response to Correct (solid line) and Incorrect (dotted line) in naïve viewers.

LPP (900–1000 ms)

The ANOVA performed on LP values did not show any statistically significant differences.

2.3.2 Source localization results

A swLORETA inverse solution was applied to the voltage recorded in the N400 time window in response to correct actions. The dipoles (see table 2.2) show the activation of a network or cortical region that was very smilar in both groups. In particular it included the left and right fusiform gyrus (BA37), the uncus, the parahippocampal area (PPA), the somatosensory area (right superior parietal lobule, BA7), and the right inferior temporal gyrus (BA20) (Fig.2.5).

Table 2.2 | Talairach coordinates (inmm)corresponding to intracranial generators explaining theN400 surface voltage recorded in response to correct basketball actions in the 450–530 ms time window, according to swLORETA, in basketball players (Power RMS = 222 µV) and naïve viewers (Power RMS = 250 µV). Magnitude in nAm; BA = Brodmann areas

Basketball players							
Magnitude	**T-x [mm]**	**T-y [mm]**	**T-z [mm]**	**Hemisph.**	**Lobe**	**Gyrus**	**BA**
8.19	50.8	-55	-17.6	R	T	Fusiform Gyrus	37
6.98	21.2	-24.5	-15.5	R	Limbic	Parahippocampal Gyrus	35
6.97	-18.5	-8	-28.9	L	Limbic	Uncus	36
6.78	-38.5	-44.8	-16.9	L	T	Fusiform Gyrus	37
6.65	21.2	9.1	-27.5	R	Limbic	Uncus	38
6.61	50.8	-0.6	-28.2	R	T	Middle Temporal Gyrus	21
5.93	1.5	-36.6	-1.3	R	Cereb	Anterior Lobe, Culmen	
5.15	21.2	-63.8	59	R	P	Superior Parietal Lobule	7
4.88	-58.5	-8.7	-21.5	L	T	Inferior Temporal Gyrus	20
Naïve viewers							
Magnitude	**T-x [mm]**	**T-y [mm]**	**T-z [mm]**	**Hemisph.**	**Lobe**	**Gyrus**	**BA**
7.33	50.8	-55	-17.6	R	T	Fusiform Gyrus	37
7.28	21.2	-24.5	-15.5	R	Limbic	Parahippocampal Gyrus	35
7.20	50.8	-33.7	-23.6	R	T	Fusiform Gyrus	20
7.05	-18.5	-8	-28.9	L	Limbic	Uncus	36
6.91	21.2	-63.8	59	R	P	Superior Parietal Lobule	7
6.84	-38.5	-44.8	-16.9	L	T	Fusiform Gyrus	37
6.63	21.2	9.1	-27.5	R	Limbic	Uncus	38
6.35	50.8	-0.6	-28.2	R	T	Middle Temporal Gyrus	21

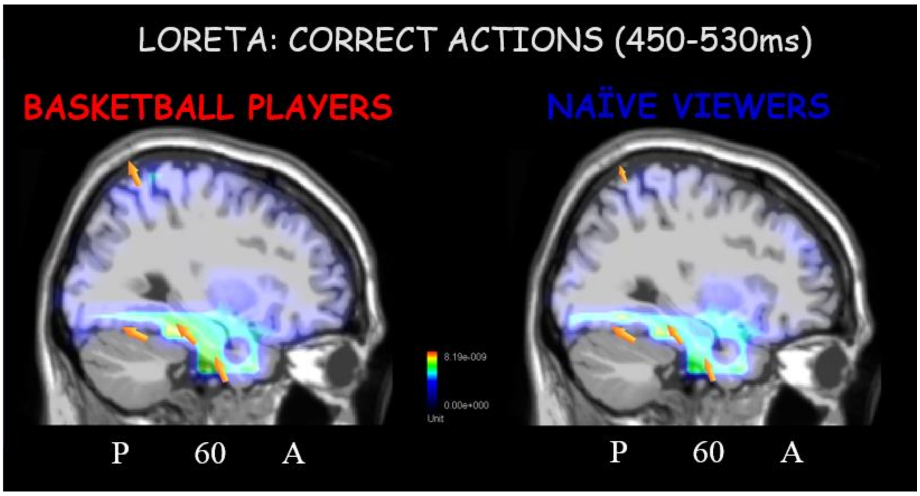

Fig. 2.5. Sagittal views of the N400 active sources for correct waves as recorded in basketball players (Left) and naïve viewers (Right) according to swLORETA analysis during the 450–530 ms time window. The different colours represent differences in the magnitude of the electromagnetic signal. The electromagnetic dipoles are shown as arrows and indicate the position, orientation and magnitude of dipole modeling solution applied to the ERP waveform in the specific time window. Numbers refer to the displayed brain slice in sagittal view.

A swLORETA inverse solution was applied by subtracting ERPs of correct from incorrect actions in the in the 450-530 ms time window. The list of active dipoles was different between the two groups (see Table 2.3). In particular, we observed strongest sources of activation located in the right inferior and superior temporal gyrus, the right parietal cortex (BA 39, 40), the right premotor cortex (BA 6), and the left precentral gyrus (BA4) in basketball players, and in the middle frontal gyrus (BA 10,46) in naïve viewers (Fig. 2.6).

Table 2.3 | Talairach coordinates (in mm) corresponding to intracranial generators explaining the N400 surface difference-voltage. Correct action ERPs are subtracted from incorrect action ERPs in the 450–530 ms window, according to swLORETA, in basketball players (Power RMS = 36.1 µV) and naïve viewers (Power RMS = 15.7µV). Magnitude in nAm; BA = Brodmann areas

Basketball players

Magnitude	T-x [mm]	T-y [mm]	T-z [mm]	Hemisph.	Lobe	Gyrus	BA
10.71	60.6	-16.8	-14.8	R	T	Inferior Temporal Gyrus	20
10.19	31	9.1	-27.5	R	T	Superior Temporal Gyrus	38
9.22	-28.5	-97.5	-5.7	L	O	Lingual Gyrus	18
8.99	60.6	-55	-17.6	R	O	Fusiform Gyrus	37
8.59	-8.5	-0.6	-28.2	L	Limbic	Uncus	28
7.10	60.6	-41.5	42.9	R	P	Inferior Parietal Lobule	40
6.93	50.8	-61.8	41.2	R	P	Inferior Parietal Lobule	39
6.41	40.9	-75.2	-19.1	R	Cereb	Posterior Lobe, Declive	
6.38	-28.5	55.3	7	L	F	Middle Frontal Gyrus	10
6.07	50.8	33.4	23.1	R	F	Middle Frontal Gyrus	46
4.70	1.5	-29.4	26	R	Limbic	Cingulate Gyrus	23
4.33	21.2	52.4	33.7	R	F	Superior Frontal Gyrus	9
3.77	1.5	-33.4	61.6	R	F	Paracentral Lobule	6
3.55	-18.5	-23.2	62.4	L	F	Precentral Gyrus	4

Naïve viewers

Magnitude	T-x [mm]	T-y [mm]	T-z [mm]	Hemisph.	Lobe	Gyrus	BA
4.30	-38.5	43.4	23.9	L	F	Middle Frontal Gyrus	10
3.44	50.8	34.3	14.2	R	F	Middle Frontal Gyrus	46
3.33	1.5	57.3	-9	R	F	Medial Frontal Gyrus	10
3.18	31	37.2	-10.5	R	F	Middle Frontal Gyrus	11
3.00	70.5	-36.6	-1.3	R	T	Middle Temporal Gyrus	21
2.76	-58.5	2.4	29.4	L	F	Precentral Gyrus	6
2.08	11.3	12.4	30.3	R	Limbic	Cingulate Gyrus	24
2.06	-8.5	-6.3	37.4	L	Limbic	Cingulate Gyrus	24
1.74	-38.5	-86.4	-12.4	L	O	Inferior Occipital Gyrus	18
1.46	-18.5	-58.9	14.5	L	Limbic	Posterior Cingulate	20
1.40	21.2	-91.3	29.7	R	O	Cuneus	19

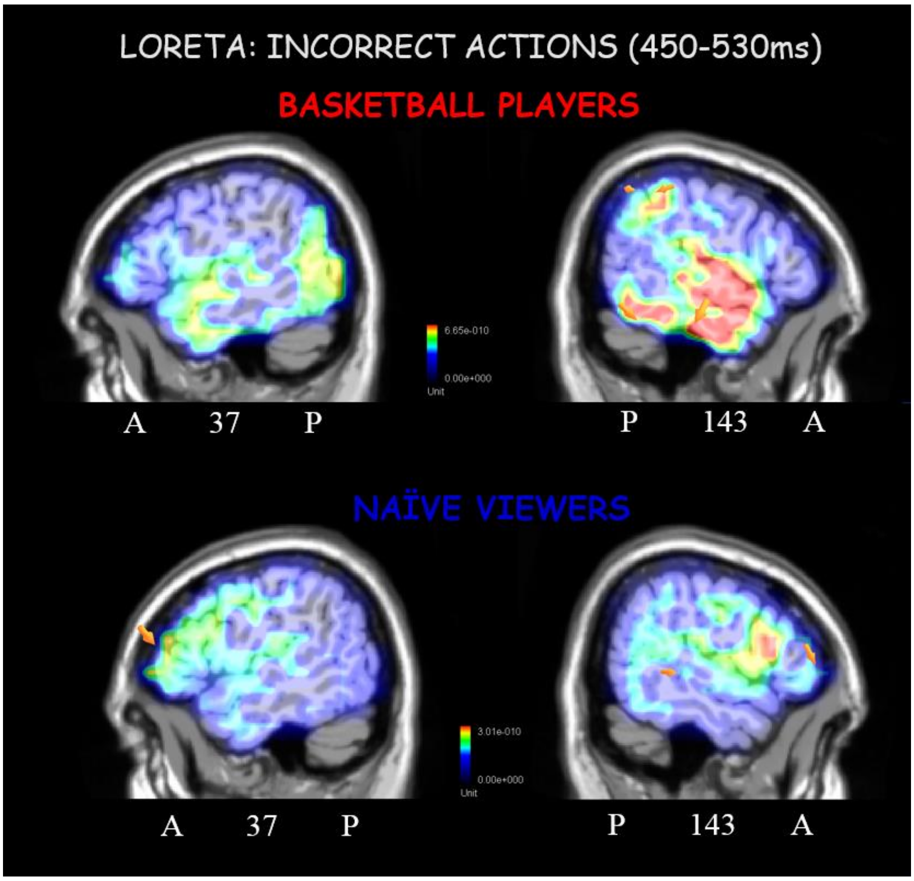

Fig. 2.6. Sagittal views of the N400 active sources for correct/incorrect waves as recorded in basketball players (Top) and naïve viewers (Bottom) according to swLORETA analysis during the 450–530 ms time window. The different colours represent differences in the magnitude of the electromagnetic signal (in nAm). The electromagnetic dipoles are shown as arrows and indicate the position, orientation and magnitude of dipole modeling solution applied to the ERP waveform in the specific time window. Numbers refer to the displayed brain slice in sagittal view: the left section belongs to the right hemisphere and the right one to the left hemisphere. Note that the scale is different, and the signal was much stronger in the players' brain.

2.4 Discussion

In this study, we investigated the semantic processing associated to actions related to a long-lasting sport training. We explored how correct and incorrect actions are processed by experts and inexperts. Our hypothesis was that the N400 response might reflect the semantic knowledge learned through a specific training. In this view, we expected to observe a greater amplitude of the N400 response to incorrect basketball actions in skilled brain compared to naïve ones. Thus, the aim of this study was to explore the semantic processing related to complex actions learned by exercise. As in the previous study, the stimuli were only visually presented.

In this work, we presented 200 pictures (100 correct and 100 incorrect) portraying basketball players performing different basketball actions. Ten expert judges previously evaluated the correctness or incorrectness of the actions showed in the pictures. The judges valued the basketball actions using a 3 point Likert scale (2 = correct action; 1 = impossible to judge from the picture, I am unsure, 0 = incorrect action).

In order to keep the subject focused on visual stimulation, the task consisted of responding to photos showing empty basketball courts by pressing a response key with the index finger of the left or right hand. The subjects had to ignore all other photos.

Regarding the electrophysiological results, the statistical analyses revealed a significant interaction between Group x Action correctness. Post-hoc comparisons showed a greater N400 amplitude in response to incorrect actions compared to correct ones only in basketball players. No stimulus content-dependent modulation (correct vs. incorrect actions) of ERPs was found at any scalp site in the naïve viewers. As we mentioned in the Introduction of this chapter, previous studies revealed a greater N400 response to incoherent and purposeless behavior compared to coherent and goal directed ones (Proverbio et al. 2009; Sitnikova, 2003). In addition, in this study we focused on the ability to recognize and detect semantically correct or erroneous actions learned through a specific training.

To our knowledge, few studies tried to investigate this aspect using nonlinguistic stimuli. Indeed, most previous works studied the semantic knowledge learned through a long-lasting verbal training. For example, in the domain of language, some studies focused on the modulation of the N400 according to the individual’s proficiency with a language. Some evidences showed that a brief language training is able to elicit a N400 effect to semantic incongruity (McLaughlin et al., 2004). Other studies on bilinguals showed that they exhibited a N400 priming and semantic congruity effects in both of their languages. However, this effect varied as a function of language proficiency and age of acquisition (Kutas & Federmeier, 2011). Other evidences indicated a similar N400 effect in musicians. In particular, the results of some works revealed that the presentation of inconsistent musical stimuli elicited a greater N400 response compared to consistent ones (Besson et al. 1994; Proverbio et al. 2014) (We will examine in more detail the evidences on semantic processing in music in the next chapter).

Thus, in light of these previous evidences, our data suggested that the action coding was automatically performed and that only skilled people were able to detect the violation of basketball rules. Indeed, the results revealed no N400 effect to the Action Correctness in naïve viewers. This evidence suggested that their brains were unable to discriminate correct basketball actions from incorrect basketball actions.

Overall, the electrophysiological data indicates that a long-last training produces effects on the semantic knowledge also in nonlinguistic field.

In addition, in this study the N400 effect was found over the anterior sites. This result is line with previous evidences that indicated that the N400 elicited by pictures has a more anterior scalp topography than the N400 observed in most language studies (e.g., McPherson & Holcomb, 1999).

Regarding the source localization results, the swLORETA inverse solution applied to the voltage recorded in the N400 time window in response to correct actions revealed a similar pattern of activation between the two groups. The brain areas involved were: the left and right fusiform gyrus (BA37), the uncus, the parahippocampal area (PPA), the somatosensory area (right superior parietal lobule, BA7), and the right inferior temporal gyrus (BA20). The parahippocampal gyrus, might be involved in scene processing, spatial processing (Kravitz et al. 2011) and body spatial position analysis (Moser et al. 2008).

In addition, in both groups, the swLORETA indicated that pictures of players in action might have activated the right fusiform gyrus (BA37), a region that may include both the fusiform face area (FFA) (Grill-Spector et al., 2004) and the fusiform body area (Schwarzlose et al. 2005), regions that are involved in human faces and bodies processing, respectively. Finally, the swLORETA indicated the possible activation of the superior parietal lobule, known to be involved in action observation of reaching movements (Cattaneo et al. 2009).

Moreover, to investigate the neural mechanism allowing the basketball players to discriminate correct from incorrect actions, a swLORETA inverse solution was applied by subtracting ERPs of correct pictures from incorrect ones. swLORETA indicated sources of activation located in the right inferior and superior temporal gyrus, the right parietal cortex (BA 39, 40), the right premotor cortex (BA6), and the left precentral gyrus (BA4) in basketball players. These areas might be part of the human mirror system (MNS) and contain neurons that respond to the observation of biological actions such as grasping, looking or walking (Hamilton et al., 2008; Rizzolatti et al. 1996; Iacoboni et al. 2005; Pelphrey et al. 2004; Saxe et al. 2004).

In conclusion, the results of the present investigation showed that an intensive sport training is able to modulate the N400 response, reflecting the semantic processing associated to action repertoires learned through imitation and exercise.

3. Processing of correct and incorrect audio-visuomotor information in musicians: an electrophysiological investigation.

[This research has been published in: Proverbio AM, Calbi M, Manfredi M, Zani A (2014). Audio-visuomotor processing in the Musician's brain: an ERP study on professional violinists and clarinetists, *Scientific Reports (Nature), 4: 5866*]

3.1 Introduction

In the third experiment, we explored how a long-lasting musical training affected the N400 amplitude to semantic violation when stimuli are presented using a multisensory modality. We focused on the effects of the integration of auditory and visual stimuli on the N400 response.

In daily life, most external information is received from visual and auditory senses. Visual and auditory information are received separately and integrated into the human brain, and thus people get a comprehensive understanding of the outside world. In recent years, several studies investigated the multisensory information processing.

Previous studies on multimodal processing during language comprehension have often investigated the relationship between speech and lip movements by exploiting the McGurk effect (Özyürek, 2007), a linguistic phenomenon observed during audiovisual incongruence (McGurk & Mac Donald, 1976; Colin et al., 2002; Mottonnen et al., 2002; Sams et al., 1991): when the auditory component of one syllable (e.g., \ba\) is paired with the visual component of another syllable (e.g., \ga\), the perception of a third syllable (e.g., \da\) is induced. These studies showed that visual information from articulation interacts with the auditory information quite early, that is, within 200 ms during audio/visual speech observation (Özyürek, 2007). Indeed, several studies investigated the phenomenon focusing on the effect on the Mismatch Negativity (MMN). Indeed, several studies investigated the phenomenon focusing on the effect on the Mismatch Negativity (MMN). The auditory MMN is a fronto-central negative potential with sources in the primary and non-primary auditory cortex and a typical latency of 150-250 ms after the onset of the deviant stimulus (Leino et al., 2007). The amplitude of the MMN response depends on the degree of variations/changes in the expected auditory percept, reflecting the cortical representation of auditory-based information (Näatänen, 1990). For example, in a study by Sams and colleagues (1991), Finnish /pa/ syllables were presented together with a videotaped face articulating either the concordant syllable /pa/ (84% of stimuli) or the discordant syllable /ka/ (16%). The magnetic responses to infrequent perceptions elicited a specific waveform that was considered analogous to a mismatch response.

Other studies have focused on the semantic processing of audiovisual stimuli. In other terms, they explored the semantic processing of stimuli that require audio-visual integration. The results of some studies revealed that semantically inconsistent speech or natural sounds with pictures or videos could elicit N400 effects (Plante et al., 2000; Puce et al. 2007; Cummings et al., 2008: Liu et al., 2011). For example, Cummings and colleagues (2008) compared behavioral and electrophysiological indices associated with semantic processing of Words and Environmental Sounds in Pre-adolescent children (7–9 years), Adolescent children (12–14 years), and Adults (18–25 years). They compared children and adults' behavioral and electrophysiological responses (the N400 effect) during the processing of words and environmental sounds presented in semantically matching and mismatching picture contexts. They found that semantically inconsistent speech or natural sounds with pictures could elicit

N400 effects in all three groups. When compared to adults, children showed longer latencies and larger amplitudes of the N400 effect for Environmental Sound.

Very few works investigated the semantic processing of audiovisual stimuli related to a well-known ability. For example, learning to play a musical instrument requires acquisition of both visual and auditory information. In addition, evidence revealed that music could activate brain mechanisms related to the processing of semantic meaning. Indeed, electrophysiological evidences pointed out that the presentation of semantically inconsistent musical stimuli elicited greater N400 responses compared to consistent ones only in musicians (Besson et al., 1994; Koelsch et al., 2004; Daltrozzo & Schön, 2008). For example, in 1994, Besson and colleagues presented short musical phrases that ended either in a congruous or a ‘harmonically’, ‘melodically’, or ‘rhythmically’ incongruous note to musicians and non-musicians. The results revealed a greater N400 response to incongruent end-notes in musicians compared to nonmusicians. In addition, this study revealed that the N400 effect varied as a function of subject's familiarity with the melodies and the type of incongruity.

In light of these evidences, we wondered if audiovisual information related to a specific knowledge might be processed differently according to the viewers’ type of expertise. Thus, we analyzed the processing of semantic violations related to a specific musical skill. In particular, we investigated if a long lasting musical training affected the N400 amplitude to semantic violation in skilled and unskilled brains in a different way.

To this aim, we recorded the brain activity during audiovisual presentation of congruent vs. incongruent sound-gesture movie clips in professional musicians and in age-matched university students. We considered two different musical instruments to verify if the detection and the processing of a semantic violation was strongly related to the type of expertise.

To make the task feasible for both naïve and expert subjects, all participants had to discriminate a 1-note vs. 2-note execution by pressing one of the two buttons. We predicted that the audio-video inconsistency would be clearly recognizable only by musicians skilled in their specific instrument (i.e., violinists for the violin, and clarinetists for the clarinet). Previous studies that investigated musical elements that were not specifically related to semantic aspects of the musical learning, found a Mismatch Negativity (MMN) effect when deviant or inconsistent audiovisual musical stimuli were presented. Unlike these previous works, since we assumed that we manipulated the semantic aspects of the audiovisual information, we expected to find a N400-like negative response. In particular, we expected to find a great N400 response in the musicians' brains to the semantic violations relative to the instrument that they played and a strong attenuation of the N400 response in naïve brains. This response could occur later because of the dynamic nature of the stimulus (movies lasting 3 seconds).

3.2 Methods

3.2.1 Participants

Thirty-two right-handed participants (8 male) were recruited to participate in this study. The musician group involved 9 professional violinists (3 males; mean age = 26 years, SE = 3.54) and 8 professional clarinetists (3 males; mean age = 23 years, SE = 3.03). The naïve group included 15 age-matched University students (2 males; mean age = 23.5 years, SE = 2.50) with no experience in music. The violinists' mean age of acquisition (AoA) of musical abilities was 7 years (SE = 2.64), whereas the clarinetists' mean age of acquisition of musical skills was 10 years (SE = 2.43). All had normal or corrected-to-normal vision, and reported no history of neurological illness or drug abuse. Their handedness was assessed by means of the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985), a laterality preference questionnaire reporting right-handedness and right ocular dominance for all participants. The experiment was conducted with the understanding and the written consent of each participant. Three controls were excluded from statistical analyses because of EEG artefacts.

3.2.2 Stimuli

The stimulus set was created by videotaping a clarinetist and a violinist performing a musical score. The musical score consisted in 200 measures (in 4/4 tempo): 84 single note measures (1 minim) and 116 double note measures (2 semiminims). There were no repeated notes. We created 200 movie clips (one for each measure) from the two videos in which the clarinetist and the violinist executed the musical score. In addition, we created 200 incongruent movie clips by substituting the original sound of the measure with the sound of the next measure using Windows Movie Maker 2.6.

In order to be validated, and to be sure that musicians detected the sound-gesture incongruity, all the stimuli were presented to 20 musician attending Conservatory classes. The judges evaluated whether the sound-gesture movie clip were correct using a Likert 3 point scale (2 = congruent; 1 = I am not sure; 0 = incongruent). The video clips of clarinet and violin were shown to judges that were expert in a specific instrument. At the end of this process, we selected 188 congruent (97 clarinet, 91 violin) and 180 incongruent (88 clarinet, 92 violin) video clips (Fig.3.1).

Fig 3.1. (Top) Exemplars of video clips relative to clarinet and violin instruments. (Bottom) An extract of the musical score.

The stimulus size was 15 X 12 cm subtending a visual angle of 7° 30’ 6’’. The mean luminance was measured by means of a Minolta luminance meter, and luminance values were compared across classes by a one-way ANOVA ($F_{1, 74} = 0.02$, $p > 0.5$) that proofed stimulus equiluminance between the two video clips (violin = 15.75 cd/m2; clarinet = 15.57 cd/m2). Audio sound values were normalized to -16 dB using the *Sony Sound Forge 9.0* software, by setting a fixed value of the root mean square (RMS) of a sound corresponding to the perceived intensity recorded at intervals of 50 ms.

It is important to specify that each movie clip lasted 3 seconds. In particular, during the first second, the musician prepared himself to perform the notes but he did not play. Therefore, the tones were executed during the second second.

3.2.3 Procedure

Movie clips were presented randomly mixed for 3000 ms at the center of a PC screen. The interstimulus interval lasted 1500 ms. To make the task feasible for all groups, participants had to respond as accurately and quickly as possible to the execution of 1-note or 2-note, by pressing a response key with the index or the middle finger, respectively. The two hands were used alternately during the recording session. We counterbalanced the order of the hand and task conditions across subjects.

Participants were comfortably seated in a darkened, acoustically and electrically shielded test area. They faced a high-resolution VGA computer screen located 114 cm from their eyes. They were instructed to gaze at the centre of the screen, where a small dot served as the fixation point, and to avoid any eye or body movements during the recording session.

Stimuli were presented at the centre of the screen and were randomly mixed in 16 different (8 for each instrument) short runs that lasted about 3 minutes each. The order of presentation differed across the subjects. Audio stimulation was administered using a set of headphones. All participants were unaware of the study's aim. However, at the end of the experiment, only musicians reported some awareness about their own instrument's sound-gesture incongruence.

3.2.4 Electroencephalographic recording

The EEG was continuously recorded from 128 scalp sites at a sampling rate of 512 Hz by means of ANT-EEprobe 3.1. system. Horizontal and vertical eye movements were also recorded. Linked ears served as the reference lead. The EEG and electro-oculogram (EOG) were amplified with a half-amplitude band pass of 0.016–100 Hz. Electrode impedance was kept below 5 kΩ (Fig.3.2).

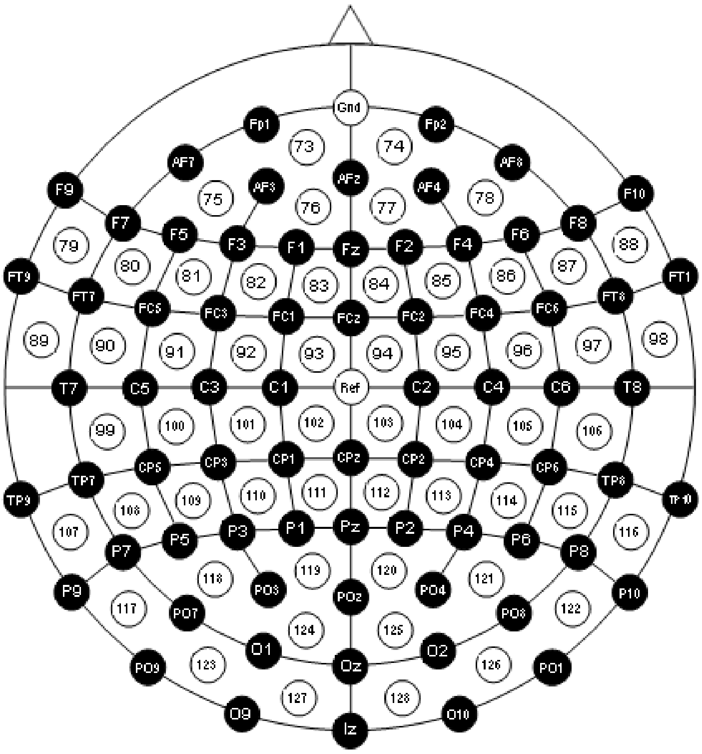

Fig.3.2. EEG recording layout, with 128 electrodes distributed over the whole surface.

3.2.5 Statistical analyses of ERPs

Computerized artefact rejection was performed before averaging to discard epochs in which eye movements, blinks, excessive muscle potentials or amplifier blocking occurred. The artefact rejection criterion was peak-to- peak amplitude exceeding 50 μV, and the rejection rate was 5%. EEG epochs were synchronized with the onset of stimuli presentation. Evoked-response potentials (ERPs) were averaged off-line from 100 ms before through 3000 ms after stimulus onset. ERP components were identified and measured with respect to the baseline voltage, which was averaged over the pre-stimulus interval from -100 ms to 0 ms.

As mentioned above, each movie clip lasted 3 seconds but during the first second the musician just prepared his position to perform the sound. Therefore, the real sound-gesture stimulus started 1000 ms after the onset of the video clips.

The choice of electrode sites and time windows for measuring and quantifying ERP components of interest was based on previous literature. The peak latency of the N170 response was measured at occipital-temporal sites (PPO9h, PPO10h) in the 150–200 ms time window. The mean amplitude of the N400-like response was measured at the fronto-central sites (FCz, Cz, and CPz) in the 1500–2000 ms (500-1000 ms *post-sound stimulation*) time window (Table 3.1).

Different repeated-measures ANOVAs were carried out on ERP latency and amplitude values relative to occipito-temporal N170 and N400 responses. The factors of variance included 1 between-group factor (Groups: musicians, naive subjects) and 3 within-group factors: Instrument (own instrument, other instrument), Condition (congruent, incongruent), Electrode (depending on the ERP component of interest), and Hemisphere (left, right). Multiple comparisons of means were performed by means of the post- hoc Fisher's tests.

In this experiment source analysis was performed according to the swLORETA method (standardized and weighted Low Resolution brain Electromagnetic Tomography) with ASA software (ANT Software BV). A detailed description of the swLORETA has been provided in the previous chapter. swLORETA was applied by subtracting ERPs of Own Instrument congruent videos from Own Instrument Incongruent videos in the in the 500–1000 (post-sound stimulation) time window.

ERP COMPONENT	TIME WINDOW	ELECTRODES
N170	150–200 ms	PPO9h, PPO10h
N400	1500–2000 ms	FCz, Cz, and CPz

Tab. 3.1. ERP components of interest for the present study

3.3 Results

3.3.1 Behavioral results

ANOVA (F 1, 27 = 0.28; $p > 0.05$) performed on accuracy did not revealed any statistical differences between the two groups. In addition, the percentage of errors was very low (below 2%) in both groups. ANOVA performed on response times indicated longer RTs ($p < 0.02$) in musicians (2840 ms, 1840 post-sound latency, SE = 81.5) than controls (2614 ms, 1641 post-sound latency, SE= 81.5).

3.3.2 Electrophysiological results

Occipito-temporal N170 (150-200 ms)

The ANOVA computed on the latency of the posterior N170 component showed a significant main effect of Hemisphere (F 1, 22 = 11.36; $p < 0.05$), revealing faster N170 latencies over the LH (173 ms, SE = 2.1) compared to the RH (180 ms, SE = 2.5). The ANOVA revealed also the significance of Group (F 1, 22 = 9.2; $p < 0.05$): post-hoc comparisons indicated faster latencies of the N170 response in Musicians during the presentation of his/her Own instrument videos (164 ms, SE = 3.9) compared with the Other Instrument videos (176 ms, SE = 4.2; p < 0.05) and compared with controls (183 ms, SE = 4.1; p < 0.05) (Fig. 3.3).

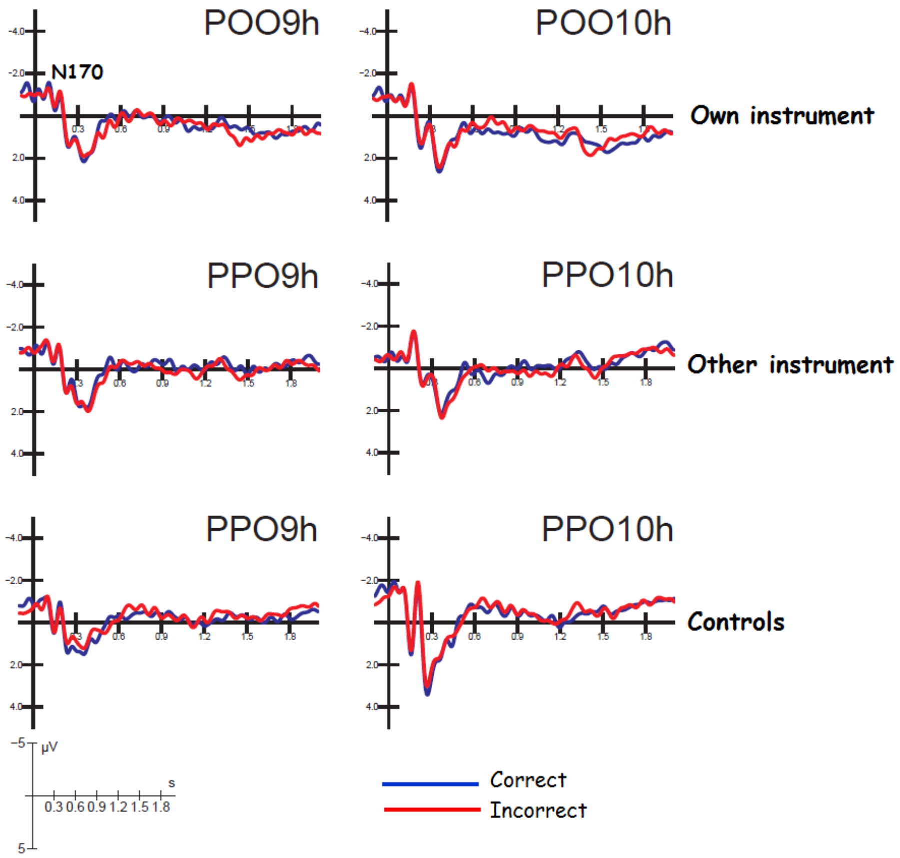

Fig. 3.3. Grand-average ERPs recorded at posterior sites in response to Congruent (blue line) and Incongruent (red line) stimuli in the three groups.

N400 (500-1000 ms post-sound stimulation)

ANOVA computed on the mean amplitude of the N400-like component revealed a significant main effect of Electrode (F 2, 44 = 7.78; p < 0.01), indicating that the negative deflection reached its maximum amplitude over the anterior sites (Fcz = -1.89 µV, SE = 0.42) compared with the central (Cz = -1.78 µV, SE= 0.44) and centroparietal (Cpz = -1.25 µV, SE= 0.42) sites (Fig.3.4). ANOVA also revealed a significant main effect of Condition (F 1, 22 = 7, 35; p < 0.05) showing a greater N400 amplitude in response to Incongruent videos (21.84 µV, SE = 0.42) compared to Congruent videos (21.44 µV, SE = 0.42). In addition, the significant

Electrode x Group interaction (F 2, 44= 3.25; $p < 0.5$) showed a larger N400 response over the anterior sites in the control group (Fcz = -2.79 μV, SE = 0.60; Cz = -2.25 μV, SE = 0.62; CPz = -1.86 μV, SE = 0.60) compared to the musicians (Fcz = -0.99 μV, SE = 0.60; Cz = -1.31 μV, SE = 0.62; CPz = -0.64 μV, SE = 0.60). Furthermore, the significant Instrument x Condition x Group interaction (F 1, 22 = 11, 73 $p < 0.05$) revealed that the N400 amplitude was strongly modulated by Condition only in musicians. Moreover, post-hoc comparisons indicated significant N400 enhancement in response to Incongruent (-0.86 μV, SE = 0.74) vs. Congruent Own instrument videos (-0.23 μV, SE= 0.76). Finally, no significance differences was observed in musicians in response to Incongruent (-1.53 μV, SE= 0.67) vs. Congruent Other instrument videos (-1.31 μV, SE= 0.63).

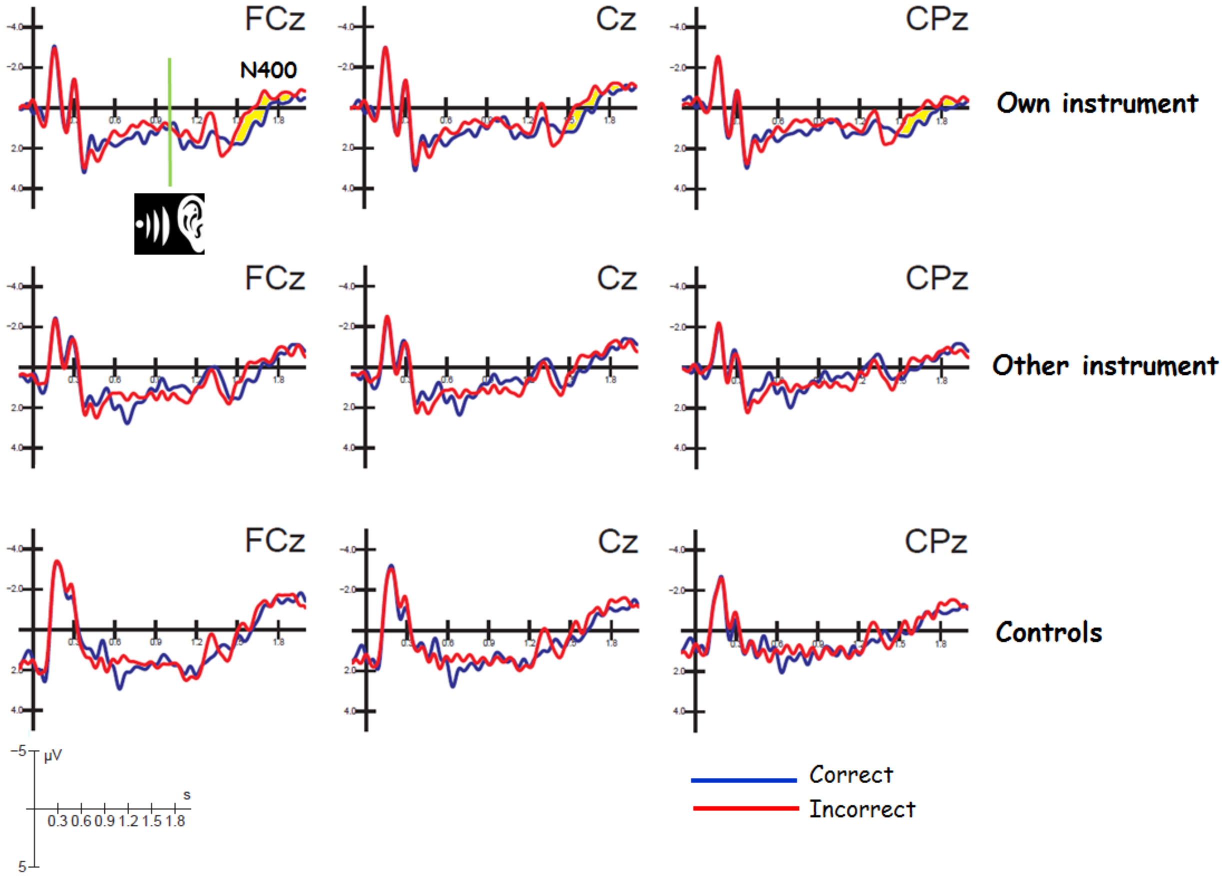

Fig. 3.4. Grand-average ERPs recorded at anterior, central and posterior sites in response to Congruent (blue line) and Incongruent (red line) stimuli in the three groups.

3.3.3 Source localization results

To investigate the neural mechanism enabling the musicians to discriminate a correct from an incorrect sound-gesture stimulus, a swLORETA inverse solution was applied by subtracting ERPs of Own Instrument Congruent videos from Own Instrument Incongruent videos in the in the 500–1000 (post-sound stimulation) time window.

The list of dipoles (Table 3.2) indicated a source of activation located in Left and right superior frontal gyrus (BA 10), the right superior temporal cortex (BA 38) and the middle temporal gyrus (BA21), the premotor cortex (BA6), the inferior frontal area (BA 44) and the inferior parietal lobule (BA 40) (Fig.3.5).

Table 3.2 | Talairach coordinates (in mm) corresponding to intracranial generators explaining the N400 surface difference-voltage. ERPs of Own Instrument Congruent videos are subtracted from ERPs of Own Instrument Incongruent videos in the post-sound 500–1000 ms time window in musicians (Power RMS = 51.8 μV)

Musicians

Magn.	T-x [mm]	T-y [mm]	T-z [mm]	Hemisph.	Lobe	Gyrus	BA
11.38	-8.5	64.4	16.8	L	F	Superior Frontal Gyrus	10
11.05	-28.5	53.4	24.8	L	F	Superior Frontal Gyrus	10
9.46	40.9	55.3	7	R	F	Middle Frontal Gyrus	10
8.08	50.8	-0.6	-28.2	R	T	Middle Temporal Gyrus	21
7.59	31	9.1	-27.5	R	T	Superior Temporal Gyrus	38
7.23	60.6	-55	-17.6	R	O	Fusiform Gyrus	37
7.02	50.8	-33.7	-23.6	R	T	Fusiform Gyrus	20
6.82	-38.5	-8	-28.9	L	T	Middle Temporal Gyrus	21
6.77	-58.5	-8.7	-21.5	L	T	Inferior Temporal Gyrus	20
6.07	40.9	-75.2	-19.1	R	Cerebellum		
7.08	-18.5	-8	-28.9	L	Limbic	Uncus	36
4.76	-58.5	-30.4	34.9	L	Pariet	Inf. Parietal Lobule	40
4.31	21.2	-91.3	29.7	R	Occip	Cuneus	19
3 .9	1 .5	-85 .4	-19,8	R	Cerebellum		
3.88	-8 .5	-1 .1	65	L	F	Superior Frontal Gyrus	6
3.55	-58 .5	14 .3	12 .5	L	F	Inferior Frontal Gyrus	44
2.94	-18 .5	-63 .8	59	L	P	Superior Parietal Lobule	7
2.37	11 .3	29 .5	58 .7	R	F	Superior Frontal Gyrus	6

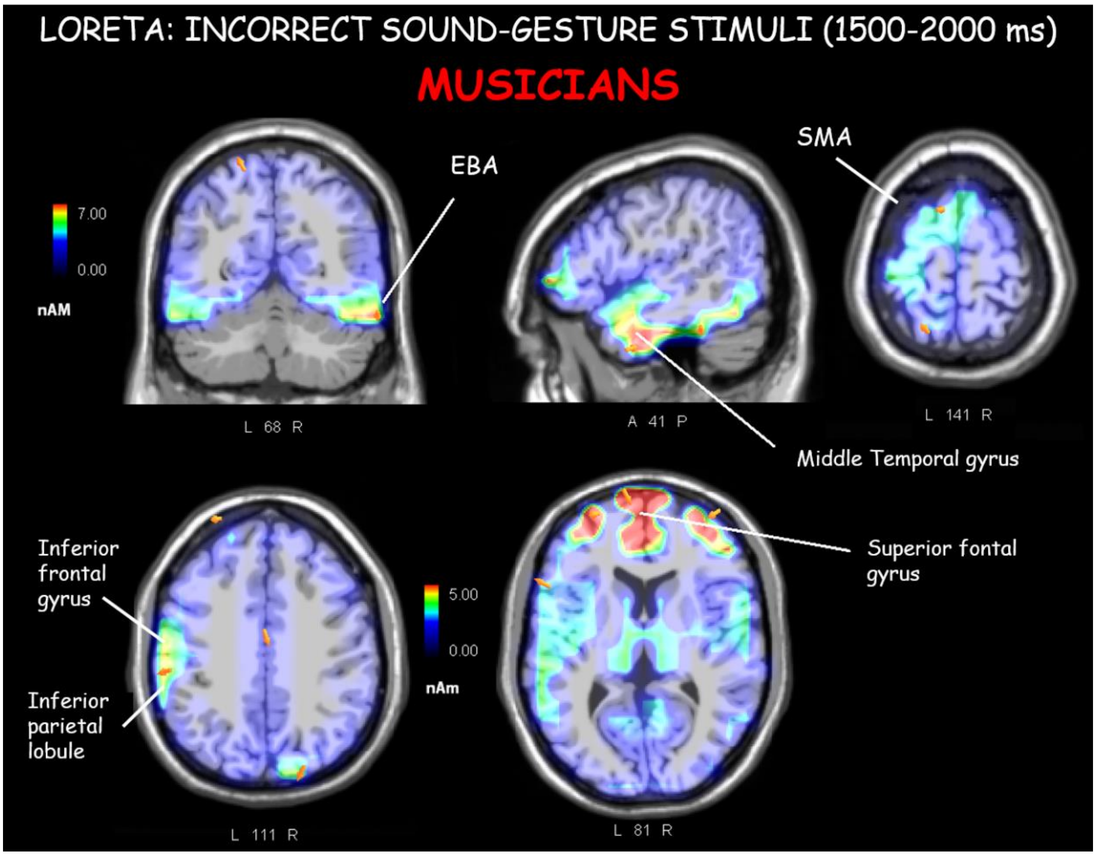

Fig. 3.5. Coronal, Sagittal and Axial views of N400 active sources for the processing of incongruent sound-gesture stimuli according to swLORETA analysis during the 500–1000 (post-sound) time window. The different colors represent differences in the magnitude of the electromagnetic signal (in nAm). The electromagnetic dipoles are shown as arrows and indicate the position, orientation and magnitude of dipole modelling solution applied to the ERP waveform in the specific time window.

3.4 Discussion

In this study, we explored the semantic processing related to a specific skill learned by imitation and exercise. In particular, we investigated how a long lasting musical training affected the N400 amplitude to semantic violation when stimuli are presented via audiovisual modality. Indeed, in this study, we focused on the effects of the integration of auditory and visual stimuli on the N400 response.

To this aim, we presented 198 congruent and 198 incongruent musical video clips to 12 musicians and 12 naïve viewers while their EEG was recorded. In the videos, a clarinetist and a violinist played the same score with their own instruments. The sounds were similar in pitch, intensity, rhythm and duration. To make the task feasible to all groups, the participants had to discriminate a 1-note vs. 2-note execution by pressing one of two buttons.

According to our hypothesis, if the ability to recognize a semantic violation were mediated by the experience, we would have expected to observe a greater N400 response to incongruent video clips only in musicians and only to videos related to their own instrument.

The behavioral results did not show any effect of audiovisual congruency on behavioral performance in the three groups. In addition, the ANOVA performed on response times revealed that musicians were slower than controls, probably because of their musical advanced knowledge.

The electrophysiological results showed faster latencies of the N170 response in musicians than controls during the presentation to Their Own Instrument videos compared with the Other Instrument videos. Previous studies showed that the N170 component is enhanced for classes of objects (picture, words, faces) for which viewers have visual expertise (Rossion et al, 1999a, 1999b; Proverbio et al., 2007; Proverbio et al., 2009; Proverbio et al., 2013; Tanaka and Curran, 2001). Therefore, the result found in this study might indicate an effect of visual familiarity for the musical instrument.

Furthermore, the analysis revealed an enlarged N400 response at the anterior frontal sites in the 500–1000 ms post-sound stimulation time window (i.e. 1500-2000 ms post-stimulus) only in musicians' brains and only for videos of Their Own Instrument. Previous studies, focusing on the integration of auditory and visual stimuli, have found that semantically inconsistent speech, natural sounds with pictures or videos could elicit N400 effects (Plante et al., 2000; Puce et al. 2007; Cummings et al., 2008; Liu, 2011). For example, in a recent ERP study, Liu and colleagues (2011) investigated the integration of natural or non-natural auditory and visual information by presenting videos of real-world events with semantically consistent or inconsistent natural sound or speech. For instance, a video of festive fireworks exploding in the sky was paired with the consistent/inconsistent sound or verbs (recorded as speech by a male voice reading). Videos with inconsistent natural sound/speech elicited N400-P600 effects compared to videos with consistent natural sound/speech.

It is important to notice that these previous studies investigated semantic violations related to the so-called ‘world knowledge’ that includes human actions in ecological environments or real-word events (Proverbio & Riva, 2009; Hagoort et al., 2004). Differently, we focused on the effects of experiences shaped by a specific long-lasting musical training. With regard to this topic, the results of the study described in chapter 2 showed that the N400 response is sensitive to semantic violations in visual processing of actions related to sport training. In particular, we observed that the N400 amplitude to violations was a function of the observers’ expertise. In the present study, we introduced the effect of multisensory presentation on the processing of semantic violations in skilled and unskilled brains. In light of these evidences, the N400 effect to incongruent sound-gestures pairs in musicians might indicate that only skilled brains were able to recognize an action-sound violation. In addition, we observed that this effect occurred only in musicians for videos of Their Own Instrument. This result strengthens the idea that the ability to detect a semantic violation is strongly modulated by the proficiency within a specific context.

Finally, a swLORETA inverse solution was applied by subtracting ERPs of congruent videos of Own Instrument from incongruent videos of Own Instrument in the 500–1000 (post-sound stimulation) time window. The results revealed a strong source of activation in the premotor cortex (BA6), the inferior parietal lobule (BA40) and the inferior frontal area (BA44). Previous studies showed that these regions play a role in action recognition and understanding and, consequently, they could be considered part of the Human mirror neuron system (MNS) (Hamilton et al., 2008; Rizzolatti et al., 1996; Iacoboni et al., 2005; Pelphrey et al., 2004; Saxe et al., 2004).

We can observe that this pattern of brain activation is very similar to that observed in basketball players during the processing of incongruent actions (see chapter 2). Moreover, Calvo and colleagues (2005) found similar results during an fMRI study in which they investigated whether the brain processes related to action observation are modulated by the expertise and motor repertoire of the observer. To this aim, videos of ballet or capoeira actions were presented to groups of ballet dancers, capoeira dancers and inexpert control subjects. The authors contrasted the brain activity when dancers watched their own dance style versus the other style. They found greater bilateral activations in premotor cortex and intraparietal sulcus, right superior parietal lobe and left posterior superior temporal sulcus when expert dancers viewed movements that they had been trained to perform compared to movements they had not.

Recently, Lahav and colleagues (2007) conducted an fMRI study to investigate whether the human action-recognition system (MNS) responds also to sounds found in a more complex sequence of newly acquired actions. To test this hypothesis, they trained a group of nonmusicians to play a piece of music by ear. Afterwards, they monitored brain activity in subjects while they listened to the newly acquired piece. They found a pattern of brain activation that included the Broca's area, the premotor region, the intraparietal sulcus, and the inferior parietal region (regions considered to be part of the MNS). Moreover, they observed that the presentation of the practiced notes in a different order activated the network to a much lesser degree, whereas listening to an equally familiar but motorically unknown music did not activate this network. According to the authors, these findings suggested the existence of a "hearing–doing" system, highly dependent on the individual's motor repertoire.

In light of these evidences and given the similar pattern of brain activations, we can consider the N400 effect observed in this study in musicians as the electrophysiological manifestation of a “hearing–doing” system related to non-verbal long-lasting gesture-sound learning.

In addition, swLORETA showed the activation of the superior temporal gyrus (BA38), a region involved in sound perception (Beauchamp et al., 2004b) and the activation of the superior and middle frontal gyrus (BA10). Previous studies revealed that this latter area might be related to an involuntary attentional orientation to visual/sound discrepancies at pre-perceptual level (Giard et al., 1990; Rinne et al., 2000).

Finally, swLORETA revealed a focus of activation in the fusiform gyrus that includes the extrastriate body area (EBA, BA37) involved in the visual perception of the body parts, and fusiform face area (FFA) (Grill-Spector et al., 2004) and the fusiform body area (Schwarzlose et al., 2005), involved in human faces and bodies processing.

In conclusion, the results of this study demonstrated that only expert musicians were able to detect the semantic violation of audiovisual information learned through a long-lasting musical training. In addition, the data revealed that the semantic violations related to a motor musical repertoire affected the N400 amplitude even when stimuli are presented using a multisensory modality. Finally, swLORETA indicated that a specialized cortical network in musicians might be involved in the sound-gesture pairs processing, as a result of musical training.

4. When a hit sounds like a kiss: an electrophysiological exploration of semantic processing in visual narrative

[This research has been carried out in collaboration with Neil Cohn and Marta Kutas]

4.1 Introduction

In this work, we investigated the processing of semantic violations associated to words that evoked specific sounds in comics. As we described in chapter 3, previous electrophysiological studies investigated semantic violations to stimuli presented through a multisensory modality. The results of these studies revealed a great N400 response to semantic incongruities related to multisensory information (Plante et al., 2000; Puce et al. 2007; Cummings et al., 2008; Proverbio et al., 2014).

Some other studies have investigated the semantic processing to different stimuli that are both visually presented. For example, some of them contrasted the semantic processing related to words and pictures. In 1992, Nigam and colleagues carried out an ERP study in which they compared the processing of words and pictures in a sentence reading task. They wanted to investigate whether the N400 response was related specifically to activity in a language system or it could be considered an index of a common semantic system (Morton & Patterson, 1980; Riddoch et al., 1988; Nelson et al., 1977; Potter & Faulconer, 1975; Seymour, 1973; Durso & Johnson, 1979; Snodgrass, 1984; Theios & Amrhein, 1989) that is accessed by both types of stimuli. In this study one group of subjects read sentences that ended with congruous or incongruous words and a different group of subjects read sentences that ended with congruous or incongruous pictures. The results showed that the N400 recorded in the Pictures Condition was identical to the N400 elicited by words in terms of amplitude, scalp distribution, and latency. These results might suggest that the N400 is an index of the activity in an amodal semantic system (Nigam, 1992).

In a similar study, Ganis and colleagues (1996) performed an ERP investigation using a paradigm that combined words and pictures presentation. As in the previous work, the goal of this study was to investigate whether or not words and pictures access a common semantic system. To this aim, they presented sentences, one word at a time, to a group of 28 undergraduates. Each sentence ended with a written word or a picture. Both pictures and word could be semantically congruous or semantically incongruous with the sentence. Results showed that both words and pictures generated a greater N400 response to incongruous relative to congruous sentence endings. They noticed that pictures and words elicited a different scalp distributions: the N400 effect for words was larger posteriorly than it was for pictures. Also, the N400 response to pictures was associated with a longer duration negativity over frontal sites. The authors concluded that written words and pictures when they terminate sentences are processed similarly, but not by identical brain areas.

The studies described so far investigated the semantic analysis by embedding words and pictures into sentence contexts. In addition, the comprehension of the critical stimuli (words or pictures) did not require inference processing for the integration in the previous sentential context.

In most naturalistic pictorial contexts, including most comic strips, some written stimuli evoke auditory information. This is the case of a particular class of words called *onomatopoeia*

(Fig. 4.1). According to the definition by Webster (1964) an onomatopoeic word phonetically imitates or suggests the source of the sound that it describes.

In 2005, Han and colleagues conducted an fMRI study to examine the neuroanatomical areas related with onomatopoeia and phainomime (a particular class of Korean words) word recognition. The two types of words were visually presented while participants performed a lexical decision task (to avoid habituation effects during fMRI scanning). The results showed that the onomatopoeic word recognition activated the bilateral occipital lobes and superior midtemporal-gyrus, whereas the phainomime words recognition activated left SMA and bilateral cerebellum as well as bilateral occipital lobes.

Fig.4.1. Example of onomatopoeia in comics

Onomatopoeias and sound effects have long been a staple of comics, particularly those featuring superheroes and other action figures. Furthermore, if only the sound effect is provided, without depicting their associated actions, its comprehension can potentially generate inferential processing. In this context, the presentation of the onomatopoeic word could require the generation of inferences for understanding an undepicted event.

Often times, onomatopoeic sounds in comics accompany actions star, a conventionalized star shaped “flash” presented in comic strips that usually indicates the culmination of an event (Fig. 4.2).

Fig.4.2. Example of onomatopoeic sound and action star in *Peanuts* comic strips.

In visual narrative, the climax of a sequence is represented by a narrative "Peak" (Cohn, 2013a). According to the theory of *Narrative Grammar of sequential images*, each image plays a categorical role based on its narrative function within the overall visual sequence. The basic categories of Visual Narrative Grammar are: Establisher (E), that sets up an interaction without acting upon it; Initial (I), that initiates the tension of the narrative; Prolongation (L), marking a medial state of extension, often the trajectory of a path; Peak (P), that marks the height of narrative tension and point of maximal event structure; Release (R), in which the tension of the interaction is released (Cohn, 2013a, 2013b, 2014).

The action star panel in comics could replace different types of actions in a representation. However, because action stars show a large "flash" of an event, we know that an action takes place, in particular a violent and sudden action, but we do not know anything more than this. This generalized quality means that this panel typically replaces a Peak panel, that represent culmination of events. However, because action stars do not show the actual events that take place, this information must be inferred from the contents of the surrounding panels (Cohn, 2013a).

In a previous experiment, Cohn (Cohn, under review) examined action stars' structural and inferential roles in a visual narrative sequence by comparing viewing times between sequences with coherent Peaks, action stars, blank panels, and anomalous Peaks. The results of this study revealed that Coherent Peaks were always viewed faster than anomalous Peak, while action stars and blank panels were viewed considerably faster than both coherent and anomalous Peaks. According to the author, this difference was likely due to the amount of visual information between these panels: action stars and blank panels had less visual information than coherent and anomalous Peaks.

Moreover, action stars were viewed significantly faster than blank panels at the critical panel position, despite being more visually rich. The author sustained that these shorter viewing times could suggest that action stars play a felicitous functional role in the narrative at the Peak position. Furthermore, panels following action star panels were as slow as panels following blank panels and anomalous Peaks. The author concluded that, overall, these results were consistent with the idea that action stars play a structural role as Peaks in the narrative grammar and motivate the generation of inference for their undepicted events.

In light of these results, we investigated the integration of sounds and pictures when both stimuli are presented in the same visual modality by using written onomatopoeia. We thought that using text within action stars of visual narratives would have allowed us a way to investigate multimodal processing facilitated by stimuli presented in the same sensory modality, avoiding the effect of a multisensory presentation on the semantic processing. We therefore used action stars to investigate how inferences are drawn from complex situations that may not be visible, and whether those inferences would vary based on their congruity with the narrative sequence. According to our hypothesis, if an onomatopoeic word evoked the representation of an implied event relative to the previous visual narrative, it should activate that associated, yet unseen, semantic information. Moreover, we might expect a different brain response depending on how congruous the onomatopoeic word is with the context of the preceding narrative.

To test these hypotheses, the brain activity during the presentation of 100 wordless *Peanuts* comic strips was analyzed in 28 University students with experience in reading comics. We recorded EEG to critical images where the climactic image of each strip was replaced with action star panels containing four different types of words: Onomatopoeic panels contained an onomatopoeic word coherent with the context (“Pow!”), Descriptive panels included a word describing the hidden action (“Impact!”), Anomalous panels used an onomatopoeic word incoherent with the context (“Smooch!”), and “Grawlix” panels used strings of symbols used in comics to represent swearwords (Walker 1980) (“$#@&!?”).

4.2 Methods

4.2.1 Participants

Twenty-eight right-handed (Oldfield, 1971) undergraduate students (12 males) were recruited from the University of California, San Diego. Participants were native English speakers between 18 and 27 years of age (M = 20.9, SE = 1.92). Participants had normal or corrected-to-normal vision, and reported no major neurological or general health problems or psychoactive medication use. Each participant provided written informed consent prior to the experiment and received course credit and/or $7/h for participating.

Participants' comic reading fluency was assessed using a questionnaire (VLFI) that asked participants to self-rate the frequency with which they read various types of comics, read books for pleasure, watched movies, and drew comics, both currently and while growing up. In this study, participants had a mean comic-reading fluency of 17.82 (SE = 6.36). An idealized average VLFI score would be 12, with low being below 7 and high above 20 (Cohn et al., 2014). All participants knew Peanuts.

4.2.2 Stimuli

Graphic sequences were created using black and white panels scanned from the Complete Peanuts volumes 1 through 6 (1950–1962) by Charles Schulz (Fantagraphics Books, 2004–2006). Peanuts comics were chosen because (1) they have systematic panel sizes and content with repeated characters and situations; (2) their content is recognizable to most people; (3) there is a large corpus of sequences to draw from; and (4) they feature fairly consistent and recurrent themes (various sports, building snowmen, Lucy skipping rope, Linus and Snoopy fighting over a blanket, etc.).

One hundred coherent four-six-panel long Normal sequences were created. Standard daily Peanuts strips are four panels long. We created novel four-six-panel experimental sequences by combining panels from existing comic strips, to ensure that any familiarity with specific Peanuts strips would not lead to episodic memory effects on the Normal sequences. In order to eliminate any influence of written language on comprehension, we used panels without text, or panels where text was deleted in Adobe Photoshop. All panels were adjusted to a single uniform size.

Normal sequences related to a common semantic theme: baseball, football, golf, piano playing, kite flying, weather (snow, rain, sunshine), seasonal activities (making snowmen, throwing snowballs, leaves falling off trees, etc.), and others.

All sequences had a coherent narrative structure (the basic canonical pattern of Establisher-Initial-Peak-Release), as defined by Cohn's theory (Cohn, 2013a). Across the normal sequences, the climactic image (Peak) of each strip was replaced with action star panels containing four different types of words: Onomatopoeic panels contained an onomatopoeic word coherent with the context ("Pow!"), Descriptive panels included a word describing the hidden action ("Impact!"), Anomalous panels used an onomatopoeic word incoherent with the context ("Smooch!"), and "Grawlix" panels used strings of symbols used in comics to represent swearwords ("$#@&!?") (fig.4.3).

Therefore, we considered four conditions (Onomatopoeic, Descriptive, Anomalous and Grawilix).

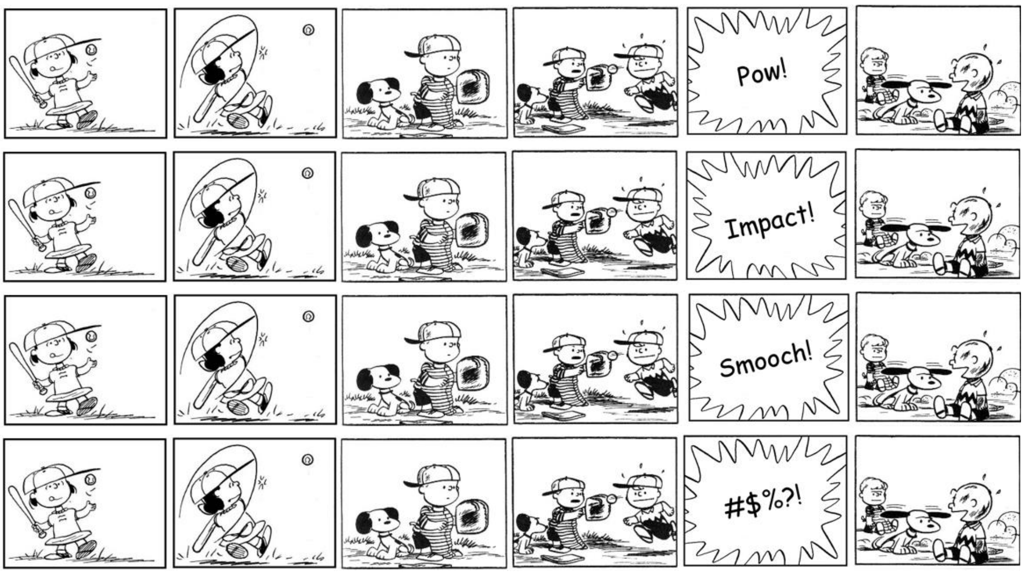

Fig. 4.3. Exemplars of pictures used as stimuli in the Onomatopoeic (firs row), Descriptive (second row), Anomalous (third row) and Grawlix strips (fourth row).

Onomatopoeic, Descriptive, Anomalous and Grawlix strings, used in the action star panel, have been balanced in terms of length, varying between 3 and 13 characters. The number of the characters has been multiplied for their frequency of appearance across the words in each condition (i.e. if three-character words were present nine times in the Onomatopoeic condition, we will have 9x3=27). An ANOVA (F 2, 18=.33; $p > 0.5$) revealing that the average values (number of characters x their frequency) were not significantly different across the conditions (Onomatopoeic =53.4, SD =20.7; Descriptive = 49, SD = 15.31; Grawlix = 59.8, SD = 15.2). In addition, the Onomatopoeic and Descriptive action star words were balanced in terms of orthographic neighborhood density (according to the CELEX database). An independent samples t-test revealed that the means of the two conditions were not significantly different ($p > 0.5$; Onomatopoeic = 4.6, SD = 4.56; Descriptive = 6.35, SD = 5.23). We also balanced the Onomatopoeic and Descriptive action star words in terms of number of repetitions (i.e. how many times a word appears in a condition) and an independent samples t-test showed that the average numbers of word repetitions were balanced across the two classes of stimuli ($p > 0.5$; Onomatopoeic = 3.13, SD = 1.28; Descriptive = 3.40, SD = 1.72). Finally, Onomatopoeic and

Descriptive words were not balanced in terms of frequency of the orthographic form according to the CELEX database. Indeed, an independent samples t-test revealed that the average values of the two conditions were significantly difference ($p < 0.01$; onomatopoeic = 4.13, SD = 7.18; descriptive = 56.44, SD = 70.07).

The stimulus set included 100 Strips (25 strips for condition), 100 action star panels, 596 panels for condition: 6 panels x 97 strips (582 panels), 5 panels x 2 strips (10 panels), 4 panels x 1 strip (4 panels). The action star panels appears in the second to the sixth panel positions, with equal numbers of action star panels at each position. There were also 100 fillers in each condition. A total of four lists (each consisting of 100 strips in random order) were created, with the four conditions counterbalanced across each list.

4.2.3 Procedure

The participants were tested in a single experimental session lasting about one hour. Participants were seated in front of a monitor in a sound-proof, electrically shielded recording chamber. Before each strip, a fixation cross appeared for a duration of ~1400 ms. Experimental and filler strips were presented panel-by-panel at the center of the computer screen. Each panel lasted ~1650 ms. When the strip concluded, a question mark appeared on the screen and participants had to evaluate if the strip was easy or hard to understand by pressing one of the two hand-held buttons (fig. 4.4). The response hand was counterbalanced across participants and lists.

The participants were familiarized with the stimulus presentation parameters and the task via a practice block of 4 strips. Feedback was provided to train them in this; as necessary, the practice block was repeated until they demonstrated high accuracy while fixating properly. Experimental and filler sentences were then presented in 5 blocks (two long and three short), with short breaks between blocks and a longer break halfway through the experiment. The participants were instructed not to blink or move during the experimental session. After the experiment, a post-test questionnaire asked participants to reflect on the nature of the sequences to see if they were consciously aware of any specific patterns or characteristics of the sequences they had viewed. The experiment had six sections and five breaks.

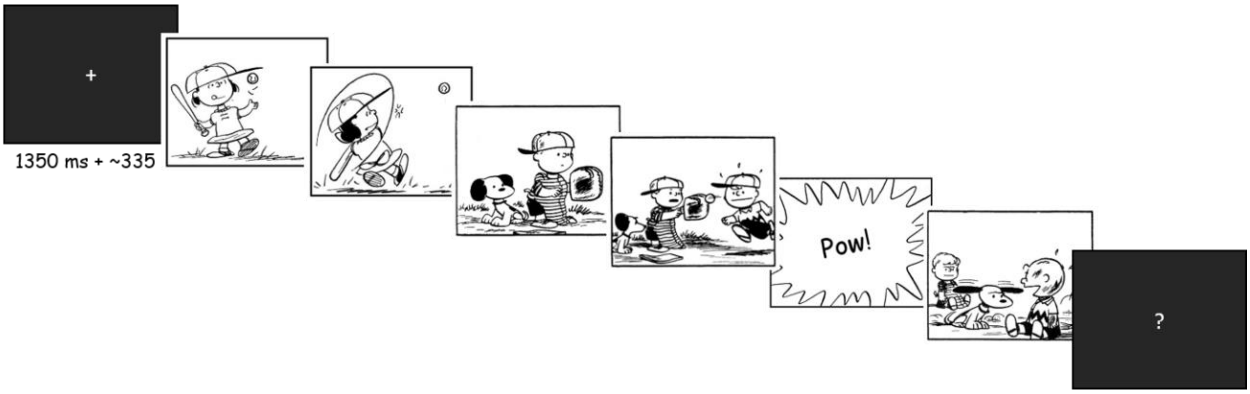

Fig.4.4. Task: participants were instructed to evaluate if the strip was easy or hard to understand by pressing one of the two hand-held buttons.

4.2.4 Electroencephalographic recording parameters

The electroencephalogram (EEG) was recorded from 26 electrodes arranged geodesically in an Electro-cap, each referenced online to an electrode over the left mastoid. Blinks and eye movements were monitored from electrodes placed on the outer canthi and under each eye, also referenced to the left mastoid process (fig. 4.5). Electrode impedances were kept below 5 KΩ.

The EEG was amplified with Grass amplifiers with a pass band of 0.01 to 100 Hz and was continuously digitized at a sampling rate of 250 samples/second.

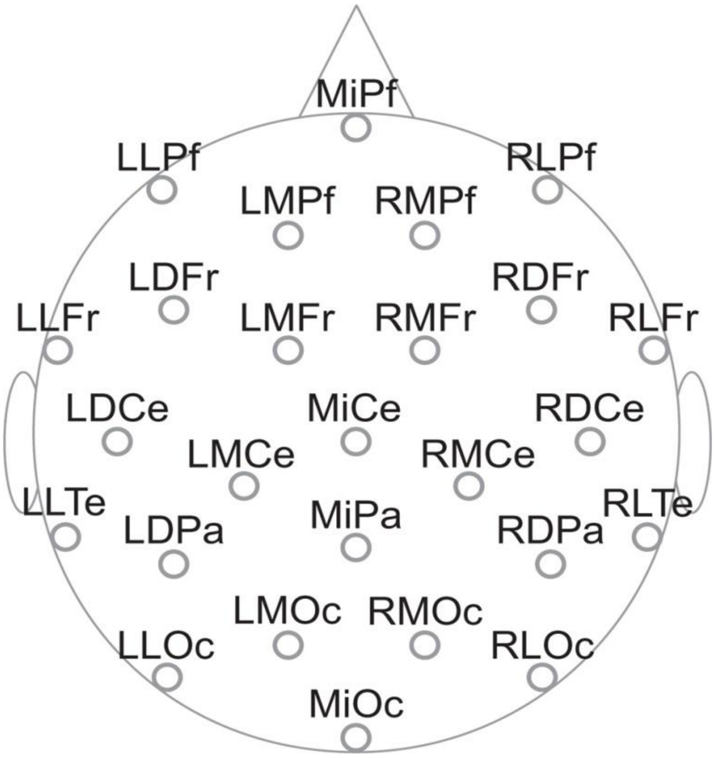

Fig.4.5. EEG recording layout, with 26 electrodes distributed over the whole surface.

4.2.5 Statistical analysis of ERPs

Trials contaminated by blinks, muscle tension (EMG), channel drift, and/or amplifier blocking were discarded before averaging. Approximately 9% of critical panel epochs were rejected due to such artifacts, with losses distributed approximately evenly across the four conditions. Individual participant averages were then averaged together to obtain a grand average ERP for each condition. To obtain ERPs for the four critical panel types, each participant's EEG was time-locked to critical panels. ERPs were computed for epochs extending from 500 ms before stimulus onset to 1500 ms after stimulus onset.

Three ERP components of interest were identified: an occipital lateral N2, a N400 and a Late Positivity Potential (LPP). The mean amplitude of the lateral-occipital N2 response was quantified at LLOc and RLOc electrode sites in the 150–250 ms time window. The mean amplitude voltage of the N400 response was measured at the MIPf, LMFr, RMFr, LMCe, MICe, RMCe, LDPa, MIPa, RDPa, LLOc, RLOc electrode sites in the 300–500 ms time window. The mean amplitude of the LPP was considered in the 600-800 ms time-window and measured on several electrodes (LMPf, MIPf, RMPf, LMCe, MiCe, RMCe, LDPa,MiPa, RDPa) (Tab. 4.1)

Mean amplitude of each component was analyzed by a repeated measures ANOVA with Condition (4 levels: Onomatopoeic, Descriptive, Anomalous, Grawlix) and Electrode sites (levels depending on the components). Multiple comparisons of means were performed by means of the post- hoc Fisher's tests.

ERP COMPONENT	TIME WINDOW	ELECTRODES
N2	**150-250 ms**	LLOc, RLOc
N400	**300–500 ms**	MIPf, LMFr, RMFr, LMCe, MICe, RMCe, LDPa, MIPa, RDPa, LLOc,
LPP	**600-800 ms**	LMPf, MIPf, RMPf, LMCe, MiCe, RMCe, LDPa,MiPa, RDPa

Tab. 4.1. ERP components of interest for the present study

4.3 Results

4.3.1 Behavioral results

The ANOVA performed on the Ratings of coherence showed that the sequences with anomalous action stars (60%, SE=0.02), were considered significantly less coherent (F 3, 81= 19.96, p<0.01) than the Onomatopoeic (77%, SE=0.02), the Descriptive (79%, SE=0.02) and the Grawlix (71%, SE=0.03). The sequences with the Grawilix (71%, SE=0.03) were considered significantly less coherent than the Descriptive (79%, SE=0.02) and Onomatopoeic strips (77%, SE=0.02), but more coherent than Anomalous (60%, SE=0.02). No differences were found between the Onomatopoeic and the Descriptive strips (fig.4.6).

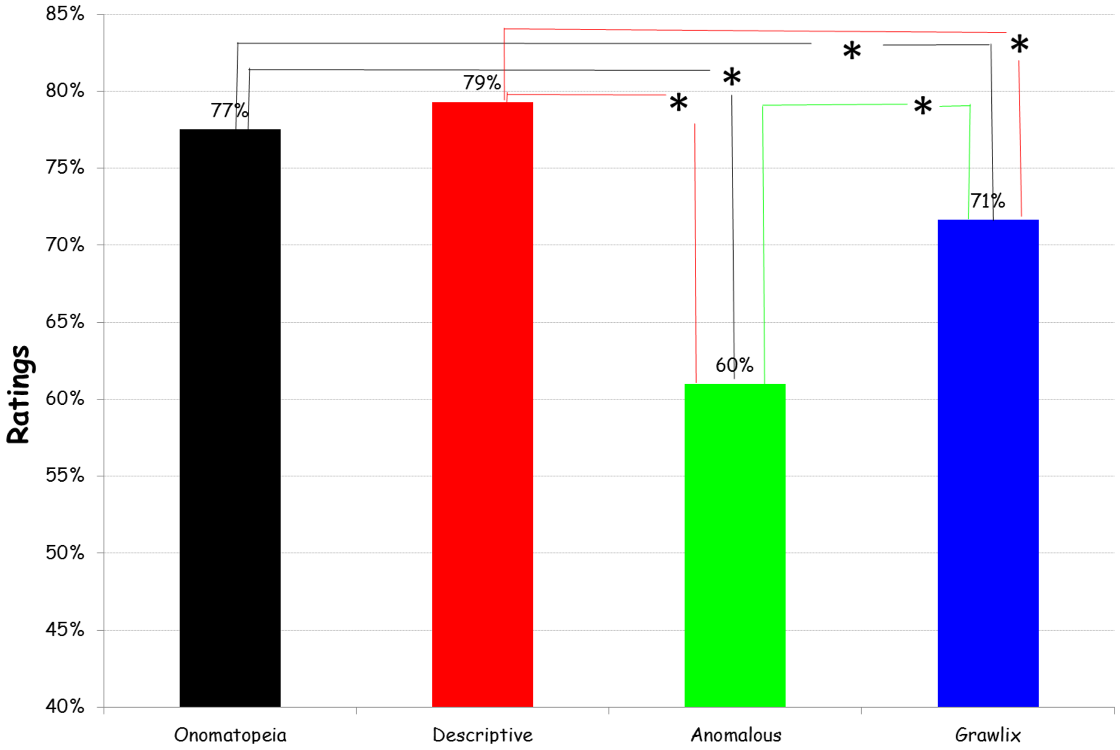

Fig. 4.6. Ratings of strips' coherence.

4.3.2 Electrophysiological results

N2 (150-250 ms)

The ANOVA computed in the first time window (150-250 ms) revealed a significant main effect of Hemisphere (F 1, 27 = 27.90, $p < 0.01$), showing a greater negativity over the left (3.76 µV, SE = 0.55) than the right hemisphere (5.57 µV, SE = 0.63). Moreover, the further significant interaction Condition x Hemisphere (F 3, 81) = 14.65; $p < 0.01$) revealed that, over the left hemisphere, the response was significant more negative to the Descriptive critical panel (3.02 µV, SE = 0.53) compared to the others (Onomatopoeic: 3.83 µV, SE = 0.56; Anomalous: 3.81 µV, SE = 0.60; Grawlix: 4.39, SE = 0.65). Conversely, the response to the Grawlix critical panel was significantly more positive ($p < 0.01$) than the others (Fig. 4.7).

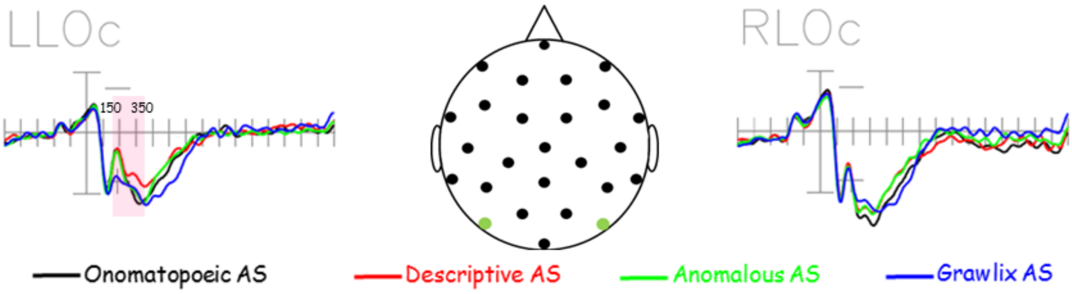

Fig. 4.7. Grand-average ERP waveforms recorded at occipital sites in response to Onomatopoeic (black), Descriptive (red), Anomalous (green) and Grawilx (blue) critical panels.

N400 (300-500 ms)

The ANOVA computed on the mean amplitude of the N400 (300–500 ms) component showed a significant main effect of Condition (F (3, 81) = 5.85, p<0.05), revealing a much greater amplitude responses to Anomalous critical panel than Onomatopoeic ($p < 0.05$; Anomalous = 1.13 µV, SE= 0.53; Onomatopoeic = 2.06 µV, SE= 0.64) and Grawlix ones ($p < 0.05$; Grawlix = 2.78 µV, SE= 0.74). No statistical differences were found between the Anomalous and the Descriptive critical panels (p = n.s.; Anomalous = 1.13 µV, SE= 0.53; Grawlix = 2.78 µV, SE= 0.74). Moreover, the N400 response was significantly greater to Descriptive and the Anomalous critical panels compared to Grawlix ones ($p < 0.05$; Anomalous = 1.13 µV, SE= 0.53; Descriptive = 1.40 µV, SE= 0.73; Grawlix = 2.78 µV, SE= 0.74). No statistical differences were found between the Onomatopoeic and the Descriptive critical panels and between the Onomatopoeic and the Grawlix critical panels.

The further significance of Electrode (F(10, 270) = 24.51; p<0.01) revealed a larger N400 potential at frontal sites (LMFr= -0.30 µV, SE=0.75; MiPf= -0.34 µV,SE=0.88; RMFr= -0.10 µV,SE=0.80) than central sites (LMCe = 0.96 µV, SE=0.72; MiCe = 0.04 µV, SE=0.81; RMCe = 1.17 µV, SE=0.80) and the parieto-occipital sites (LDPa = 2.92 µV, SE=0.57; MiPa = 2.71 µV, SE = 0.73; RDPa = 4.61 µV, SE=0.70; LLOc = 3.56 µV, SE = 0.53; RLOc = 5.14 µV, SE = 0.62). Moreover, the N400 response was greater on the left than the right sites only over the parieto-occipital sites ($p<0.01$; LDPa=2.92 µV, SE=0.57; RDPa=4.61 µV, SE=0.70; LLOc=3.56 µV, SE=0.53; RLOc=5.14 µV, SE=0.62). Moreover, the interaction Condition x Electrode (F (30, 810) = 5,66; $p < 0.01$) revealed that the difference between the Onomatopoeic and the Descriptive critical panels was significant over the MiPf (Onomatopoeic: 0.37 µV, SE = 1.18; Anomalous: -0.54 µV, SE = 1.07) and the LLOc (Onomatopoeic: 4.64 µV, SE = 0.59; Anomalous: 0.78 µV, SE = 0.77) and RLOc (Onomatopoeic: 6.04 µV, SE = 0.67; Anomalous: 3.44 µV, SE = 0.66) electrodes ($p < 0.05$).

The difference between the Onomatopoeic and the Anomalous critical panel was significant at all sites (except LMfr, RMfr, RDpa). Also, the analysis revealed that the difference between the Onomatopoeic and the Grawlix critical panel was statistically significant only over the LMCe (Onomatopoeic: 1 µV, SE = 0.72; Grawlix: 2.37 µV, SE = 0.87), MiCe (Onomatopoeic: 0.13 µV, SE = 0.88; Grawlix: 1.45 µV, SE = 0.95), RMCe (Onomatopoeic: 1.22 µV, SE = 0.87; Grawlix: 2.47 µV, SE = 0.98), LDPa (Onomatopoeic: 2.88 µV, SE = 0.60; Grawlix: 4.05 µV, SE = 0.70), and the MiPa sites (Onomatopoeic: 2.08 µV, SE = 0.90; Grawlix: 3.13 µV, SE = 0.99). The difference between the Descriptive and the Anomalous critical panel was significant only at MiPa (Descriptive: 1.43 µV, SE = 0.95; Anomalous: 4.20 µV, SE = 0.58), RDPa (Descriptive: 3.78 µV, SE = 0.84; Anomalous: 5.05 µV, SE = 0.62), LLOc sites (Descriptive: 3.61 µV, SE = 0.53; Anomalous: 0.78 µV, SE = 0.77), RLOc sites (Descriptive: 5.03 µV, SE = 0.68; Anomalous: 3.44 µV, SE = 0.66) sites. Finally, the difference between the descriptive and the grawlix and between the anomalous and the grawlix critical panels were significant at all sites (except MIPf) (Fig.4.8 and Fig. 4.9).

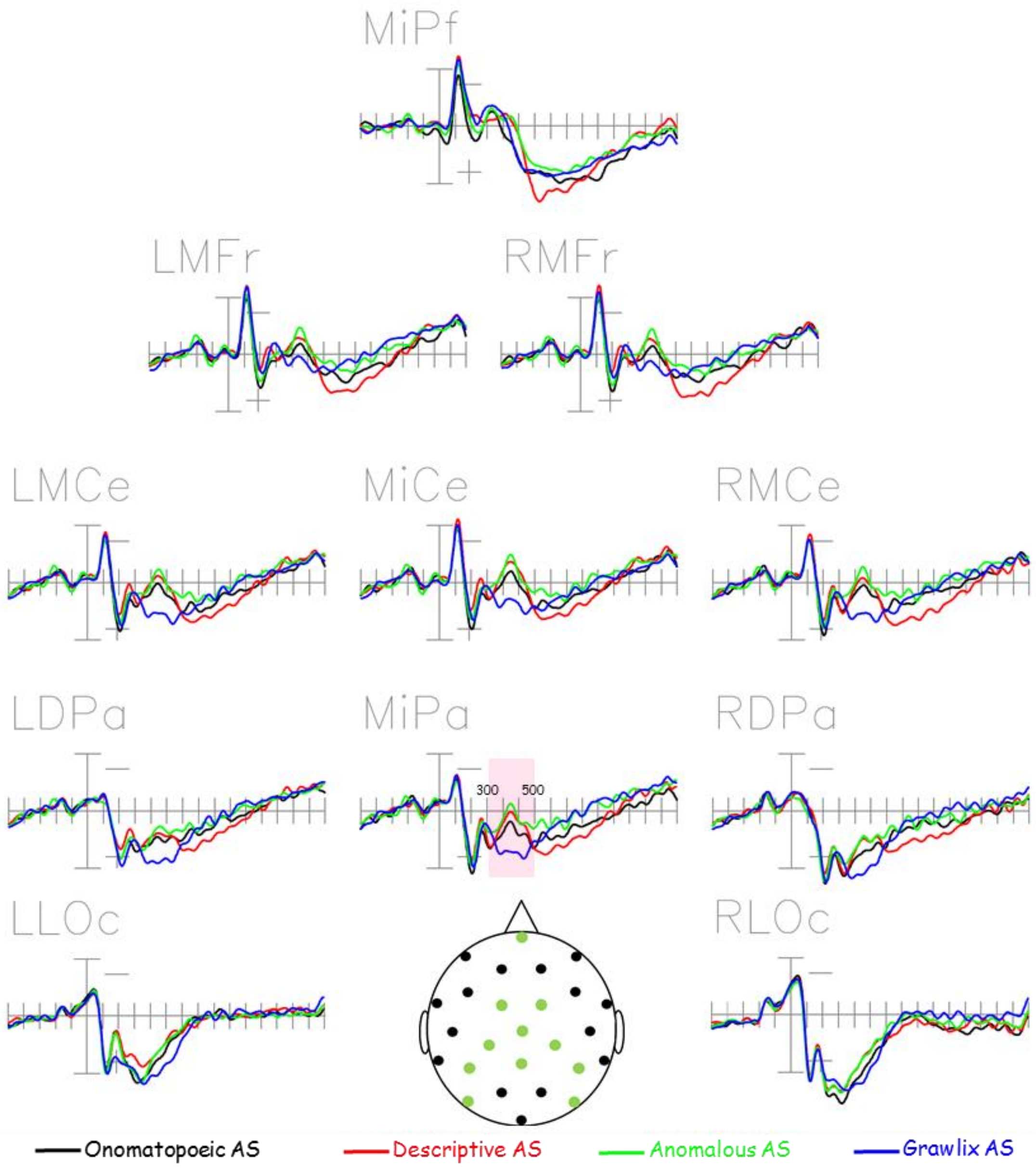

Fig. 4.8. Grand-average ERP waveforms recorded at frontal, central, parietal and occipital sites in response to Onomatopoeic (black), Descriptive (red), Anomalous (green) and Grawilx (blue) critical panels.

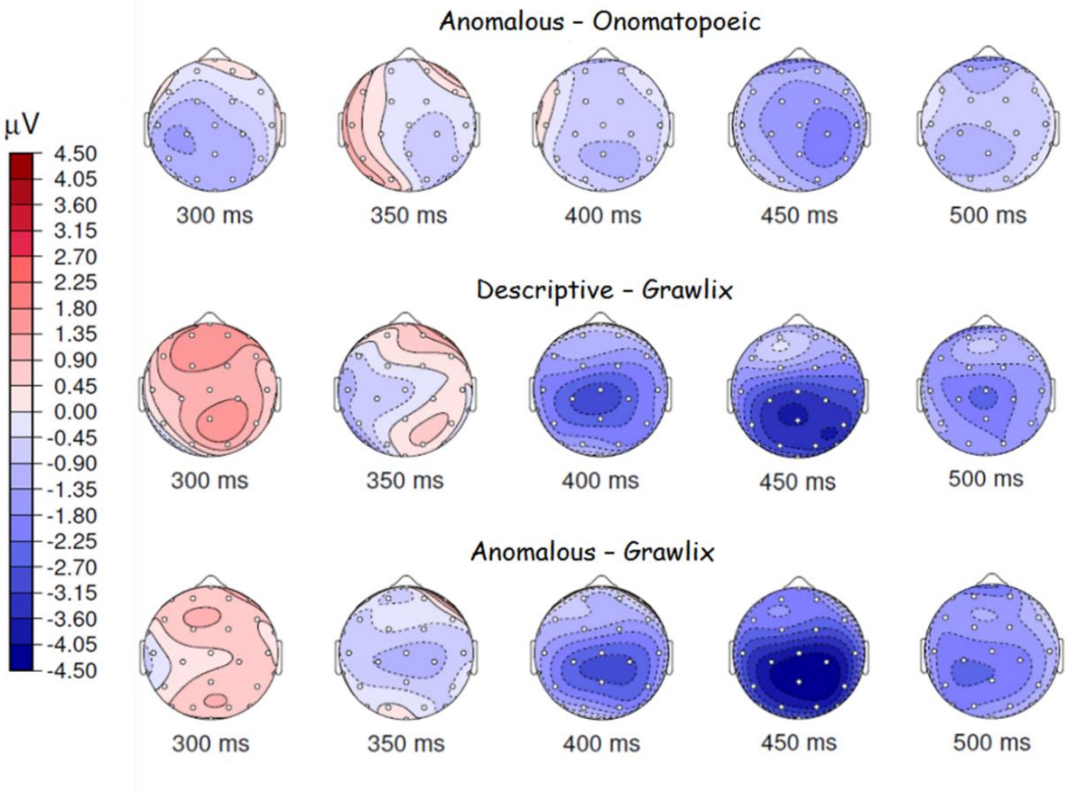

Fig. 4.9. Topographical difference maps performed by plotting difference voltages obtained by subtracting ERPs to anomalous from ERP to onomatopoeic critical panel (first row), descriptive from grawlix critical panel (second row) and anomalous from grawilx critical panel (third row) in the N400 latency range.

LPP (600-800 ms)

The analysis revealed that the late positivity component was significantly affected by Condition (F (3,81) = 4.92, p < 0.01) and was of greater amplitude in response to Descriptive critical panel (3.64 µV, SE = 0.76) compared to the others (Onomatopoeic: 2.28 µV, SE = 0.51; Anomalous: 1.57 µV, SE = 0.62; Grawlix: 2 µV, SE = 0.55).

In addition, data revealed a significant main effect of Electrode (F (8, 216) = 3.59, p < 0.01) that showed that the LP component was significantly more positive to MiPf (p < 0.01; 4.55 µV, SE = 1.22) compared to the other electrode sites (LMPf: 2.34 µV, SE = 0.75; RMPf: 2.42 µV, SE = 0.75; LMCe: 2.14 µV, SE = 0.47; MiCe: 1.90 µV, SE = 0.53; RMCe: 1.99 µV, SE = 0.48; LDPa: 1.95 µV, SE= 0.38; MiPa: 2.13 µV, SE = 0.43; RDPa: 1.90 µV, SE = 0.43) (Fig. 4.10 and 4.11).

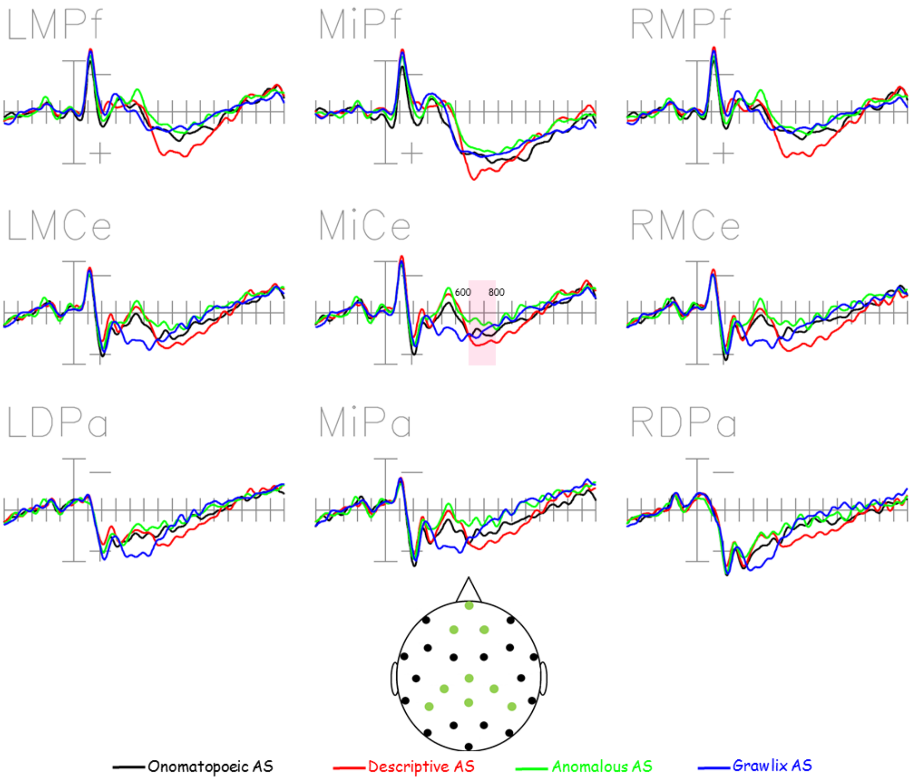

Fig. 4.10. Grand-average ERP waveforms recorded at frontal, central and parietal sites in response to Onomatopoeic (black), Descriptive (red), Anomalous (green) and Grawilx (blue) critical panels.

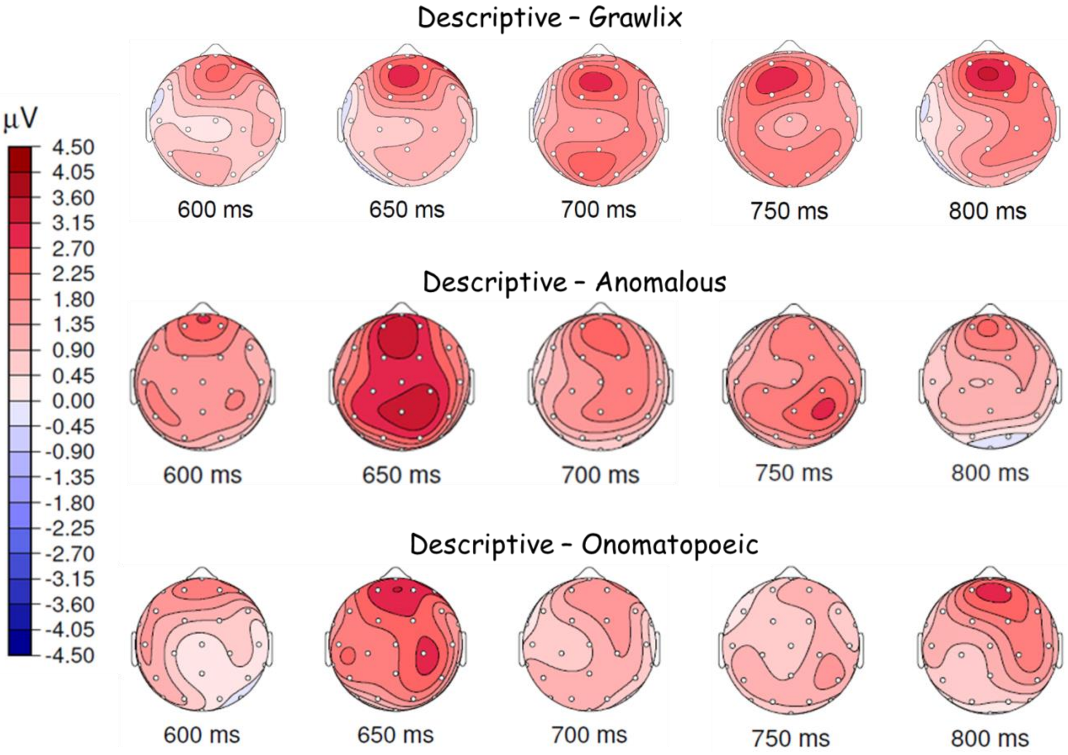

Fig. 4.11. Topographical difference maps performed by plotting difference voltages obtained by subtracting ERPs to descriptive from ERP to grawlix critical panel (first row), descriptive from anomalous critical panel (second row) and descriptive from onomatopoeic critical panel (third row) in the LPP latency range.

4.4 Discussion

In this study, we investigated the cross-modal understanding of language integrated into the context of visual narratives (e.g., comics). In particular, using action stars, we analyzed how inferences are drawn from complex situations that may not be visible, and whether those inferences would vary based on their congruity with the narrative sequence. To this aim, we presented 100 wordless *Peanuts* comic strips to 28 University students while their EEG was recorded. We contrasted the brain activation during the presentation of comic strips containing four different types of words embedded in the action star panel: onomatopoeic word coherent with the context ("Pow!"), Descriptive word, describing the hidden action ("Impact!"), onomatopoeic anomalous word, incoherent with the context ("Smooch!"), and "Grawlix", symbols used in comics to represent swearwords ("$#@&!?"). According to our hypothesis, if an onomatopoeic word evoked the representation of an implied event relative to the previous visual narrative, it should activate that associated, yet unseen, semantic information. We also manipulated the "congruency", expecting different brain response depending on how congruous the onomatopoeic word is with the context of the preceding narrative.

The statistical analyses performed over the posterior scalp sites evidenced that the mean amplitude of the posterior early negative response was greater over the left than the right hemisphere. This result was similar to previous evidences revealing that a left-lateralized early negative component (180–200 ms) (Cohen et al., 2000) is strongly responsive to orthographic stimuli. This early component is also known as N170, and it is considered the electrical signature of the visual word form (VWF) system, a left inferior temporal region specifically devoted to the processing of letter strings (Cohen et al. 2000).

In addition, our results revealed a greater response to the Descriptive critical panels compared to the others. This finding would suggest that this early negative component was more sensitive to the describing words depicted in the critical panel compared to onomatopoeic ones and Grawlix strings. The N170 responds more to well-structured (legal pseudo-words) than poorly structured (illegal) letter- strings (Cohen et al., 2002), to words than pseudo-words (Kronbichler et al., 2004) and to high than low frequency words (Proverbio et al., 2008). It also has been demonstrated that the modulation of this early component is mediated by the experience. Indeed, the results of a study by Proverbio et al. (2013) revealed that the N170 was much larger in response to visually presented words than to musical notes in a group of non-musicians.

In addition, all but the Grawlix panel elicited a large N400 amplitude, greater to Anomalous onomatopoeia and Descriptive words and smallest to the congruent Onomatopoeic word. This finding are similar to those found in studies that investigated the N400 effects related to the processing of words embedded in sentence contexts (Federmeier et al., 2007; Federmeier and Kutas, 1999; Kutas et al., 1984). Indeed, some evidences revealed that, in a sentential context, the modulation of N400 is affected by the semantic constraints of the sentence. In fact, evidences showed that the context is able to preactivate features of likely upcoming words, facilitating the processing of the words that share semantic or orthographic features with the predicted word (Kutas & Federmeier 2000; Laszlo & Federmeier, 2009). In 2007, Federmeier and colleagues investigated the contextual effects of sentence constraint and cloze probability on the modulation of the N400. They presented *strong constraint sentences* that ended with critical word of high cloze or low cloze probability. In addition, they presented weak constraint sentences that ended with critical word of medium cloze or low cloze probability. The results showed that N400 amplitudes were graded by expectancy and seemed to index the benefit of contextual information.

Thus, in the comic strip context, it is possible that the increased N400 response to the anomalous action star panel would reveal the difficulty of retrieving the meaning of the onomatopoeic word that is incongruent with the context. Conversely, the attenuation of the

N400 in response to the action star panel in the onomatopoeic strip may suggest that the onomatopoeic word was easier to interpret. Finally, we found that the Grawlix ERP was positive in this window. This result may reflect a physical violation (McCallum e al., 1984).

After the N400 response, only the Descriptive panel elicited a fronto-central late positivity. In a recent review, Van Petten and Luka (2012) investigated the late positive components elicited by words that are potentially more or less predictable from preceding sentence context. They identified two distinct late positive components with different scalp topographies, one (posterior) associated with semantically incongruent words and one (frontal) associated with congruent words. In particular, the latter would reflect disconfirmed lexical predictions, rather than unexpected concepts (Van Petten & Luka, 2012; Thornhill & Van Petten, 2012). Thus, in this study, the greater late positivity observed in response to the Descriptive critical panels compared to the others, would suggest a continued processing of the word and its relation to the visual narrative. We will further investigate the meaning of this evidence by performing a second study in which we will analyze the congruency of the descriptive words.

In sum, the results of this study demonstrate that lexical information, carrying different event meaning, can be incrementally incorporated into the representation of a visual narrative by ~ 300 ms. In addition, we can speculate that these findings would suggest an interactive processing of the semantic multimodal interaction, in which top-down and bottom-up information are processed together. Indeed, since stimuli are presented in the same sensory modality (visual), the semantic processing of inputs would not be influenced by the previous recognition and integration process of different sensorial information.

General discussion and conclusions

Semantic memory refers to general knowledge about the world, including concepts, facts and beliefs (Yee et al., 2013). Some authors reported that the representations of knowledge result in flexible concepts that can vary depending on the task and context, as well as on individual experience (Yee et al., 2013).

In the Introduction of this dissertation, we described several theories that tried to explain how different types of conceptual knowledge are acquired, stored and retrieved. Each of these models makes assumptions at a different level in a hierarchy of questions about the organization of conceptual knowledge (Caramazza & Mahon, 2003).

An electrophysiological instrument to explore the access to the semantic memory is the N400, an event-related brain potential (ERP) waveform that reflects the difficulty to integrate incoming information with previous information (Proverbio et al. 2010). Results from early investigations that used the N400 component as a tool to explore the semantic processing (Kutas & Hillyard, 1980, 1984; Bentin et al., 1985), suggested that semantic memory might contain representations of individual concepts that have connections characterized by different strength (Hutchison, 2003; Zacks & Tversky, 2001; Fischler & Bloom, 1985; Bower et al., 1979). Moreover, previous investigations indicated that the processing of semantic violations might be modulated by the level of experience and familiarity in specific contexts. In particular, it has been shown that the N400 response could be modulated by the familiarity and appropriateness of information included in the so-called "world knowledge" (Proverbio et al.

2009; Proverbio & Riva, 2009; Hagoort et al., 2004; West & Holcomb, 2002; Sitnikova et al. 2003) belonging to a specific repertory (i.e. learned through a specific artistic/motor or linguistic long-lasting training) (Proverbio et al., 2012; Proverbio et al., 2014; , Weber-Fox and Neville, 1996; Proverbio et al., 2002; Ardal et al., 1990; Koelsch et al., 2004; Daltrozzo & Schön, 2008; Besson et al., 1994). However, it is still not clear how and when knowledge related to different contexts and different levels of expertise is integrated into the brain.

Furthermore, it has been shown that the N400 component is sensitive to semantic violations related to a wide range of stimulus types across modality. In this regard, one early line of N400 work tested long-standing questions about whether semantic memory is organized in a single, amodal system (similarly accessed by stimuli with different physical properties, such as pictures and words) or as comprising a number of distinct (sub)systems (reviewed in Kutas & Federmier 2000).

Thus, in light of these evidences, in this doctoral thesis we deepened and clarified the role of two elements on the semantic processing of a given information: i) expertise and ii) sensory modality. Specifically, we focused our attention on the effects of the experience related to a specific knowledge and the sensory modality of the incoming stimulus. In particular, we investigated the electrophysiological processing to semantic violations in different kinds of contexts. More specifically, we examined the processing of knowledge that requires the integration of automatic, rapid processing of emotional facial expressions into contexts of everyday life and the effects of experiences shaped by a specific artistic/motor training. Therefore, we explored the effects of semantic violations, related to learned knowledge, on the amplitude and morphology of the N400 component.

In addition, we also attempted to verify if the difficulty (or ease) to integrate the incoming information into the semantic memory is affected to some extent by the sensory modality of the information. In other words, we wondered if the semantic processing related to different kinds of experience is also influenced by perceptual factors of the incoming stimuli. To this aim, we investigated the sensitivity of the N400 to semantic violations related to several kinds of information presented in different sensory modalities.

We carried out four studies in order to analyze these aspects. In the first study, we investigated the semantic processing related to knowledge that are not learned through an explicit training, but that requires the integration of automatic and fast processing of emotional expressions into situations of everyday life. In particular, we observed that the semantic processing to complex misfortunate situations varies according to the type of facial expressions showed by the victims. Indeed, the data provided by this experiment revealed that the N400 amplitude is modulated by the difficulty or ease to integrate the facial expression of the victims in the context. In addition, the anterior scalp distribution of the N400 component observed in this study was very similar to the N400 morphology found in other picture studies. Indeed, several evidences pointed out that the N400 response elicited by pictures revealed a more anterior scalp distribution compared to the N400 response found in language studies (McPherson & Holcomb, 1999; Federmeier & Kutas, 1999).

It is important to mention that in this first study the N400 was preceded by two early component (N170 and N220) that reflect the first processing of facial expressions depicted in the misfortunate situations. In particular, we observed a greater amplitude of these early components during the observation of the Comic stimuli compared to the Affective and the No-face ones.

Previous neuroimaging studies have investigated different aspects of face recognition in humans, suggesting a spatial and temporal dissociation in the processing of identity and emotion (Münte et al., 1998; Sergent et al., 1994). Different neural networks have been found for processing specific facial emotions, with the involved areas including cortical (prefrontal, frontal and orbito-frontal cortices, occipito-temporal junction, cingulate cortex and secondary somatosensory cortex) and subcortical structures (amygdala, basal ganglia and insula) (Damasio et al. 2000; Gorno-Tempini et al. 2001; Kesler-West, 2001). Some evidences revealed that amygdala is involved in processing fearful faces (Adolph et al., 1994; Morris et al., 1998; Vuilleumier et al, 2001) and sad faces (Blair et al, 2001; Schneider et al., 2000), while the cingulate sulcus could be implicated in happy faces processing (Kesler-West et al., 2001;Phillips et al., 1998). In addition, angry faces could activate the orbital frontal regions (Blair et al., 1999) and disgust seems to activate basal ganglia and insula (Calder et al., 2000; Phillips et al., 1997). Most of these evidences provide evidence of a dissociation as well as an overlapping of the cerebral structures involved in processing different facial emotions (Batty and Taylor, 2003). Other studies investigated the timing of different emotional processing. For example, Batty and Taylor (2003) presented a large number of unfamiliar faces expressing the six basic emotions (anger, happiness, fear, surprise, disgust and sadness; Ekman and Friesen, 1971) in addition to neutral faces, to 26 young adults while recording event-related potentials (ERPs). ERPs showed latency and amplitude differences among emotional expressions from 140 ms (N170 component). In particular, the data revealed that positive emotions evoked N170 significantly earlier than negative emotions and the amplitude of N170 evoked by fearful faces was larger than neutral or surprised faces. The authors concluded that the data support a model of automatic, rapid processing of emotional expressions.

In our study, the bewildered and disoriented expression depicted in the Comic stimuli could be considered a life-threatening facial expression because it shares several facial features with the fearful expression, including eye widening. Thus, the greater N170 amplitude found in response to Comic stimuli compared to the others might reflect rapid and automatic processing, analogous to those involved in fearful faces processing. We can also speculate that the typical bewildered facial expression showed by people involved in a misfortune might be considered another independent basic facial expression of emotion. Further investigations are necessary to explore and clarify this point.

Moreover, we also found a greater anterior N220 response during the perception of Comic stimuli in comparison to the Affective and No face ones. In a previous study, Proverbio and colleagues (2009) indicated that the anterior N2 response could reflect the activity of the orbitofrontal pleasure circuit during perception of social information. Indeed, the orbitofrontal pleasure circuit is active during the observation of many kind of positive and pleasant emotional social information (Bartles & Zeki, 2004; Leibenluft, Gobbini, Harrison, & Haxby, 2004; Nitschke et al., 2004). In addition, Goel and Dolan found that the appreciation of humor involved the activation of the central reward system in the medial ventral prefrontal cortex (MVPFC). Thus, since we found a significant correlation between the comic effect size of the N220 amplitude and subjective funniness ratings, we argue that the N220 early response elicited by the bewilderment expression depicted in the Comic stimuli might be considered the electrophysiological index of the orbitofrontal pleasure circuit that is modulated by the funniness of the Comic stimuli.

In light of this evidences, we can conclude that the results of our study reveal that the rapid, automatic encoding of emotional facial expressions influences the semantic processing related to misfortunate real-life situations.

While in the first experiment we explored the semantic processing of information that are not mediated by experience or learning, the experiment described in chapter 2 focused on the effects of experience related to a specific long-lasting training. In particular, we analyzed the semantic processing related to correct and incorrect basketball actions. We observed that a group of basketball players showed a great N400 response to semantic violations in visual processing of incorrect actions. Previous evidences revealed that people are more accurate in comprehending actions that are present in their own motor repertoire compared to those actions that are not (Buccino et al., 2004). Moreover, recent studies showed that this ability increases with motor expertise (Calvo-Merino et al., 2005). For example, some psychophysical and transcranial magnetic stimulation works investigated the perceptuo-motor processes and neural correlates of the athletes' ability to detect and predict erroneous actions (Aglioti et al., 2008; Tomeo et al., 2012). They showed that the athletes were more efficient than controls in predicting and detecting errors by reading the body kinematics. Similar findings have also been found in studies that investigated the processing of actions related to specific styles of dance (Calvo-Merino et al., 2005, 2006; Orgs et al., 2008; Ibanez, 2014). For example, in a study performed by Ibanez and colleagues (2014), high-density event-related potentials were recorded in experts, beginners and naïves participants while they observed realistic videos of Tango steps with different levels of execution correctness. The results revealed a greater negativity (N400) to incongruent than incongruent Tango steps only in the expert group. Similarly, in a recent ERP work, Orlandi and Proverbio (2014) investigated the effect of motor expertise in a group of professional dancers. Specifically, the authors presented 212 video clips in which a professional dancer performed a motor action. Each video was followed by a second video that could be identical to the previous one (“same” videos) or different (“different” videos) along 3 dimensions (time, body, space). The results showed a greater amplitude of the N400-like component to “different” videos compared to “same” videos in dancer group.

In light of these evidences, we can sustain that the data found in our study indicate that the fine motor expertise directly affected action observation modulating the ability to comprehend complex actions related to specific repertoires. In addition, the electrophysiological evidence found in our study could be considered a sign of a “resonance mechanism” that allows for the embodied mapping of action kinematics (Ibanez, 2014; Aglioti et al., 2008; Tomeo et al., 2012). In the next section, we shall discuss the neural source of the N400 response found in this study.

Moreover, an anterior scalp distribution of the N400 response was found also in this study. We assume that, similarly to the first study, the scalp distribution of the N400 might be due to the stimulus modality (actions) used in the experiment.

Taken together, the results from these two experiments suggested that the semantic processing of a given information is affected by the level of experience related to both a specific repertory and to automatic and not experience-mediated processing.

Similarly, in the third chapter we investigated the semantic processing related to a specific skill learned by imitation and exercise. In particular, we analyzed the processing of semantic information related to a long-lasting musical training. The results found in this study confirmed that the proficiency within a specific context is able to modulate the brain response to semantic anomalies. In addition, this study revealed that the ability to detect an error related to a motor repertoire is influenced by the expertise of the observers in several domains and across different sensory modalities presentation. Indeed, in this study we focused on the effects of the integration of auditory and visual information on the semantic processing. The results pointed out the time window of the N400 response to semantic violations of sound-gesture stimulus pairs was similar to those observed in the studies on unisensory visual information. However, in this study we noticed that the N400 response spread more over central-posterior areas of the scalp compared to the N40 morphology found in the previous studies. Interestingly, a similar scalp distribution of the N400 was found in previous studies that investigated semantic processing of audiovisual information (Plante et al., 2000; Puce et al. 2007; Cummings et al., 2008).

Overall, these data indicated that a long lasting training affects the N400 amplitude to semantic violation related to a specific repertoire even when the stimuli are presented using a multisensory modality.

In study 2 and study 3, in order to locate the possible neural source of the N400 response, different swLORETA source reconstructions were performed on the brain voltages recorded in the Congruent and Incongruent conditions in the N400 time window. The swLORETA analysis indicated the activation of a widespread cortical network (especially in expert viewers) that was very similar to that involved in semantic processingaccording to the results of a meta-analysis (Binder et al., 2009; see Introduction). Indeed, the meta-analysis identified a network of brain regions involved in semantic processing: i) the posterior inferior parietal lobe (AG and portions of SMG), ii) the lateral temporal cortex (MTG and portions of ITG), iii) the ventral temporal cortex; iv) the DMPFC, v) the IFG, vi) the ventromedial prefrontal cortex (VMPFC), and vii) the posterior cingulate gyrus.

In addition, to investigate the neural mechanism enabling the expert viewers to discriminate a correct/congruent from an incorrect/incongruent stimulus, the swLORETA inverse solution was applied by subtracting ERPs of correct/congruent videos/pictures from incorrect/incongruent videos/pictures in the N400 time window. It is very interesting to notice that a similar pattern of brain activation has been found in response to incongruent/incorrect stimuli in both studies. Indeed, the results revealed a strong source of activation in the premotor cortex (BA6), the inferior parietal lobule (BA40) and the inferior frontal area (BA44), the inferior temporal gyrus (BA20) and the superior temporal gyrus (BA38) in expert viewers. Previous studies suggested that these regions could play a role in action recognition and understanding and, therefore, they could be considered part of the human mirror neuron system (MNS) (Hamilton et al., 2008; Rizzolatti et al., 1996; Iacoboni et al., 2005; Pelphrey et al., 2004; Saxe et al., 2004).

Finally, in the last work we investigated the integration of sounds and pictures when both stimuli are presented in the same visual modality. In particular, we explored the semantic processing related to congruent or anomalous onomatopoeia, a particular type of language that has long been a staple of comics. The results showed that semantically incongruent words that evoked specific sounds in comics elicited a great N400 response in a group of University students with experience in reading comics. The novelty of this study was that we investigated the multimodal processing when stimuli are presented in the same sensory modality, avoiding the effect of a multisensory presentation on the semantic processing. In line with previous language studies (McPherson & Holcomb, 1999), we observed that the N400 response to the critical words presented in this study elicited a more central scalp distribution compared to the studies that used picture presentations.

In this dissertation, we investigated the electrophysiological processing to semantic violations in different kinds of context and using different sensory modalities. Previous works pointed out that although there are broad similarities (in wave shape, time course, and functional sensitivity of the N400 effect), there are also important differences (especially in terms of scalp topography) in the response to different types of meaningful items (Federmeier & Kutas, 2001). For example, prior electrophysiological investigations suggested the existence of a single semantic store shared by pictures and words (see Introduction; Nigam et al., 1992 Ganis et al., 1996; Kutas & Hillyard, 1980, 1984). However, other evidences indicated that the electrophysiological responses to words and pictures differ in scalp distribution, implicating non identical neural generators (Ganis et al., 1996; Holcomb & McPherson, 1994).

Even though much of the discussion examined in previous works focused on comparisons of pictures and words, our evidences extend the debate to a wide range of stimulus types presented in different contexts. Overall, the morphological, functional, and temporal properties of the effects found in our results suggest similar semantic processing elicited by paradigms using words, static pictures and videos as stimuli. However, we also observed several differences among the results of these experiments. For example, we noticed a frontal scalp distribution of the N400 response only in the experiments in which the stimuli used were static pictures (Exp. 1 and Exp. 2). In addition, even if we did not measure it, we observed that the N400 to pictures was preceded by an overlapping earlier negativity (the N300).

Moreover, we noticed a difference in the time-course of ERPs between the experiments that included pictures (Exp. 1 and Exp. 2) and words (Exp. 4) and the study that involved video clips (Exp. 3). In particular, we observed a longer latency of the N400 response to incongruent stimuli presented in the experiment 3, compared to the N400 latency observed in the other studies. This long latency might be explained by the variability in the timing of identification of different sequences of actions that constitute the sound-gesture pattern. On the other hand, we can speculate that the integrations of different sensorial information required by a multisensory presentation, take long time to be processed. Further investigations will be necessary to clarify this point.

Overall, the results of this doctoral thesis revealed that the semantic processing of a given information is strongly affected by the level of expertise related to specific training or based on knowledge that do not require an explicit learning. In addition, our results suggest that the level of proficiency in a specific knowledge affects the semantic processing regardless the sensory modality of the information.

Moreover, our data shed some light on the long-standing question about how a class of knowledge that can be conveyed by stimuli characterized by different perceptual elements is stored and processed. It is important to underline that previous studies limited their analysis to words and pictures. The multiple semantic system models hypothesize that pictures and words are processed in distinct, specialized semantic systems (Paivio, 1971, 1986, 1991; Shallice, 1988). In contrast, common semantics system, or "single-code", models hypothesize that words and pictures converge on a single, common semantic store (e.g., Caramazza et al., 1990; Glaser et al., 1992; Potter & Faulconer, 1975; Pylyshyn, 1980; Riddoch et al., 1988; Snodgrass & McCullough, 1986).

In general, we found no significant differences in the time course with which the different classes of stimuli are processed. This evidence makes unlikely the hypothesis that stimuli characterized by different perceptual factors are processed and stored in completely independent systems. However, we found the N400 effect to static pictures, words and videos shows slightly different ERP scalp distributions, implicating nonidentical neural generators (Ganis et al., 1996; Holcomb & McPherson, 1994). Thus, this evidence suggests that the representation derived from stimuli presented under different perceptual factors may be partially nonoverlapping (Federmeier & Kutas, 2001; Ganis et al., 1996). In other words, the slightly different morphology of the N400 found in response to the stimuli across the four experiments, suggests that perceptual factors might affect the semantic processing.

These findings are in line with the idea that semantic information may be distributed over multiple cortical areas. Although all areas may be involved in the representation of semantic information in general, each area preferentially processes information from a particular modality. According to this view, the relative contribution of the various areas will differ for different types of information (Federemeier & Kutas, 2001; Small et al., 1995).

In conclusion, these studies suggested that the semantic system is affected by both experience-dependent knowledge and automatic, not experience-mediated processing. In addition, the topographic differences found to different class of stimuli suggest that (partially) nonoverlapping neural areas could be implicated in meaning construction.

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