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Multistable visual phenomena. The role of executive functions in the perceptual reversal tasks.

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A mia madre

Aknowledgments

I want to thank my supervisor, Prof. Costanza Papagno for guiding me throughout these years.

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A special thanks to my daughter. It is only thanks to her that I found the smile again.

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Introduction

Vision is the most used sensory modality to acquire information and knowledge about the external world. Reaserchers have always been fascinated by how information from the eyes is coded into neural terms, into the language of the brain, and reconstituted into experience of surrounding objects. Indeed, seeing objects involves many sources of information beyond those reaching the eye when we look at an object. It generally involves knowledge of the object derived from previous experience, and this experience is not limited to vision but may include the other senses. In addition, as pointed out by Gregory (1966) “objects are far more than patterns of stimulation: objects have pasts and futures; when we know its past or can guess its future, an object transcends experience and becomes an embodiment of knowledge and expectation without which life beyond the simplest is not possible”. The complexity of visual perception is exemplified by a particular visual phenomenon: the multistable perception. Multistability refers to the phenomenon of perceptual switching between possible interpretations of an unchanging stimulus (Farkas et al., 2016). Since a long time, figural multistability attracts the attention of psychologists, because understanding how this phenomenon occurs might help one to understand perceptual processing in general. Figural multistability appears to be a necessary consequence of the normal functioning of our visual system, and hence it is something that any theory of visual processing should be able to account for by means of the mechanisms that explain normal, or correct, perception (Garcia-Pérez, 1989). This interest has generated much research aimed at determining a) which factors control the alternation in interpretations and b) the neural mechanisms underlying multistable perception. Two hypotheses were proposed to explain these visual phenomena: bottom-up and top-down. The role of higher cognitive and low-level sensory processes in visual multistable phenomena is still debated in the literature.

In this thesis, I investigated the role of higher cognitive processes in figural reversal tasks. Specifically, the first chapter is dedicated to describing the multistable perceptual phenomenon and its characteristics. In particular, the hybrid model (Long and Toppino, 2004) will be illustrated; in this model the integration of bottom-up and top-down processes is theorized. In the second chapter, empirical evidences about the functional and neural correlates of perceptual reversal are reported. Particular emphasis will be given to the studies concerning the role of attention in the multistable visual phenomena.

In the third chapter, the first experimental task is described. In this first study, I investigated the role of the right dorsolateral prefrontal and right ventral occipitotemporal cortices in figural reversal, by means of transcranial magnetic stimulation (TMS). Part of this chapter reports two pilot studies. In the pilot I, I selected the reversible stimuli for the experimental task. Pilot II aimed at examining the feasibility of the experimental task.

In the fourth chapter, the active and passive perceptual switching and the bias-effect of adaptation to an unambiguous version of reversible stimuli will be addressed. Therefore, a pilot study and two experimental tasks will be described in this chapter.

Summary, general discussion and conclusion will be reported in the fifth and sixth chapters.

1. The multistable perception

The sensorial system does not reproduce faithfully the external world. Actually, our mind constantly organizes sensory activity in order to perceive objects and events and to coordinate sensorimotor responses directed towards a specific goal (Windmann et al., 2006). von Helmholtz (1821-1894) suggested that human perception is not only related to objects, but it arised from fragmentary information. Therefore, the perceived information is inadequate and ambiguous to build a reliable percept. So, the involvement of central cognitive processes, such as memory or thought, is necessary in order to integrate and elaborate the missing information. An inferential unconscious mechanism is believed to be at the basis of this process. This mechanism depends on past experiences of the subject and it allows interpreting the incomplete or ambiguous image.

In order to investigate the complex nature of visual processing, researchers have repeatedly studied a particular class of visual phenomena known as reversible, or ambiguous, figures. Examples of such figures include the Necker cube, Boring's wife/mother-in-law figure, and many others (Long & Moral, 2007). The proximal retinal patterns produced by these reversible figures do not produce stable perceptions-the unchanging retinal stimulus can be perceived in more than one way without any concurrent change in the physical nature of the distal stimulus. This characteristic of the figures is named perceptual ambiguity. In addition, these figures generate spontaneous perceptual fluctuations between distinct perceptual interpretations. This characteristic of subjective instability is referred to as perceptual reversibility or instability (Hochberg and Peterson 1987; Long and Toppino 2004). In general, these visual phenomena are categorized as multistable perception.

1.1 Multistable visual phenomena: definition and characteristics

Specifically, multistability refers to the phenomenon of perceptual switching perception between possible interpretations of an unchanging stimulus (Farkas et al., 2016). In other word, the multistable perception occurs when a single phisical stimulus produces different alternatives in subjective perceptions. There is consistent evidence that every stimulus pattern offers the possibility of more than one interpretation. However, the perceptual system has developed specific criteria which favor one interpretation (Kruse and Stadler, 1995), but in the case of multistable stimuli a continuous switching between two interpretations remains possible.

The fact that perception oscillates between more interpretations, without changes in the external stimulus, makes ambiguous figures a fruitful tool to investigate the visual and cognitive processes involved in the interpretation of the retinal stimulus and of the visual awareness (Andrews et al., 2002; Kornmeier & Bach, 2004; Leopold & Logothetis, 1999). Kanizsa (1980) suggested that a correct theory must consider optical illusions as valuable real indicators of how the visual system works, in other words they are a natural experimental condition that allows investigating the underlying organization of the visual system.

Kruse and Stadler (1995) suggested seven different types of patterns that induce a continuos change of the perceptual interpretation:

1. *Fluctuations of complex patterns* (Figure 1). This image directly shows the activity of the perceptual system in search of order and stability.
2. *Figure-ground tristability*. The Rubin's vase (Figure 2) is a classic example of this category. Two simple lines may be the boundary both of two profiles of face to the right and to the left and of the vase in the center. It is impossible to

simultaneously perceive the elements, because the contour belongs to only one of them (Metzger 1975b).

3. *Multistability of symmetry axes*. Every figure with more than one symmetry axis suffers from this kind of instability, because the perceptual system can obviously realize one at a time. For example, every equilateral triangle has three symmetry-axes which determine where the triangle is pointing (Attneave, 1971). In Attneave's triangles there are several triangles with vertices that point to the same direction; during a period of continuous viewing, they seem repeatedly to change direction.
4. *Multistability of 2-dimensional projections of 3-dimensional bodies*. The famous Necker-cube (Figure 4a), for istance, consists of a two-dimensional representation of a three-dimensional wire frame cube. Schröder's staircase (Figure 4b), Mach's book (Figure 4c) and many others belong to this category (van Leeuwen, 1993; Zimmer, 1994).
5. *Multistability of actually 3-dimensional objects*. In this category, the Ames rotating trapezoidal window is more representative (Figure 5). The Ames trapezoid or Ames window is a style of window, which, when observed frontally, appears to be a rectangular window but is, in fact, a trapezoid. The window is mounted on a rod connected to an electric motor that rotates it about its vertical axis. When it is observed with one eye from about 3 meters or with both eyes at 6 meters, or more, the window appears to rotate through 180 degrees and then seems to stop momentarily and reverse its direction of rotation. Therefore, it is not perceived veridically to be rotating continuously in one direction but instead is misperceived to be oscillating, reversing its direction once every 180 degrees.
6. *Multistability of motion direction in apparent moviment*. The stroboscopic alternative movement introduced by von Schiller (1933) is a visual stimulus consisting of two alternating images located at opposite corners of an

imaginary rectangle, presented with an intermediate blank phase between each image. The images continuosly change their position. They appear to move (hopping) horizontally or vertically. The circular apparent movement demonstrated by Kruse et al. (1991, 1994) also pertains to this category (Figure 6).

7. *Multistability of meaning attribution*. This category includes images to which two different meanings can be attributed. The Rabbit-duck illusion is an example (Figure 7), in which a rabbit or a duck can be seen.

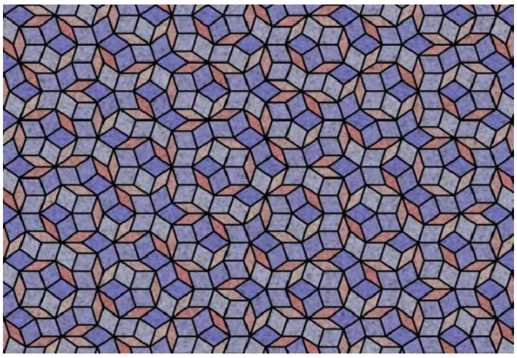

Figure 1. Multistable pattern. In this immage is possible to see innumerable different structure.

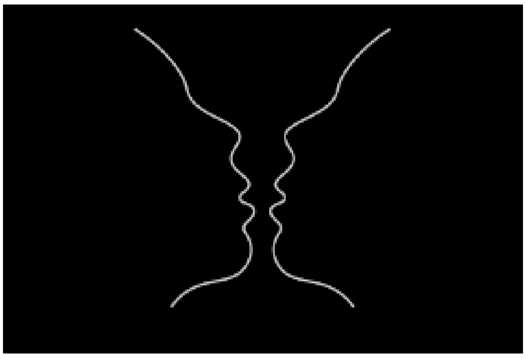

Figure 2. Rubin's vase. Two simple line may be the boundary both of two profile of face to the right and to left and of the vase at the center.

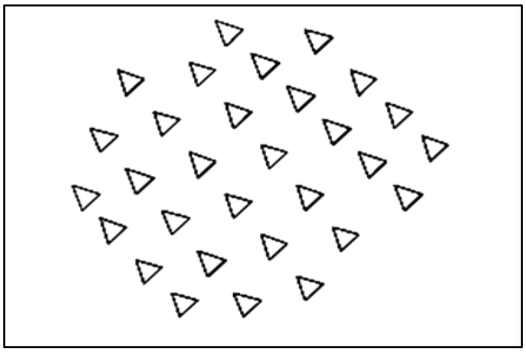

Figure 3. Attneave's triangles.the perceived direction of the vertices changes with prolonged viewing.

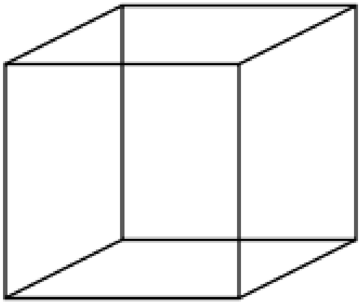

Figure 4a. Necker cube. Intersections between two lines do not indicate which line is on top of the other and that below: it is not possible to indicate which side is pointing the observer and what is behind the cube.

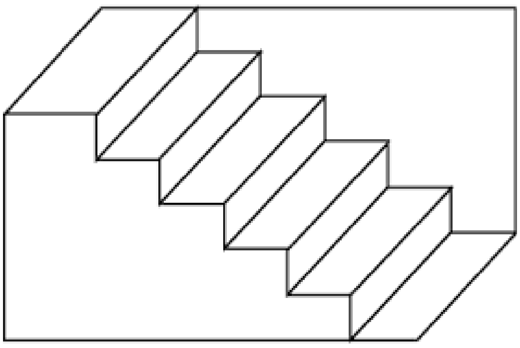

Figure 4b. Schröder's staircase) is an optical illusion which is a two-dimensional drawing which may be perceived either as a drawing of a staircase leading from left to right downwards or the same staircase only turned upside down.

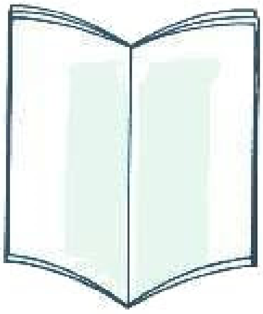

Figure 4c. Mach's book may be seen as an open book with pages facing you, or as the covers of a book, with the spine facing you.

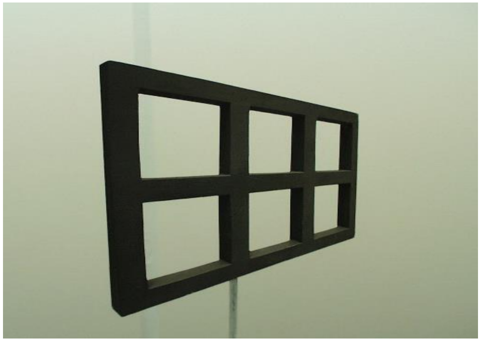

Figure 5. The ames rotating trapezoidal window when observed frontally, appears to be a rectangular window but is, in fact, a trapezoid. When observed the window appears to rotate through less than 180 degrees. The exact amount of travel that is perceived varies with the dimensions of the trapezoid. It seems the rotation stops momentarily and reverses its direction. It is therefore not perceived to be rotating continuously in one direction but instead is mis-perceived to be oscillating.

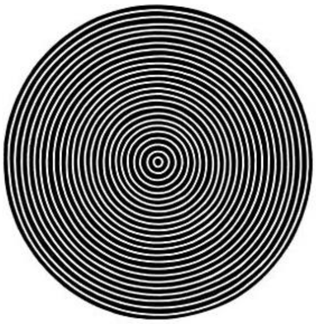

Figure 6. Circular apparent movement.

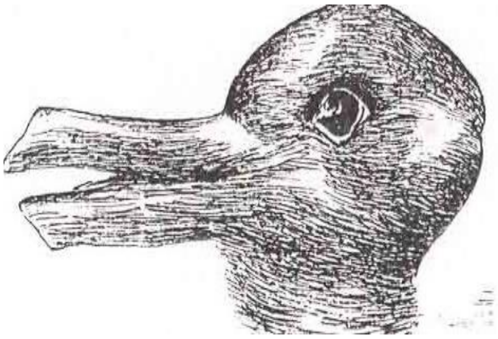

Figure 7. The Rabbit-duck illusion is an ambiguous image in which a rabbit or a duck can be seen.

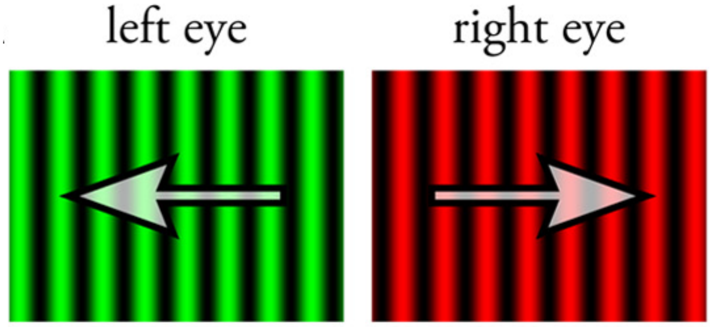

Figure 8. Example of stimulus used to generate binocular rivalry: two distinctly colored (red/green) sinusoidal gratings that drifted in opposite lateral directions (i.e., left/right) one presented to the right eye and one in the left eye.

In all these categories, spontaneous reversals are always possible. Ususally, the first reversal takes some time, up to three minutes, but then the reversion rate cotinuously increases, until it is stabilized at a rate that is specific for different people. The individual differences of the reversion rate range from about 60/min to about 1/min (Kruse and Stadler, 1995). Klintman (1984) suggested that the individual reversion rate would depend on a cognitive-style variable called "cognitive flexibility" wich includes originality in thinking (Klintman, 1984) and ability to imagine (Kruse et al., 1992).

The "binocular rivalry" also falls within the multistable visual phenomena. This phenomenon occurs when two dissimilar stimuli are presented to the eyes, and perception alternates between multiple interpretations (Frassle et al., 2014) (Figure 8). Leopold et al. (1995) give a clear explanation of this phenomenon: when two retinal images are largely different, normal binocular fusion becomes impossible, and the visual system turns into an unstable state; when somebody artificially creates such situation, by placing completely non matching stimuli in front of one's two eyes, the brain trend is to choose rather than compromise. This choice manifests itself in complete perceptual suppression of one of the competing stimuli, while the other remains entirely visible. The dominance of the visible stimulus is only temporary, however, and after a few seconds the suppressed stimulus rises to the conscious level, as the previously dominant stimulus fades away.

Gregory (1997) suggested a classification of optical illusions, dividing those into 4 classes: distortions, ambiguities, fictions, paradoxes.

He suggested that the first two have a physical or physiological nature. They are generated by confusion in the stimulus during transit between the object and its two-dimensional retinal representation. Conversely, the last two, namely fictions and paradoxes, have a cognitive-psychological nature; they depend on an erroneous interpretation of the stimuli provided by the visual system.

In other word, Gregory (1997) described these percepts as an incomplete hypothesis that requires an integration with prior knowledge, thus he considers the perceptual processes as a problem-solving activity.

Indeed, the main feature of the multistable perception is ambiguity. Ambiguity generates a switching between percepts without any change of the physical characteristics of the stimulus (Attaneave, 1971). Actually, all sensory stimuli can be considered ambiguous, but the automatic disambiguation processes prevent to perceive this instability (Kruse and Stadler, 1995; Andrew et al., 2002), except for multistable stimuli. Probably this depends on specific characteristics of multistable stimuli: uniqueness, inevitability, stochasticity.

The “uniqueness” refers to the occurrence of a single perceptive interpretation at a time and can be attributed to a fundamental principle of decoding that belongs to the sensory receptors. Perceptual alternations, in fact, occur in a sudden and total manner as if the visual system oscillates between two percepts equally existing a priori.

The “inevitability” refers to the fact that the oscillation between the two possible percepts occurs during the entire observation time.

The “stochasticity” refers to the fact that temporal dynamics, such as the frequency of the oscillations, and the dominance of a percept, show particular characteristics of stochasticity and independence. Specifically, the periods of perceptual dominance during time observation show unimodal and asymmetric distributions. Therefore, they have been treated as theoretical probability distributions (Braun and Mattia, 2010).

Finally, Kruse and Stadler (1995) argued that there are different stages of multistable perception: a stimulus has a specific number of possible organizations, but only some of these meet a neural attractor wich results in a figural organization that is created by attention. Then the switching between percepts is a function of the varying strenght of attractors. The experienced alternatives of specific figural organizations may be linked to specific meanings. If the meaning switches from one to another, the figural organization changes, too. Certain organizations that do not come to attention spontaneously may be learned (Figure 9). Thus, according to these authors, the multistable perception can be defined also as a switching between two or more attractors. The attractors are ordered states of high stability surrounded by instability.

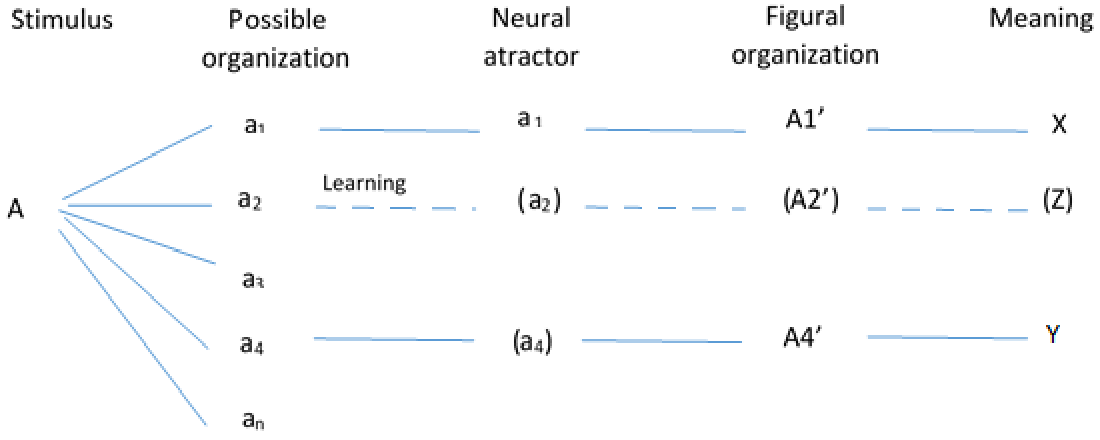

Figure 9. The stages of multistable perception (Kruse and Stadler, 1995).

These several forms of perceptual multistability exhibit comparable dynamics, with distribution of dominance durations associated with a given perceptual state being unimodal and skewed toward longer durations (Klink et al., 2008; Leopold and Logothetis, 1999; van Ee, 2005). The similarity of their dynamics suggests that those different forms of multistability may arise from comparable, although not necessarily identical, underlying neural events.

However, experimental evidences about neuronal mechanisms underlying the multistable perception are conflicting. The hypothesized processes in the multistable perception include fluctuations in attention, eye-movement changes, accommodation changes, stimulus complexity effects, natural cortical rhythms, expectancy effects, volitional effects on perception, satiation in the flow of cortical activity, fatigue of localized neural channels, cyclical decision processes, perceptual learning, perceptual hypothesis testing, preference for novelty, cyclical cortical "search" processes, and more. In all cases, the hypothesized processes are not considered as unique to the reversible-figure situation; rather, these processes are proposed as normal visual processes that are more clearly revealed in the multistable stimuli situation (Long & Toppino, 2004). Some studies (see paragraph 1.1.1) suggested that the underlying mechanisms to the multistable perception are automatic and involuntary while other studies (see paragraph 1.1.2) hypothesized that multistable perception involves the activity of higher cognitive areas and, therefore, voluntary processes such as the attention.

In other words, the multistable perception processes have been categorized as bottom-up and top-down theories (automatic vs. cognitive processes). In additon, Long and Toppino (2004) proposed a "hybrid model", according to which the multistable perception is influenced from both bottom-up and top-down processes at various levels.

1.2 Bottom-up hypothesis

The bottom up hypothesis assumes that the perception of multistable stimuli depends on peripheral, automatic and involuntary processes.

Specifically, the perceptual reversal is primarily based on a rivalry between two competing perceptual interpretations at early processing levels—that is, between the retina and the corresponding receptive fields of the primary visual cortex (Blake et al., 2003). Indeed, the reversal of figures depends on stimulus properties such as the intensity (Lynn, 1961), figural completeness (Babich & Standing, 1981), and continuity of presentation (Leopold et al., 2002; Orbach et al., 1963).

Thus, the figural reversion would be due to relatively autonomous brain processes that are: a) strictly dependent on the characteristics of the stimulus; b) localized on specific retinal regions undergoing arousal, adaptation and recovery processes; c) largely independent on higher cognitive processes.

Many previous studies support this hypothesis. Reversal rates were measured varying physical features of ambiguous figures (e.g. Ammons & Ammons, 1963; Brigner & Deni, 1990; Washburn, et al., 1931), varying the ambiguous figures presentation mode (Orbach et al., 1963), or while presenting an unambiguous preadapting stimulus preceding the ambiguous one at the same position (e.g. Carlson, 1953; Emerson, 1979; Hochberg, 1950), or presenting the stimulus at different positions in the visual field (Orbach & Zucker, 1965; Toppino & Long, 1987).

Boring (1942) and Necker (1832/1964) were among the first to promote a bottom-up explanation. They suggested the first version of the *focal-feature hypothesis*, according to which the "different focal regions or areas" of the ambiguous figure favor different global interpretations of the stimulus, i.e. the different points of a figure are assumed to favor one of the two perceptual alternatives. Thus, the interpretation of the figure depends on the perceived feature that receives the early processing, while the reversion figural reflects the shift in the primary processing from a focal area of figure to another (Toppino, 2003).

The *focal-feature hypothesis* placed the locus of the perceptual reversal in the "optical" rather than "mental" processes (Necker, 1832/1964). Other researches seem to confirm the role of eye movements in the multistable visual perception. For example, Ellis & Strak (1978) showed that changes in the fixation point are associated with switching, and Ruggieri & Fernandez (1994) reported that particular eye movements correlated with instructions to produce a particular interpretation of a reversible figure. In the past, several studies have shown that the fixation of different locations of a figure promotes one or the other of perceptual responses (Chastain & Burnham, 1975; Garcia-Perez, 1989; Hochberg a& Peterson, 1987; Peterson & Gibson, 1991).

Another bottom-up hypothesis assumes that in the multistable visual perception the switching between two possible percepts is caused by a passive adaptation of local neural units during the early stages of visual processing (Toppino and Long, 1987). When both interpretations are recognized, these will automatically alternate as a result of fatigue or neural satiety in the visual cortex involved in early processing of stimuli (Blake, 1989; Kohler, 1940). In other words, the neural channels tend to selectively tune to particular characteristics of the retinal stimulus and the continuous stimulation of neural selective channels temporarily alter their response by reducing their sensitivity and their ability to respond to following stimuli until recovery (Toppino & Long, 2004).

In order to support this hypothesis the inversion rates over time were studied. In fact, the increase in the number of inversions, during few minutes of observation, seems to confirm the assumption that the underlying neural activity at each perceptual response moves from a period of fatigue (or satiety) to a recovery (Kohler, 1940). Therefore, the observer experiences reversal when the fatigue threshold value is reached. In this way, while the second set of neural channels is dominant and approaches the fatigue threshold value, the first set can dissipate fatigue and so on. However, the neural channels cannot recover all the fatigue, therefore the reversals will be more and more close in time (Dornic, 1967).

Ilg et al. (2008) studied the relation between the stimulus frequency and the reversal rate, and therefore systematically varied the stimulus frequency and analyzed the resulting percept duration. They showed that the percept duration, with the reversal rate, significantly depends on the stimulus frequency (with higher frequencies resulting in faster percept reversals). The robust effect of the stimulus frequency on the reversal rate confirmed the dependence of the percept on primary stimulus properties, such as and continuity of presentation. According to authors, these effects of exogenous stimulus properties on the reversal rates suggest that bottom-up effects influence perceptual reversals of ambiguous stimuli on early processing levels. In addition, the results of continuity support a sensory model. Leopold et al. (2002) showed that spontaneous reversals of multistable percepts can be slowed when stimuli are viewed intermittently (the visual stimulus is periodically removed from view) rather than continuously. This evidence is against the notion that perceptual reversals are governed by an autonomous oscillator that operates independently of the visual stimulus. They interpreted this finding as an expression of bottom-up influences.

The effects of “adaptation” or " reverse-bias effects" (Long and Toppino, 2004) are usually cited to support the bottom-up model of figural reversal.

In the first paradigm, the researcher exposes the observer to an unambiguous version of reversible figure and then to an ambiguous version, in order to adapt the neural structures related to one of the percepts (Hochberg, 1950; Long et al., 1992). In these studies, the observer, after prolonged exposure to an unambiguous version, reports the alternative version of the subsequently viewed ambiguous stimulus. Exposure to the unambiguous stimulus presumably selectively adapts and weakens the neural structures underlying that particular interpretation of the ambiguous figure, allowing “no-adapted” neural networks to become dominant.

The second paradigm showed that when two or more multistable stimuli are presented the reversals are independent. For instance, when two cubes of Necker, are simultaneously presented one inside the other or side by side, the observer experiences the reversal of the cubes independently (Long and Toppino 1981; Long et al., 1983; Toppino and Long, 1987).

Finally, several researchers have reported the localized effect. If a Necker cube is viewed for several minutes when it is moved to a different location in the visual field, reversal rate returns to baseline (Spitz & Lipman, 1962). Similarly, Howard (1961) and Toppino & Long (1987) used the rotating Necker cube figure and demonstrated that a change in retinal location produces a return to baseline in the response pattern. In a closely related vein, Toppino and Long (1987) also demonstrated that adaptation to a figure of one size and then viewing a cube of a different size shows no carryover from the adaptation phase to the test phase. These demonstrations are especially strong evidence for the involvement of relatively localized processes, which is easily modeled with known cortical structures receiving input from restricted retinal regions (i.e., localized receptive fields).

A final category of findings that have been cited by various investigators to support a model of figural reversal that is dependent on sensory processes is the “stimulus effect on figural reversal”. These findings involve stimulus effects whose role is predicted for a stimulus-driven model involving early cortical processes. Complete figures reverse more rapidly than incomplete ones; and continuous viewing produces more reversals than intermittent viewing. Each of these manipulations has been interpreted to impact relatively early in cortical structures which analyze stimulus features and in which slowly building adaptation effects critically dependent on these stimulus characteristics are believed to occur (Long and Toppino, 2004).

1.3 Top-down hypothesis

In the past, several authors proposed the hypothesis that multistable visual phenomena are based on central cognitive processes such as imagination and attention.

For example, Fugel (1913) suggested a variation of the focal hypothesis, arguing that eye movements and attention can dissociate. Flugel (1913) suggested that the direction of attention, rather than of eyes, is critical for the perception of one or the other interpretation of the ambiguous figure. Previously, Lange (in Toppino and Long, 2004) and Gordon (1903) speculated that the "inversions" of reversible figures depend on a change in attentional focus. Therefore, at the beginning of the XX Century there was already a consensus that the locus of figural reversals was in the central rather than in the peripheral processes.

In the 60’s and 70’s, the critical role of top-down processes, such as learning, attention and decision-making, has been increasingly recognized. The concept of automaticity of reversion was replaced by the concept of the observer's flexibility. Observers actively processe retinal information using their own internal resources.

Therefore, the "top-down" hypothesis suggests that reversal takes place during perceptual interpretation, therefore, at the highest level of visual hierarchy (Long and Toppino, 2004).

Gregory (1974) considered individual perceptions as elaborated hypotheses based on comparison between previously stored data and new data. The Necker cube, as the figure duck / rabbit, has two or more perceptive hypotheses, equally reasonable, which are considered in turn. In order to support a cognitive model of reversion figural, Long & Toppino (2004) classified the results of several studies based on five fundamental features:

1. *Volitional effects on figural reversal*. Since the 1800s, it has been demonstrated that observers have some degree of control over figural reversals. For example, Helmholtz claimed that an observer can produce intentionally a “change of inversion” in a figure as the Schroeder staircase (see Figure 4b) if “we recall vividly the image of its contrary form” (as cited in Vicholkovska, 1906, p. 276).

   The empirical investigation of volitional control has taken two main forms in the literature: a) observers are instructed to “hold” a particular interpretation of the figure (e.g., Liebert & Burk, 1985; Peterson & Gibson, 1991; Washburn & Gillette, 1933) while a control group of observers are given “neutral” instructions; b) observers are instructed to either “hold” the current percept or “switch” the figure as rapidly as possible (e.g., Pelton & Solley, 1968; Struber & Stadler, 1999). The results showed that both types of instructions significantly affect figural reversal, either varying the duration for which a given percept is reported or altering reversal rate in the direction of the instructional set.

   In an interesting study by Toppino (2003) the observers were instructed to view a Necker cube passively or to intentionally hold a designated orientation of the cube. Simultaneously, fixation location was varied so as to bias processing of focal features that favored a particular perceived orientation. Depending on the combination of conditions, the demands of intentional instructions and fixation location were either compatible or incompatible.

The hypothesis was if both factors depended on selecting certain focal features for primary processing, they should have produced interactive effects. The results showed that both variables produced additive (independent) strong effects. Furthermore, when a very small cube was used to reduce the probability of the selective processing of the focal features, the effect of the location of the fixation was eliminated, while the effect of intentional instructions was not reduced. These findings supported the argument for an important role of cognitive control in figural reversal. They showed that voluntary control could be independent of selectively processing particular focal features.

2. *Knowledge of reversibility*. Rock et al. (1977; 1992; 1994) demonstrated that the observer's knowledge of the reversible character of the figure influences the reported reversion rate: if the observer does not know that the figure is potentially bistable shows few reversals. So, if perceptual reversal depended only on passive neural processes it could not explain why these are influenced by familiarity and practice.
3. *Learning effects on figural reversal.* Several works demonstrated that observers exhibit learning effects with bistable figures. For example, it has been demonstred that the negatively accelerating rate of reversals reflects a standard learning curve (e.g., Ammons, et al., 1959).

   The negatively accelerating response pattern has been re-conceptualized to reflect an active cognitive process. Studies that support this hypothesis used conditions that eliminate the role of transient adaptation effects. In general, studies on learning effects on figural reversal demonstrate progressive changes in the observer’s reported reversals over repeated viewing periods under conditions in which transient adaptation effects are excluded.

For example, observers report more reversals over repeated sessions spaced by weekly intervals (e.g., Donahue & Griffitts, 1931; Long et al., 1983). Although transient adaptation effects would appear to be excluded by long intersession periods, an increase in reversals is found.

Solley & Santos (1958) found that successive 2-s presentations of biased figures accompanied by verbal reinforcement produced a progressively stronger likelihood that the standard Necker cube would be seen in the biased version.

4. *Expectancy effects on figural reversal*. A short presentation (less than 5 seconds) to visually relevant information (showing an unambiguous version of the stimulus before the ambiguous version), at the categorical level (showing a figure which belongs to the same category of one of the interpretations of the ambiguous figure) or contextual level (the perception of an ambiguous figure can be altered depending on the context in which it is presented) can affect the perception of one or the other interpretation of the ambiguous stimulus.

   Specifically, Botwinick (1961), Leeper (1935), and Fisher (1967) demonstrated that showing an unambiguous version of the reversible figure prior to the traditional ambiguous versionaffected the observer in that he/she wasmuch more likely to report the normally ambiguous figure in the biased interpretation. Similar results were obtained when prior verbal information (i.e., a verbal description of one of the alternatives) was used to bias one or the other interpretation of the ambiguous figure.

   Bruner & Minturn (1955) demonstrated that the context altered observer's perception of an ambiguous figure (i.e., the figure 13 seen as the letter B or the numbers 1 and 3, depending on whether the stimulus was embedded within other letters or other numbers).

   In addition, presenting pictures of the same category as one or the other interpretation of the ambiguous figure (e.g., drawings of people vs. drawings of animals presented prior to viewing the rat–man ambiguous figure; see Figure 10) can affect the observer in that he/she is more likely to report the primed interpretation of the ambiguous figure (Bugelski & Alampay, 1961).

5. *Effects of a secondary task on figural reversal*. If perception of bistable figure does not involve higher cognitive processes, it should not be affected by introducing a second task. Reisberg (1983) and Reisberg and O'Shaughnessy (1984) found that the introduction of a secondary task increases the time to report the first reversal of a reversible figure, as well as it decreases the rate with which subsequent reversals occur. In other word, the figural reversals require "perceptual judgments" that compete with the secondary task for working memory: the perception is considered as a resource-limited, problem-solving process.

Figure 10. Rat/man

1.4 Hybrid model

In light of the above it, it seems particularly significant as told by Garcia-Perez (1989): "*it is difficult to trace the boundary between what perceptual multistability owes to early visual processing, and what cognitive processing adds* *to it*". Indeed, the experimental evidences seem to support both bottom-up and top-down hypotheses.

Long and Toppino (2004) proposed a hybrid model, according to which both transient, localized sensory and global, long-lasting cognitive processes are involved in the perceptual reversals. Therefore, no single process is likely to be the determining process in figural reversal.

The idea of multilevel perceptual effects on the reversal is not new. Already Hochberg & Peterson (1987) showed that the manipulation of the subject's intentions, by instructions to hold one or the other percept, though revealing a clear top-down influence on the reversal figural, cannot eliminate reversals altogether. This led them to conclude that reversals depend on both a largely passive, stimulus-stimulus and automatic processe defined *figural instability*, and on a second component dependent on more cognitive factors (such as instructions) defined *figural malleability*. Long et al., (1992) confirmed the involvement of both sensory and cognitive processes in multistable visual phenomena. They investigated the effect of presentation of an unambiguous version of the reversible figure on viewing of the ambiguous figure. Specifically, they presented a non-reversible verision of ambiguous figures (where the observer can see only one of two percepts) before the ambiguous one. The results showed a positive-bias effect after a brief presentation (less than 5 s) of the unambiguous version, favoring the same perceptual response to the subsequently viewed ambiguous figure. However, when the adaptation period was increased (2-3 min), a reverse-bias was found. Thus, the duration of the adaptation period seems to have two different effects: short and long exposure periods seem to affect perception via top-down processes (i.e., set or expectancy) and bottom-up processes (i.e., neural adaptation), respectively.

Specifically, sensory and cognitive processes may be more or less evident depending on the observation conditions.

Long and Toppino (2004), referring to the results of studies conducted over the last decades, proposed that the perceptual experience of reversible figures involves two distinct components: ambiguity and reversibility. This distinction is the basis of their hybrid model. The first component (ambiguity) refers to the fact that a reversible figure can elicit more than one interpretation or percept. This is related to the interpretation given by the observer, and would depend on experience, previous neural representations, differences in neuronal excitatory levels and cognitive variables. The second component (reversibility) refers to the switching between possible interpretations or percepts. Thus, this allows the alternating perceptual experience, that means "the abandonment” of the previous interpretation (or dominant percept), and may reflect the operation of different processes. The authors emphasized that this component would reflect different processes from those of disambiguation, which depends on mechanisms of inhibition and adaptation neuronal.

In order to clarify the distinction between these two components, the authors argued: *“We believe that the value of treating the two perceptual experiences of ambiguity and reversibility separately is that the identification of a certain process as critical to perceptual ambiguity (or defeating that ambiguity) does not necessarily indicate that the same process is involved in the reversibility of the figure or, alternatively, that the process is involved in the same manner. To oversimplify the argument […] consider the plausible scenario in which initially the alternate perceptual interpretations (Percept A and Percept B) for a stimulus depend on active learning with that figure to establish competing internal neural representations or networks for that single stimulus pattern. We propose further that, once established, these neural representations might function subsequently* *in a relatively passive manner such that the perceptual fluctuations that occur during extended viewing may be due to very different, even noncognitive factors”.*

Specifically, the model includes several levels of information processing that accommodate both bottom-up and top-down processes.

The authors hypothesize that an early feature-extraction level encompasses (largely) automatic parallel channels (f1 . . . fn) that are selectively tuned to stimulus features (e.g., orientation, depth, motion, size, and more) localized in specific retinal areas. This is followed by intermediate levels (1A, 1B, 2A, and 2B) that receive input from the early feature-extraction level as well as from higher levels in the system that can differentially affect these neural structures and, thus, the alternate percepts of a reversible figure. Thus, descending signals from higher levels are responsible both for anticipatory effects that are established before viewing the reversible figure (e.g., context effects, volitional effects, familiarity effects) and for critical recurrent neural processes during target viewing by which the system seeks to reduce the impact of incomplete retinal information (figure 11).

Some authors (Rock et al., 1994; Horlitz & O'Leary, 1993) suggested that the resolution of the contrast between the different interpretations of the bistable figure occurs at the intermediate level. In particular, for these authors - which emphasize the role of top-down processes such as learning or “preference for novelty” in the figural reversion - the competition between the multiple interpretations of the figure should occurs within a late locus with respect to the perceptual switching that involves a post-recognition level of analysis. Such internal representations of multiple percepts of a reversible figure presumably occur beyond the primary and secondary visual cortex.

Consistent with this perspective, Leopold et al. (2002) found that the phenomenal disappearance of a figure produced through the motion-induced blindness (MIB) paradigm has the same effect on figural reversal as the physical removal of the stimulus: even if the physical stimulus and the retinal image remain unchanged, the phenomenal disappearance of the stimulus interrupts the usual configuration of the image in the same manner that physical removal of the stimulus does. This demonstration provides evidence against those models of figural reversal that suggest passive (i.e., automatic) neural adaptation, because the sensory input to the system has remained unchanged. These results do not exclude the role of neural adaptation effects, but they suggest the existence of an early locus for attentional modulation (Long and Toppino, 2004).

Therefore, the evidence indicates that the visual system is characterized by reentrant processes, i.e. iterative exchanges of neural signals among levels (DiLollo et al., 2000). In the unambigous figure, the role of these processes is to reduce the noise produced by the interaction between the ascending and descending neural pathways and, therefore, to allow the visual system to determine the most plausible distal stimulus producing the given retinal pattern (Long and Toppino, 2004). However, in reversible figures, the initial bottom-up processes activate more than a single cognitive representation and, therefore, the resulting top-down processes (reentrant) are not sufficient to confirm a unique solution to the neural input. So, perceptual ambiguity, as well as reversion, are affected by both low-level and high-level manipulations. The ambiguity, in fact, is linked to experience and familiarity of the observer with this type of figures from which depends on the construction of the different internal competitive representations, but also from the current sensitivity of these representations that can vary as a function of the excitatory level or cognitive variables.

In summary, one of the main features of this theoretical framework is that it explicitly recognizes that both sensory and cognitive processes significantly contribute to figural reversals. Long & Toppino (2004) suggest that the hybrid model has two important implications: a) "*this has the advantage of sensitizing researchers to the moderating effects of these processes on one another*"; b) this can affect the particular reversible figure selected for investigation by researchers. Indeed, bistable stimuli do not have the same degree of complexity. For example, regarding the reversible figure, the Necker cube – that requires a reversal of perspective - is less complex compared to Boring's (1930) wife/mother-in-law (figure 12) – that requires a reversal of meaning. It is very likely that the former class is less susceptible to instructional manipulations than are the latter class of figures (Struber & Stadler, 1999). Figures that require a reversal of meaning critically engage different cognitive processes or engage those processes to a different degree than figures that reverse in perspective.

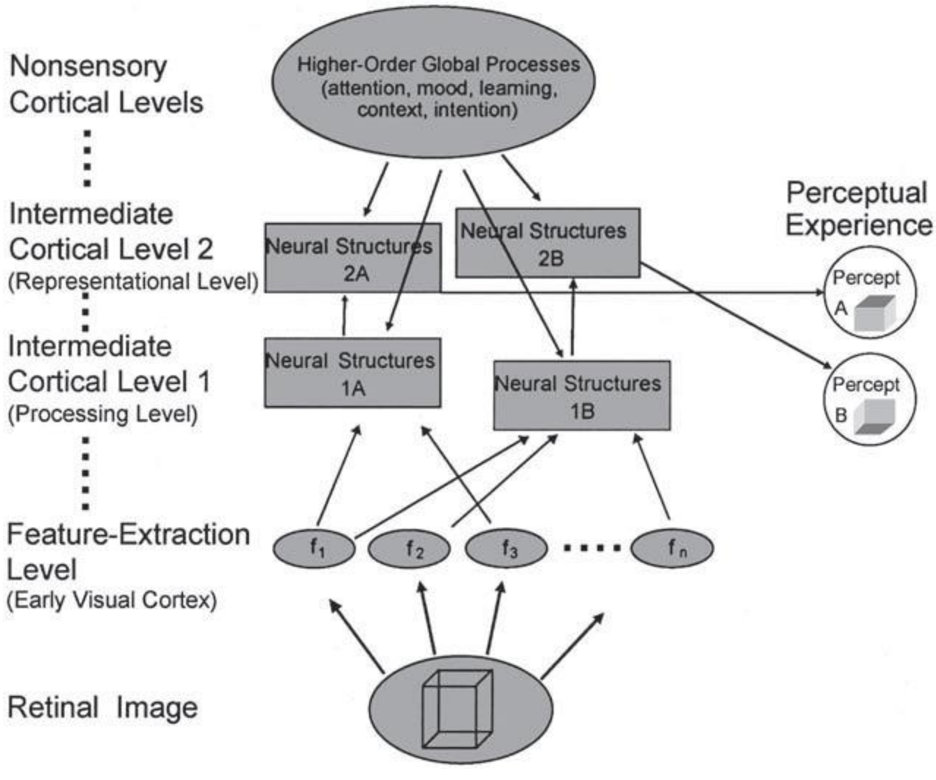

Figure 11. Hybrid model of Long and Toppino (2004).

Figure 12. Boring's (1930) wife/mother-in-law.

Other theories have been proposed to explain multistable phenomena. These theories are not classifiabile in a bottom-up, top-down or hybrid model.

In order to explain the mechanisms underlying perceptual construction, many studies proposed the self-organization theory (Maturana & Varela, 1980; Kelso, 1995) according to which systems, initially chaotic, generates states of global coherence (forms, collective behaviors, ordered structures) completely unpredictable a priori. In other words, the systems are capable of self-organization.

According to the self-organization theory the external stimuli are not causally related to perception but they are only initial conditions which stimulate self-organization processes in the brain. They induce non-specific fluctuations that must be transformed into stable states by the cognitive system. Therefore, cognition is produced by a non-linear self-organization process wich allows organisms to hold their stability (autopoiesis) (Varela et al. 1974; Maturana & Varela, 1980). The spontaneous oscillation between different percepts, in the bistable figure, is a clear example of self-organization. This oscillation can be defined as the property of a dynamic system to obtain different states of stability in a non-linear manner (Braun & Mattia, 2010; Haken, 1978, 1996). Therefore, the multistable perception can be considered as a transition between two or more different attractors (configurations that the multistable figure can assume). In other words, perception is considered an active disambiguation process.

An alternative model to explain multistable perception has been provided by Leopold and Logothetis (1999). They suggested that the perceptual switch depends on higher cognitive mechanisms on the sensory areas. These mechanisms steadily rearrange the incoming information and avoid erroneous or disadvantageous interpretations. The role of top-down processes would be essential to orientate and choose an appropriate behavior in confused environmental situations. In order to support their model, the authors referred to neuropsychological and psychophysiological evidences showing that the perceptual reversals: a) start spontaneously and are influenced by individual factors such as the mental state and attention; b) switching is facilitated by learning and is impaired by cortical lesions in non visual areas; c) perceptual dominances show temporal dynamics similar to those observed in spontaneously initiated behaviors; d) fMRI studies have showed that the cortical areas involved in higher cognitive activities are specifically activated during perceptual instability. Therefore, the multistable perception would represent the manifestation of a cognitive strategy in the case of ambiguous situations, because the perception cannot remain anchored to only one possible solution.

2. Multistable visual phenomena: empirical evidences

Multistability emphasizes the subjective experience of the perceiver, by using stimuli that are physically stable but lead to different phenomenology. Therefore, multistability phenomena play a crucial role in studies of perceptual awareness (Schwartz et al., 2012).

In order to investigate the brain activity during bistable perception, researchers used a great number of methodologies. They have been able to address whether (and in what areas) cortical activity exhibits changes corresponding to the reported perceptual changes or whether the cortical areas exhibit a constant level of activity, mimicking the unchanging physical character of the stimulus (Long and Toppino, 2004). The study of neural processes involved in multistable perception provided experimental evidences on the interaction between bottom-up and top-down mechanisms.

It is possible to distinguish two major classes of studies, namely those that have investigated cortical areas involved in the perceptual reversal process by means of functional magnetic resonance imaging (fMRI), and those that used electroencephalography (EEG) and analysis of event-related potentials (ERP) in order to obtain a precise time resolution to understand the contribution of lower and higher cognitve mechanisms in multistable perception (Eagleman, 2001). This latter produced very interesting data in order to understand the role of attention in bistable perception.

According to all contributions, a useful distinction to keep in mind is between “what competes” and “how competition takes place” (Hupé et al., 2008) between two percepts in bistable perception. “What competes” is the content of sensory experience, the components of the stimulus that have to be bound into perceptual objects, corresponding to the ‘neural events associated with the representation of a given perceptual state’ (Kang & Blake, 2010). “How competition occurs” depends on the neural processes ‘that are responsible for switches between alternative perceptual states’ (Kang & Blake, 2010). Put in a different way, the question is ‘what determines the change in perceptual organization after the observer has been perceiving the stimulus in a particular way’ (Rock, 1975). While the “what” and “how” questions are independent in principle, empirical evidence does not always provide a basis for distinguishing them unequivocally.

2.1 Functional and neural correlates of Perceptual Reversal

Although the multistable perception has been studied for more than a century (Long and Toppino, 2004), the underlying mechanisms are still unclear. Several studies focused on the question of “when” and “how” the perceptual reversal occurs. Kleinschmidt et al. (1998) used event-related fMRI to localize transient human brain activity.

Specifically, the authors defined the neural correlates of flips in visual perception by asking human observers to look at ambiguous figures during fMRI. Subjects were instructed to repetitively report their conscious experience of the visual scene by key-press, defining the occurrence of perceptual reversals and the presence of stable percepts. The figures used were "vase / faces" (Rubin, 1915) and "my wife and my mother-in-law" (Boring, 1930) to dissociate reversal-related responses from those reflecting preference for the dominant, because these two figures have little categorical difference between the two possible percepts. Contrasting perceptual reversals with perceptual stability, they found responses in prestriate visual cortical areas, most prominently in bilateral ventral occipital cortex (middle fusiform gyrus) and posterior intraparietal cortex, as well as in other occipital and some frontal areas, but not in sensorimotor cortices.

The bilateral ventral occipital and parietal responses were localized in visual areas Frontal activations were located bilaterally in ventral prefrontal areas and tfrontal eye fields, and were interpreted as a correlate of covert shifts of spatial attention. Kleinschmidt et al. (1998) found also transient de-activations associated with perceptual reversals compared to stable percepts in the calcarine cortex and the posterior thalamus (pulvinar complex) bilaterally. Given the sequence of stable visual percepts alternating with spontaneous reversals, they interpreted deactivations to indicate that activity during a stable percept, i.e. during maintained `binding', is transiently disrupted during the `de-' and `re-binding' associated with perceptual reversals. Hence, these findings suggest a crucial functional contribution of primary visual cortex to perceptual stability. This behaviour of ‘early’ visual cortex is sign-inverted to that in the ‘late’ stage of the two specialized visual pathways that displayed activity increases during perceptual reversals. Similar to primary visual cortex, the pulvinar is, by virtue of massive interconnection, a key node in the visual system and displays complex response properties that combine sensitivity to different stimulus attributes (Benevento & Port 1995). However, it differs from primary visual cortex because its activity is more readily modulated by attentional mechanisms (Robinson & Petersen 1992; LaBerge 1995). Thus, the pulvinar would have a key-role in the integration of specialized visual processing subserving perception. Therefore, the activity breakdown during a transition between two percepts could reflect the temporary absence of a clear-cut winner in the rivalry between two percepts. Conversely, regained coherence of perceptual interpretation after such a transition could be associated with high activity levels (Kleinschmidt et al., 1998). Kleinschmidt et al. (1998) suggested that the metastability perceptual related to ambiguous stimuli is associated with rapid redistribution of neuronal activity between distinct specialized cortical and subcortical structures. The results provide, therefore, experimental evidence for cognitive models of visual perception that propose widespread cooperation between functionally distinct and spatially segregated cortical areas (Damasio 1989).

Other fMRI studies suggest that non-visual areas play an important role in multistable perception. For example, Lumer et al. (1998) confirmed that the activity in the fusiform gyrus, but not in the striate cortex, was connected to the perceptual transitions during binocular rivalry. They also noticed activity in several frontal and parietal areas usually associated with various cognitive behaviors. This study showed for the first time that the frontoparietal areas are actively involved in multistable visual phenomena.

Inui et al. (2000) have examined the cerebral activity for the depth perception of the Necker cube by fMRI. They used three types of line drawing figures, the Necker cube, hidden line elimination cube and overlapping squares. Subjects were instructed to perceive both orientations of the depth of the Necker cube. They were instructed to shift their attention voluntarily during viewing overlapping squares to obtain a control for the attentional shift in perceiving the Necker cube. Results showed an activity in bilateral parietal areas during the Necker cube perception compared with other control (unambigous) conditions. Inui et al. (2000) suggested that a neural process similar to mental image manipulation occurs during the depth perception of the Necker cube and that extracting visual spatial information invokes responses in motor preparation areas such as those found to mediate motor imagery.

Tracy et al. (2005) focused on fMRI activations associated with rapid, conscious and deliberate changes in the interpretation of a constant physical stimulus. In their experiment, they manipulated instructional set (reversal and suppression) while keeping the similar perceptual stimuli. They presented the Necker cube and required to shift quickly from one percept to another. In a separate experimental condition, they used similar stimuli and asked explicity to not shift or reverse the percepts. The goal was to maximise neural activity associated with top down suppression of any switch in perceptual state. The results showed an increase of the activity in several segregated areas during reversal but not during suppression operation.

In this same study, deactivations were also found in both conditions. The decrease in activation decreases associated with active reversal relative to resting baseline revealed five significant clusters: left insula, superior temporal gyrus, right exstrastriate, right middle temporal gyrus, right anterior cerebellum and right postcentral gyrus. Activation decreases associated with active suppression relative to the resting baseline showed four areas of activation: medial frontal, left superior temporal gyrus and insula, right cuneus and precuneus and right anterior cerebellum. The medial frontal activation was posterior to the region activated during active reversal relative to suppression. Therefore, Tracy at al. (2005) found multiple, segregated areas engaged in the reversal operation, but very limited regions unique to the suppression operation in terms of activation. They considered the activation in medial frontal and cerebellar regions associated with reversal of Necker cube to be part of an internal attentional system that calls for information from sensory regions to implement and support subjective and desired percepts. They hypothesized that the cerebellum, including the dentate, is important during the anticipation of upcoming internal percepts, in order to shift visual focal attention to a new feature of the percept and make this feature salient. The authors suggested two interpretations about the role of the medial frontal cortex. According to the first hypothesis, the medial frontal cortex provides crucial information about body position, viewpoint, and object orientation. Likewise, the evidence for deactivation of this region during suppression suggests that this information has to be inhibited in order to prevent reversals. Alternatively, the frontal activity may reflect a process of task switching where this area selects the different neural pathways associated with each percept of stimulus. Indeed the medial frontal region is responsive to predictable task order, a characteristic that emerges from the expected alternations between the two views of the cube~~.~~This study showed how object recognition can occur in non sensory regions with the broader implication that when external sensory input is unchanging “top-down” processes play a larger role, probably dictating where in the processing hierarchy the percept recognition takes place.

Results in Tracy et al. (2005)’s study differ from those observing changes in sensory areas during ambiguous figures processing (Downar et al., 2000). In addition, the studies described above (Kleinschmidt et al., 1998; Lumer et al., 1998; Inui et al., 2000; Rizzolatti et al., 1994) found same brain activations during both the switch between percepts of reversible figures (without any change of the physical characteristics of the stimulus) and perception of stimulus in which the change in phsysical characteristics is real. They also found in the occipital regions that the decreased activation was lower and more posterior than that observed by Tracy et al. (2005); no activation of cerebellar and of the medial frontal area during inversions was observed. Probably these different results in (Kleinschmidt et al. (1998) and Tracy et al. (2005), are due to the use of different kinds of experimental design. Indeed, in the study of Kleinschmidt et al., (1998) 2D stimuli were used and spontaneous inversions (absence of instructions) were observed, whereas in the study of Tracy et al., (2005) depth clues were used and instructions to maximize reversals or suppressions of the ambiguous figure. Finally, studies that found an activation in the same sensory areas during stimulus perception in which the change of the phsysical characteristics is real (Downar et al., 2000; Lumer et al., 1998) used motion stimuli (rather than static lines as in the Necker cube), which probably activated the visual regions (Tracy et al., 2005). Tracy et al. (2005) hypothesized that all factors that maximized the sensitivity of the medial frontal cortex involve non-sensory aspects of the process. Finally, Tracy et al. (2005) suggested that the medial frontal cortex processes a specific type of somatosensory information (body position/perspective relative to the object) which is used to generate the mental image of the 3D cube.

Conversely, Inui et al. (2000) observed bilateral activity in premotor and parietal cortex in explicit reversal conditions of the Necker cube. This study used a very limited exposure time (2 vs 30 s exposure in Tracy et al. (2005)), with the instruction to only reverse once during that time. Premotor activation found by Inui et a. (2000) was more inferior and lateral than the medial frontal activity observed by Tracy et al. (2005). This may reflect mental imagery.

Shen et al. (2009) found that different brain regions are deputed to hold information (perceptual memory) during endogenous stabilization, whereas other areas induce perceptual reversal (a neural process of perceptual destabilization). In order to increase the neural intensity of Necker's effect, Shen et al used a lattice resulting from the combination of several Necker cubes, both in ambiguous version (without depth clues) and two unambiguous Necker lattices variants (where ambiguity is reduced by depth cues). They used a discontinuous paradigm with two experimental conditions (endogenous and exogenous) and two perceptual events (reversal and stabilization) in each condition. In the endogenous condition, two ambiguous Necker lattices were presented; for the exogenous condition, they replaced the ambiguous Necker lattice by an unambiguous Necker lattice where depth cues favored the peception of one form over the other. During endogenous stabilization, the authors found that increased activity was restricted to the right anterior portion of the superior temporal sulcus, right posterior portion of the temporal lobe, and the rigth ventral frontal cortex. During endogenous reversal, differential activity was increased in several cortical regions including the frontal lobe and the anterior portion of superior temporal gyri. These results suggested that the right anterior portion of the superior temporal sulcus and the right ventral frontal cortex hold the trace of the previous perceptual dominance; conversely, during endogenous reversal, previous perceptual dominance is interrupted. Here, the right dorsal frontal cortex modulates activity in the right ventral frontal cortex and right anterior portion of the superior temporal sulcus. This modulation induces endogenous reversal or destabilization. Then, the destabilizing signals seem to emanate from the right dorsal frontal cortex. The process of perceptual stabilization represents interference with signals favoring destabilization (Noest et al., 2007). The authors observed activity in parietotemporal cortex and occipital lobe during reversal and stabilization, both exogenous and endogenous. This suggests that low-level physical characteristics of the image do not play a major role. Shen et al. (2009) found, also, that in stimulus-driven reversal (exogenous), perceptual memory has little or no influence on perceptual processing, which is asscociated with reduced activity in the right anterior portions of the superior temporal sulcus. These observations support the idea that this portion of the temporal sulcus holds the trace of perceptual dominance (or perceptual memory). This result is in line with earlier reports that temporal lobe activity is closely correlated with percetual reversal (Sheinberg & Logothetis, 1997; Kreiman and al., 2002). Then, the authors concluded that the right anterior portion of the superior temporal sulcus reflects the perceptual stabilization or memory and this is modulated by destabilizing influences in the right frontal lobe. The role of frontal lobe in perceptual reversal was found also in clinical studies. Frontal lobe damage makes the alternative percepts of a bistable stimulus harder to identify (Ricci & Blundo, 1990; Meenan & Miller, 1994) (but see Valle-Inclan & Gallego, 2006) and impairs top-down volitional control over the perceptual sequence (Windmann et al., 2006). This may depend on impared connections between the superior temporal gyrus and the frontal cortex. However, in their study, Shen et al. (2009) did not observe a significant differential activity in the frontal lobe between the exogenous and endogenous condition, indicating that this region also contributes equally to inversions in both conditions.

In general, various studies (Long & Toppino, 2004; Kleinschmidt et al., 1998; Lumer et al., 1998; Inui et al., 2000; Tracy et al., 2005; Shen et al., 2009) have shown that the perceptual reversal involves different brain areas from the primary visual cortex, particularly the extrastriate and frontal areas.

Recent studies confirmed these findings. Kanai et al. (2010) and Kanai & Rees (2011) found a strong correlation between the number of perceptual reversals and some structural differences in the superior parietal cortex. In particular, positive associations have been observed between the density of the gray matter in circumscribed regions of the superior bilateral parietal cortex and the perceptive switching. This may depend on the different transmission of signal from the superior parietal cortex to the sensory areas. In a few words, the greater density of the gray matter in the superior parietal regions could produce stronger and more effective signals that could facilitate the perceptive switching (Kleinshmidt, 2012).

Knapen et al., (2011) found that the right frontal-parietal network is associated with perceptual transitions during bistable percetion. Specifically, they found perception transition-related activity primarily located in the right hemisphere, including the intraparietal sulcus (IPS), superior parietal lobule (SPL), and more anterior parietal areas including the right hemisphere temporo-parietal junction

(TPJ); frontal areas including the frontal eye field (FEF), the inferior frontal junction (IFJ), and the dorsolateral prefrontal cortex (DLPFC). The authors suggested that occurrence of frontoparietal activity during perceptual transitions can plausibly be attributed, at least in part, to changes in sensory experience, attentional state, and task. According to this view, the initial cause of perceptual alternation could be a destabilization of the current dominant perceptual representation, perhaps due to neural adaptation in sensory brain areas (Blake et al., 2003; Lankheet, 2006; Brascamp et al., 2006; Pastukhov and Braun, 2007; van Ee, 2009; Alais et al., 2010). Following this destabilization, frontoparietal areas might respond by initiating a reorganization through feedback signals to those same sensory areas, resulting in the formation of a new dominant percept. In this scenario, perceptual alternations would involve a cascade of events, some of them causing frontoparietal areas to activate and others caused by frontoparietal areas themselves.

Weilnhammer et al. (2013) in an fMRI experiment confirmed previous findings of greater activity in frontoparietal areas during bistable perception. In addition, they applied dynamic causal modeling to identify the neural model that best explains the observed BOLD signals in terms of effective connectivity. The authors found that enhanced activity for perceptual transitions is associated with a modulation of top-down connectivity from frontal to visual cortex, thus arguing for a crucial role of frontoparietal cortex in perceptual transitions during bistable perception.

2.2 The role of higher cognitive processes in multistable visual phenomena

Leopold and Logothetis (1999) proposed an ‘’environment exploration’’ theory to explain multistable visual phenomena. They suggested that perceptual reversals are the consequence of a generalized high-level ‘’exploratory’’ mechanism that directs selective attention in a way that forces lower-level perceptual systems to periodically ‘’refresh’’. Selective attention involves a salience increase of certain visual features such as location, color, motion, or form (Sperling et al., 2001).

The exploratory mechanism described by Leopold and Logothetis (1999) is a mechanism in which the ultimate goal is to ‘’use’’ and ‘’act upon’’ environmental information. By continually reorganizing and refreshing perceptual processing, accurate interpretation of visual input improves. In everyday situations, this central mechanism (most likely a fronto-parietal network) works with eye movement centers (the frontal eye fields) to mediate a continuous exploration of the visual scene. In bistable perception experiments, due to the ambiguity of the stimuli, the visual scene requires continual exploration, and reversals in perceptual interpretation consistently occur. Leopold and Logothetis (1999) also pointed out the similarities between control over bistable perception and other voluntary behaviors, mostly with respect to the improvement over time due to practice and learning. Specifically, they argued that like many cognitive and non-cognitive behaviors, the reversal during perception of ambiguous figures is subject to a great degree of voluntary control. As voluntary processes can initiate a motor output or affect a stimulus-contingent behavior, they can also control to a large degree which of two competing stimuli is seen. In the case of reversible figures, several studies put forward evidence that the subject’s intention plays an important role in the pattern of perceptual dominance (Lack, 1978; Collyer and Bevan, 1970). Naïve observers, for example, can nearly achieve a three-fold increase in their reversal rate if they consciously attempt to see ‘fast’ alternations rather than ‘slow’ alternations. Such control cannot be attributed to eye movements, as it does not disappear when stimuli are presented as after images or stabilized on the retina by some other means. In addition, control over perceptual reversal improves significantly with practice. It is important to note that although the theory of environmental exploration poses a critical role of selective attention (often classified as a top-down process), the authors descrided the attentional shifting as largely involuntary and automatic (bottom-up processes).

The role of higher cognitve processes in these visual phenomena seems confirmed by clinical studies. In a neuropsychological study, Windmann et al. (2006) found an interesting dissociation of voluntary control abilities in patients with frontal lobe damage. They investigated reported perceptual reversals in patients with circumscribed lesions of the prefrontal cortex and healthy control participants in three experimental conditions: hold (maintaining the dominant view), speed (inducing as many perceptual switches as possible), and neutral (no intervention). Results indicated that although the patients showed normal switching rates in the neutral condition and were able to control perceptual switches in the hold condition as much as control subjects, they found it difficult to facilitate reversals specifically in the speed condition. A possible explanation is that voluntary perceptual switching might require some form of attention-regulated ‘‘deactivation’’ or ‘‘destabilization’’ of the dominant pattern before the alternative pattern can be selected. The patients’ impairment in the speed condition, then (as well as their reduced ability to recognize the second view of the pattern), could result from a reduced ability to intentionally ‘‘let go’’ the dominant pattern instead of (or in addition to) a mere selection problem

(Windmann et al., 2006). Therefore, Windmann et al. (2006) suggested that the prefrontal cortex is not necessary for maintaining conscious representations of continuously perceived visual objects, but does seem essential for selecting and intentionally switching between competing object representations in line with current goals. These results are consitent with those of Trojano et al. (2010). Indeed, in a patient (Trojano et al., 2010) a correlation between ability to reverse the figure-ground of bistable stimuli and cognitive flexibility and selective attention was found, confirming an important role of the frontal lobe in perceptual reversal processes. The patient (female, 63 years old) suffered ischemic vascular lesions in the left half of the splenium of the corpus callosum, in the left occipital gyrus, bilateral occipitotemporal gyri, and in the inferior face of the right cerebellar hemisphere; an MRI also showed small hemorrhagic lesions in the right insula and small lacunar pontine lesion. During the Birmingham Object Recognition Battery (BORB) in order to assess neuropsychological disorders of visual object recognition, the patient showed no difficulties in recognizing and identifying objects. However, during the description of complex figures with elements of ambiguity, the patient was impaired in figure-ground structuring, reaching the identification of just a percept per time. Furthermore, the neuropsychological assessment underlined the typical difficulties of patients with frontal lobe damage, such as the reduced cognitive flexibility, selective attention and working memory disorders, as well as a short-term memory deficit. The authors tested the patient's ability to switch between percepts, by means of two tests. One tested endogenous perceptual reversal rates by presenting reversible figures; the second aimed at checking the patient’s ability to use cognitive strategies to reverse the figure-ground, by presentation of reversible figures with cues. The patient’s performance was compared with that of a control group. The patients showed difficulties to switch between percepts in both tests.The authors suggested that the difficulties were linked to reduction of cognitive flexibility, selective attention and working memory disorders, confirming the role of higher cognitive processes in perceptive reversibility (Kleinschmidt et al., 1998; Lumer et al., 1998; Tracy et al., 2005; Shen et al., 2009; Windmann et al., 2006).

Some authors (Tracy et al., 2005, Windmann et al., 2006) have supported the hypothesis that perceptive changes during perception of ambiguous figures are the result of activations and deactivations in different non-sensorial areas and in functionally distinct cortical structures (especially between the medial frontal area and the cerebellum). The evidence that the patient described by Trojano et al. (2010) was not able to operate reversal of ambiguous images coupled with specific frontal defects, is consistent with a cognitive interpretation of the perceptive deficit. In fact, she was able to quickly and clearly identify the dominant percept but not to reverse the figure-ground or use cues to move her attention between percepts.

Selective attention allows focusing cognitive resources on a specific goal, ignoring the insignificant signals (Daini, 2007). As a matter of fact, during perceptual reversals, the dominant percept must be abandoned in favour of the latter. This suggests that attention must be selectively turned towards other characteristics of the image. In addition, inhibition of the dominant precept in favour of the other one requires the use of the same sensorial information in an authentic manner, which consists in modifying the interpretation of the image that has been dominant up to that moment (Trojano et al., 2010). This ability implies the integrity of specific abilities such as cognitive flexibility and working memory. Cognitive flexibility allows the development of new strategies to be adapted to specific environmental requests; working memory allows maintaining a trace of the selected stimulus and updating the information

(Grossi and Trojano, 2002). Without these abilities, the subject appears rigid and repetitive, preferring usual and simple cognitive strategies (Grossi and Trojano, 2002).

In order to verify the possible role of superior cognitive processes such as attention in bistable perception, several studies have used event-related potential (ERPs) to measure early changes in brain activity associated with perceptual reversal.

Previous researches on brain activity associated with multistable perception used backward-averaging techniques, finding a slow, positive wave in parietal and frontal areas (Başar-Eroglu et al., 1993; Isoglu-Alkaç et al., 1998; Strüber et al., 2000). This component, named Late Positive Component (LPC; Strüber et al., 2000, Pitts et al., 2007), has a significant similarity to the P300 wave, that is correlated with cognitive and attentive processes (Verleger et al., 2005), and it provides experimental evidence in support of the top-down approach in visual perception.

Kornmeier and Bach's studies (2004, 2005) did not confirm the involvement of attentional processes in perceptual reversal processes. They identified two early ERP components related to endogenous perceptual reversals of the Necker cube. They analyzed and described these components by computing difference waves from reversal trials minus stability trials. The largest difference between the two waveforms began at 160 ms post-stimulus, peaked at 250 ms, and persisted until about 400 ms. This broad, negative, reversal-related difference was termed the reversal negativity (RN) (Kornmeier & Bach, 2004). An earlier reversal component was identified in a subsequent study, the reversal positivity (RP), and peaked at 120 ms poststimulus (Kornmeier & Bach, 2005). Kornmeier and Bach argued that the ERP traces for perceptual reversals support a low level (or bottom–up) theory of multistable perception because the differences occurred so early in the waveform. Pitts et al. (2007) investigated whether these ERP differences represent general "perceptual displacement" mechanisms that can apply to different types of multistable perceptual reversals or are specific for Necker cube reversals. To this purpose, three stimuli were used: Schröder's staircase, which elicits similar depth-orientation reversals as the Necker cube; Rubin's face/vase, which elicits figure-ground reversals; and Lemmo's cheetahs (figure 13), a novel multistable stimulus, which involves figure belongingness reversals of a natural image. Results showed differences in the components of the ERPs between inversions and stability for the three stimuli and a possible counterpart to the reverse reversal negativity was also identified: the frontal reversal positivity. Futhermore, Pitts et al. (2007) analyzed the reversal-related ERPs in such a way that allows comparisons with existing visual ERP research, particularly with studies involving spatial and selective attention (Hillyard and Anllo-Vento, 1998; Hillyard et al., 1998; Luck et al., 1994; Mangun, 1995).

An effect of early visual-spatial attention on figure inversion was suggested by an analysis of the occipital components P1 and N1. These results support a model of multistable perception where early changes in spatial attention (indicated by increments P1 and N1) modulate perceptual inversions (indicated by "reversal negativity" or "selection negativity (SeN)). Although it is difficult to localize the neural generators of ERP components, some attempts have been made to identify the neurophysiological sources of P1 and N1 components. These approaches include combining ERP and fMRI techniques in a single study (Di Russo, et al., 2001; Martinez et al., 2001), combining ERP and PET measurements (Woldorff et al., 1997), combining ERP and MEG measurements (Hopf, et al., 2002). All of these approaches provide converging evidence that the generator of the occipital P1 is located in the extrastriate cortex, either in dorsal or ventral regions, depending on the particular techniques used. The N1 generators, on the other hand, have been localized in the ventral pathway, in particular the in the occipito-temporal cortex. Enhancement of P1 and/or N1 amplitudes, therefore, may reflect an initial increase in the activity of the extrastriate cortex and a subsequent increase in occipitotemporal cortex activation. Following this initial change in extrastriate activity, cortical regions in the ventral pathway are then affected by the allocation of spatial attention and show differences in activation for reversal/stability trials (i.e., N1 enhancement for reversal trials) (Pitts et al., 2007). These results did not strictly support bottom-up or top-down theory of multistable perception, but suggest a critical role of perceptual exploration mediated by visual attentional mechanisms (Pitts et al., 2007). In a subsequent study, in order to clarify the role of attentional mechanisms in perceptual reversal, Pitts et al. (2008) recorded RN while observers maintained one of three ‘intentional approaches’, (1) try to reverse perception as often as possible, (2) try to stabilize perception for as long as possible, and (3) maintain a passive approach. Their results indicate that top-down mechanisms can affect perception of bistable figures at least as early as 150ms post-stimulus onset (indicated by amplitude enhancements of the RN component) and that postperceptual processing is affected by top-down control, indicated by late positive component (LPC) amplitude differences (Pitts et al., 2008).

Based on these studies (e.g., Kornmeier and Bach, 2004, 2006; Pitts et al., 2007, 2008), Qui et al. (2009) hypothesized that the perceptual reversal of ambiguous figure (the vase–face illusion) may not only depend on basic perceptual principles (low-level visual perception) but also can be influenced by top-down control.Therefore, there might be some difference for these early and late ERP components (N1, P1, RN or P300) between the face and vase response to the vase–face figure.

They provided a cue (face or vase) to make subjects attend the target stimuli in the vase–face ambiguous figure, and compared the spatiotemporal cortical activation patterns underlying face (face–face) or vase (vase–vase) processing to the ambiguous figure using high-density (64-channel) event-related brain potential (ERP) recordings. The ERP analysis found that the anterior N100, P160, N320 and posterior P100 and N160 were elicited by the face–face and vase–vase responses. Qui et al. (2009) suggest that the anterior N100 might reflect deployment of attention (conscious effort) to identify the target stimuli (face or vase) in early processing of the ambiguous figure, and the N320 might be the reversal negativity (RN) involved in involuntary perceptual reversals (from face to vase or reverse). In addition, the LPC might reflect post-perceptual processing supporting the view of Pitts et al. (2008).

Pitts et al., (2009) investigated the functional significance of ERP components more linked to perceptual reversion such as RN and LPC. The authors identified neural generators for the RN in inferior occipito-temporal cortex, while LPC generators were estimated to be located in superior parietal and inferior temporal regions. The authors suggest that RN could probably reflect the intermediate level in processing between sensory and central systems.

Although different techniques and methods were used to study bistable perception, the question of the role of bottom-up and top-down processes remains open. The study reported in the next chapter aimed at investigating the involvement of the dorsal prefrontal cortex and the occipito-temporal cortex in perceptual reversal tasks by means of rTMS.

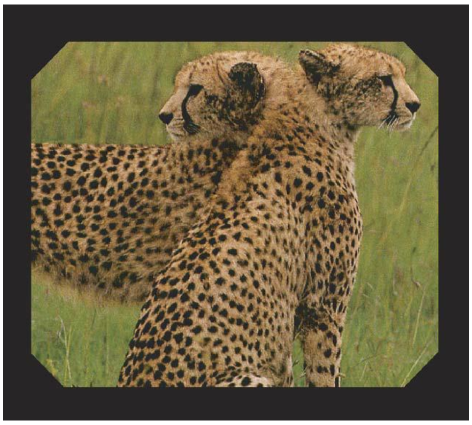

Figure 13. Lemmo's ambiguous cheetahs elicit object-belongingness reversals; that is, the cheetah in the front can appear to be looking to the right while the cheetah in the back is looking to the left or, alternatively, the cheetah in the front can appear to be looking to the left while the cheetah in the back is looking to the right

3. The role of executive functions in the perceptual reversal task: a rTMS study

3.1 Introduction

Gestalt psychologists (Kofka, 1935, Köhler 1940, Wertheimer 1923) suggested the existence of two innate tendencies that affect the vision. One follows the principles of grouping and the other the figure-ground principle: any stimulus considered as a figure pops-out in relation to the background; consequently, there is no figure without ground (Rubin, 1915). In building up a representation of the visual world, the brain has to cope with the fact that any given two-dimensional retinal image could be the projection of countless object configurations in the three-dimensional world. Although in the majority of situations this inherent ambiguity is resolved by the visual system, there are cases in which human vision alternates between different interpretations of a given stimulus. Common examples of such multistable or ambiguous stimuli include figure–ground reversals (Rubin, 1915). In these images, the distinction between figure and ground is not often clear: elements of the figure can be both figure and ground and it is impossible to simultaneously perceive the elements, because the contour belongs to only one of them (Anolli, 1998). Reversible figures offer a potentially fruitful tool to test the relationship between neural activity and sensory perception, because, in the absence of any extrinsic change in the stimulus, perceptual alternations must be due to specific brain processes that lead to conscious vision. The explanations proposed for the bistability of these figures emphasizie either bottom-up or top-down processes. The satiation theory (Köhler & Wallach, 1944) suggests that perceptual reversals are the result of the adaptation processes occurring in stimulus-driven sensory mechanisms. The activity of one perceptual mechanism supports only one of the attainable percepts, and when this mechanism fatigues, another one comes into action, and the competing percept emerges (e.g., Cohen, 1959). The cognitive explanation suggests that the reversals are caused by feedback operations of central mechanisms on lower level sensory activities (e.g., Girgus et al., 1977).

The most used techniques to investigate the underlying processes for perceptual inversions of reversible images are fMRI and ERP.

All fMRI studies agree in finding that perceptual reversal involves different brain areas from the primary visual cortex, particularly in the superior temporal sulcus (Shen et al., 2009), bilateral parietal areas, bilateral ventral occipital cortex (middle fusiform gyrus) and posterior intraparietal cortex, as well as in other occipital and frontal areas, but not in the sensorimotor cortices (Kleinschmidt et al.,1998; Inui et al., 2000; Kanai et al. 2010; Kanai & Rees, 2011). Specifically, frontal activations are located in the medial prefrontal areas (Tracy et al., 2005), ventral prefrontal areas and in the frontal eye fields bilaterally (Kleinschmidt et al., 1998, Shen et al, 2009). Results of fMRI studies seem to confirm a preminent role of higher cognitive processes in perceptual reversal. Conversaly, electrophysiological studies have provided conflicting results. Kornmeier and Bach (2004, 2005) did not confirm the involvement of higher cognitive processes in perceptual reversal. They were able to identify two early ERP components related to endogenous perceptual reversals. The authors argued that the early ERP traces for perceptual reversals support a low-level (or bottom–up) theory of multistable perception. Conversely, Pitts et al (2007, 2008, 2009) and Qui et al. (2009) found early changes in spatial attention (indicated by increments of P1 and N1) that modulate perceptual inversions (indicated by "reversal negativity" or "selection negativity (SeN)). These results suggest that perceptual reversals may not only depend on basic perceptual principles (low-level visual perception) but also can be influenced by top-down control. According to the top-down hypthesis, the frontal regions might provide an impetus to earlier visual brain regions to re-evaluate the visual input (Rees 2004; Sterzer et al. 2009). This would constitute an active role, suggesting that frontal regions “drive” or “cause” the perceptual switches. Frontoparietal regions implicated in perceptual switching (Kleinschmidt et al. 1998; Lumer et al. 1998; Lumer and Rees 1999; Inui et al. 2000; Sterzer et al. 2002; Schoth et al. 2007; Zaretskaya et al. 2010) can overlap with the frontoparietal attention network (e.g., Coull et al. 1996; Corbetta 1998; Nobre et al. 1999; Pessoa et al. 2003; Naghavi and Nyberg 2005). Indeed, several researchers have hypothesised that perceptual reorganization or reconfiguration in the visual system may be prompted by higher order regions (e.g., Leopold and Logothetis 1999; Rees 2004; Slotnick and Yantis 2005; Pitts et al., 2007; Pitts et al., 2008; Sterzer et al. 2009). This suggests that a form of (selective) attention may be responsible for perceptual switching in bistable vision. However, the precise role that the frontal cortex plays in the resolution of ambiguity remains an open question (de Graaf et al. 2011). Indeed, a similarity between frontal activations for bistable vision and for attention does not necessarily imply that the frontal activations actually cause the perceptual switches. It has repeatedly been shown that, under certain circumstances, people are able to control their bistable perception, inducing more frequent or less frequent switches between the competing conscious percepts (Pelton and Solley 1968; Liebert and Burk 1985; Horlitz and O'Leary 1993; Hol et al. 2003; Toppino 2003; Meng and Tong 2004; van Ee et al. 2005; Brouwer and van Ee 2006; Windmann et al. 2006; Kornmeier et al. 2009). It seems that attention-based theories of bistable vision might predict that the same top-down pathway, involved in voluntarily induced perceptual switching, might be involved in spontaneous switching. Yet, the neural origins of both passive and voluntarily controlled perceptual switches remain unclear, particularly concerning the role of higher order top-down regions. de Graaf et al. (2011) studied not only passive bistable vision but also voluntarily controlled bistable vision. They induced ‘‘virtual lesions,’’ with transcranial magnetic stimulation (TMS), in frontal, parietal, and 2 lower level visual cortices using an established ambiguous structure-from-motion stimulus. They found that dorsolateral prefrontal cortex was causally relevant for voluntary control over perceptual switches. In contrast, no evidence was found for an active role of frontal cortex in passive bistable vision. Thus, it seems that the same pathway used for voluntary top-down modulation of bistable vision is not used during passive bistable viewing. The study of de Graaf et al. (2011) is one of the few in which TMS was applied to investigate the neural basis of perceptual switchings. Indeed, although different approaches have been used to investigate the multistable phenomena, such as combining ERP and fMRI techniques in a single study (Di Russo, et al., 2001; Martinez et al., 2001), combining ERP and PET measurements (Woldorff et al., 1997), combining ERP and MEG measurements (Hopf, et al., 2002) few studies used transcranial magnetic stimulation (TMS). TMS is considered a standard stimulation technique for the noninvasive investigation of cognitive function (Pascual-Leone et al., 2000), whereby neural tissue is stimulated by using the principles of electromagnetic induction to generate electrical currents in the brain (Barker et al., 1985). A TMS induced change in behavior (usually measured in reaction times, RTs, or accuracy) can be used to inform models of causal relations between specific brain regions and individual cognitive functions (Robertson et al., 2003). The key features of the technique are that the TMS stimulator delivers a large current in a short period of time and the current flowing in the TMS coil produces a magnetic field that lasts for only about a millisecond. Provided that appropriate stimulation parameters are selected, such rapidly changing magnetic field easily penetrates the scalp and skull inducing an electric field sufficient to stimulate the neuronal activity and change the pre-stimulus dynamics of neuronal firing in the stimulated region (Sandrini et al., 2011). An advantage of the TMS is focality or spatial resolution that makes this technique appropriate to investigate a variety of issues in the cognitive neurosciences in general. In the study of multistable perception thanks to the high spatial resolution of TMS it was possible to establish that different regions within the parietal cortex play opposite roles in the control of bistability. Specifically, Carmel et al. (2010) stimulated a site in the right superior parietal lobule (SPL), where activity is time-locked to perceptual switches in rivalry. Offline disruption of the function of this area shortened dominance durations (increased switch rates) in binocular rivalry compared to no stimulation, whereas stimulating a control site (the homologous locus in the left hemisphere) did not. Kanai et al. (2010) found that the posterior and anterior right SPL show opposite relations to the dynamics of bistable perception. For the same bistable stimulus, disruption of the posterior SPL slowed perceptual switching, whereas disruption of the anterior SPL made it faster.

These conflicting results in the above-mentioned studies are not only attributable to the use of different methodologies but also to the difference of stimuli. In fact, some images such as Rubin's "the vase or faces" and Hill's "my wife and my mother in law" are complex and are based on the reversal figure-ground, while others, such as the "Necker cube", are based on a change in perspective and are less complex.

The aim of this study is to clarify the involvement of the right dorsolateral prefrontal cortex as well as the right ventral occipitotemporal cortex, by means of repetitive (r) TMS. The effect of rTMS over the dorsolateral prefrontal cortex is expected to affect the ability to operate perceptual reversal, and to select between the neutral and reversible image.

The hypothesis is that participants would show a reduction in cognitive flexibility and in the ability to shift attention from the dominant percept, when rTMS is delivered over the right dorsolateral prefrontal cortex. In this condition, slower reaction times are expected. Since it is assumed that the right occipito-temporal cortex is not directly involved in perceptual reversal processes, no differences are expected in this condition compared to sham condition. This type of results would support the hypothesis of a role of the right dorsolateral prefrontal cortex and thus of higher cognitive processes in the disambiguation process of reversible figures.

Since in the literature no standardization of reversible figures is reported, in this study a great number of stimuli was used, which respond to more specific criteria for figure-ground reversal. Images requiring a simple reversal of perspective were excluded.

Two pilot studies have been run before of experimental task to select appropriate material.

3.2 Pilot study I

The aim of the first pilot study was to select images with the same degree of complexity. Only images that received at least 85% of correct answers were included in the experimental task.

3.2.1 Materials and methods

Subjects

Twenty right-handed, healthy participants (ten males, mean age= 26.89 years, SD= 2.47 y, range 20-30; mean educational level = 16.66 years, SD= 2.27, range 13-18) were enrolled into the pilot study. The entire experimental procedure was approved by the Ethical Committee of the University of Milano-Bicocca and each volunteer gave written informed consent to participation. All participants were naïve as to the experimental procedure, and the purpose of the study.

Stimuli

71 black-white images (6X9, 9X6, 9x9) were used: 41 figure-ground reversible images (reversible stimuli) and 30 non-reversible images. Reversible images belonged to the “multistability of meaning attribution” category. This category includes images to which two different meanings can be attributed. The visual effect generally presents the viewer with two shape interpretations, each of which is consistent with the retinal image, but only one of which can be maintained at a given moment. This is because the bounding contour can be seen as belonging to the figure shape, which appears interposed against a formless background. If the latter region is interpreted instead as the figure, then the same bounding contour will be seen as belonging to it. A common example is Rubin's vase (also known as the Rubin face or the figure–ground vase) in wich two faces or a vase can be seen.

Non-reversible stimuli were common black-withe figures for which only one percept can be seen.

Image format was JPEG. The images from the internet were modified by GNU Image Manipulation Program (GIMP).

Procedure

Participants were presented with stimuli which subtended 5.6° (height) ×7.4° (width) of visual angle, placed in the center of a screen, 50 cm from the subject at eye level (fixation at centre) in a quiet, well lit room. 71 images were randomly presented. Each trial consisted of a fixation cross at the center of the screen for 1500 ms, followed by the appearance of the stimulus. The subject had to decide whether the image was reversible or neutral by pressing (with his/her right hand) on the keyboard “R” if the answer was “reversible image” or “N” if the answer was “non-reversible image”.

Once the trial had ended, a description of each reversible image was requested to check that the subject had actually performed the figure-ground reversal.

Several practice trials were performed, in order to familiarize with the procedure and the type of stimuli.

Statistical analyses

For each image the percentage of correct answers was considered and the mean and standard deviation on RTs were computed.

One-way Anova with stimuli (revresible, non-reversible) as within subjects variables was run on RTs of correct trials.

3.2.2 Results

34/41 reversible images were correctly reversed at least in 85% of trials (mean percentage= 91.71, SD= 5.13).

21/30 non-reversible images were correctly judged at least in 85% of trials (mean percentage= 95, SD= 5.47).

One-way Anova performed on RTs showed no significant differences between reversible and non-reversible stimuli (F(1,53)= 2.17; p= .147) (see Table 1).

3.3 Pilot study II

The second pilot study aimed at examining the feasibility of the experimental task.

3.3.1 Materials and methods

Subjects

Twenty right-handed, healthy participants (ten males, mean age= 25.84 years, SD= 3.53 y, range 20-31; mean educational level = 15.78 years, SD= 2.12, range 13-18), who did not take part in the previous pilot experiment, were enrolled in this second pilot. The experimental procedure was approved by the Ethical Committee University of Milano-Bicocca and each volunteer gave written informed consent to participation. All participants were naïve as to the experimental procedure, and the purpose of the study.

Stimuli

stimuli that had been correctly judged at least in 85% of the trials in the first pilot study were used: 34 reversible images and 21 non-reversible images. 55 additional stimuli were included. Specifically, these new stimuli consisted of the same 34 reversible stimuli but in a disambiguated version and the same 21 non-reversible stimuli modified in some details. In the disambiguated version, the figure-ground reversal was no longer possible, and only one percept could be seen. Therefore, 110 black-white images (6X9, 9X6, 9x9) were used: 34 figure-ground reversible images (reversible stimuli) and 76 non-reversible images.

The 76 non-reversible images were the same 34 reversible images in a disambiguated version and 21 non-reversible images (neutral stimuli) and the same 21 neutral modified images in some detalis.

Image format was JPEG. The images were modified by GNU Image Manipulation Program (GIMP).

Procedure

The procedure was the same as in the previous pilot study.

Statistical analyses

One-way Anova with category (reversible vs non-reversible) as within subjects variable was run on accuracy (percentage of correct answer) and RTs of correct trials. Levene's Test for equality of variances was applied.

One-way Anova with stimuli (reversible, disambiguated, neutral) as within subjects variable was run on accuracy (percentage of correct answer) and RTs of correct trials.

3.3.2 Results

There were no significant differences in accuracy between reversible and non-reversible stimuli (F(1,108)= 7.93; p= .006). Post-hoc test showed a higher percentage of correct responses for neutral stimuli compared to reversible and disambiguated (p < .005; p= .009, respectively). Means and standard deviations of percentage of correct responses are reported in table 2. Levene's test was not significant (p= .208)

There were no significant differences on RTs between reversible and non reversible stimuli (F(1,108)= 2.61; p= .108). Also, one-way Anova with stimuli (reversible, disambiguated, neutral) as within subjects variable on RTs showed no significant differences (F(2, 107)= 1.73; p= .181). Means and standard deviations of RTs are reported in table 3.

3.3.3 Summary

In the first pilot study 16/71 stimuli (7/41 reversible and 9/30 neutral stimuli) were not correctly reversed at least in 85% of trials. Therefore, they were not included in the second pilot. In the second pilot study, the selected 55 stimuli (34 reversible and 21 neutral) and 55 additional ones were included. The 55 additional stimuli consisted in the same 34 reversible stimuli but in a disambiguated version and the same 21 neutral stimuli modified in some details. Therefore, a total of 110 stimuli were included in the experimental task.

Table 1. Means, SD and range of RTs for reversible and non-reversible stimuli in pilot study I.

	N	RTs (mean)	SD	Min	Max
reversible	34	2340,06	656,68	1391,63	3637,79
non-reversible	21	2600,68	605,36	1014,95	3835,45

Table 2. Means, SD and range of accuracy for reversible, neutral and disambiguated stimuli in pilot study II.

	N	% Accuracy (mean)	SD	% Min	% Max
Reversible	34	91,91	5,07	85	100
Disambiguated	34	89,55	7,82	55	100
Neutral	42	94,64	6,93	75	100

Tabla 3. Means, SD and range of RTs for reversible, neutral and disambiguated stimuli in pilot study II.

	N	RTs (mean)	SD	Min	Max
Reversible	34	2425,199	647,1241	1321,23	3769,9
Disambiguated	34	3051,393	720,6147	2033,76	5445,11
Neutral	42	3669,548	4602,816	1775,84	32523,11

3.4 Experiment task

3.4.1 Materials and methods

Subjects

Thirty right-handed, healthy participants (fourteen males, mean age= 23.93 years, SD= 4.12 y, range 20-37; mean educational level = 15 years, SD= 2.24, range 13-18) were enrolled in the study after a screening to exclude potential adverse effects of TMS. Subjects with medical history of seizures, convulsions, loss of consciousness and traumatic brain injury, carriers of intracranial metallic objects and/or of cardiac pace-makers were excluded. The entire experimental procedure was approved by the Ethical Committee of the University of Milano-Bicocca and each volunteer gave written informed consent to participation. All participants were naïve as to the experimental procedure, and the purpose of the study.

Stimuli

110 black-white images (6X9, 9X6, 9x9), selected through the pilot studies,were used: 34 figure-ground reversible images (reversible stimuli) and 76 non-reversible images. The 76 non-reversible images included: the same 34 reversible images in a disambiguated version where some details have been modified in order to make visible only one percept; 21 non-reversible images (neutral stimuli) and the same 21 neutral modified images in some detalis. Reversible stimuli belonged to the category named "multistability of meaning attribution" (see paragraph 1.1) that includes images to which two different meanings can be attributed (Figure 14). The neutral images have been used as further control condition in addition to control task.

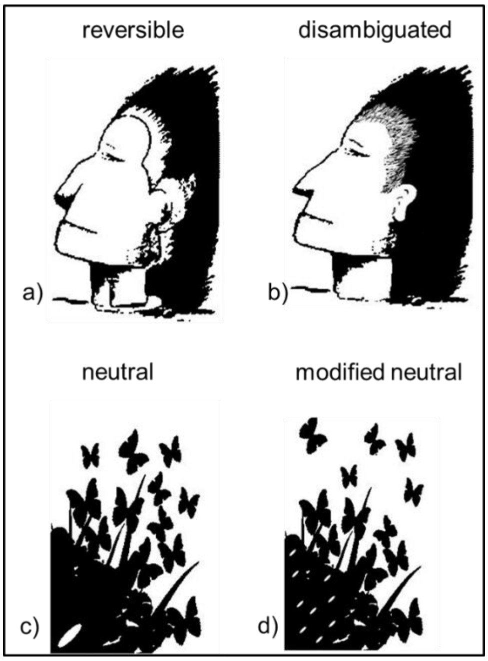

Figure 14. Example stimuli. A) Reversible figure. It is possible to see a the profile of an Indian or an Eskimo by figure-ground reversal; b) figure non-reversible. In this disambiguated version of indian/eschimo is possible to see only the profile of indian; c) neutral figure; d) neutral figure modified in some details

Experimental task

Stimuli, which subtended 5.6° (height) ×7.4°(width) of visual angle, were presented in the center of a screen, 50 cm from the subject at eye level (fixation at centre) in a quiet, well lit room. 1 Hz rTMS (off-line, 10% submotor threshold) was administered for 600 s before the task. After stimulation, 110 images were randomly presented. Each trial consisted of a fixation cross at the center of the screen for 1500 ms, followed by the appearance of the stimulus (Figure 15). The subject had to decide whether the image was reversible or neutral by pressing (with his/her right hand) on the keyboard "R" if the answer was "reversible image" or "N" if the answer was "non-reversible image".

Several practice trials were presented, in order to familiarize with the procedure and the type of stimuli.

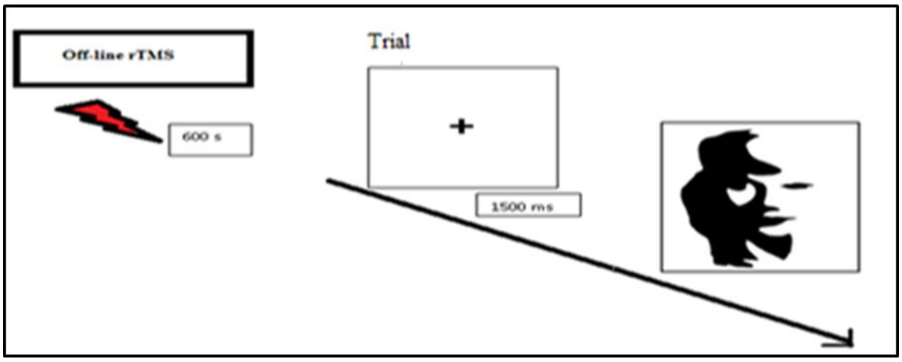

Figure 15. Experimental task. After 600 s of rTMS, 110 images were randomly presented. Each trial consisted of a fixation cross in the center of the screen, which lasted for 1500 ms, followed by the appearance of the stimulus. The subject had to judge whether the image was reversible or neutral by pressing (with his/her right hand) on the keyboard "R" if the answer was "reversible image" or "N" if the answer was "neutral image".

Control task

In order to exclude an unspecific effect of rTMS, a control task was administered before stimulation (session 1) and after the experimental procedure (session 2). A visual pattern task was prepared using checkerboards, with half of the squares black and half white. The task was divided in 2 blocks. Each block included 18 trials. In each trial a first checkerboard was presented on a computer screen for 500 ms. This was followed by a 2000 ms interval with a blank screen, after which a second checkerboard was presented, which could be identical to the previous or different for the position of one square (Figure 16). Subjects were asked to judge whether the two checkerboards were the same or not by pressing one of two response keys. The size of the checkerboards used in the task was established based on the results of a preliminary test, performed prior to the experiment. In this test, checkerboards of increasing size were used: 3×4, 4×5, 5×6, 5×7 and 5×8. For each of the 6 possible sizes, 15 trials were presented. The biggest checkerboard correctly matched in 85% of trials was then used in the experiment (Romero Lauro et al., 2010).

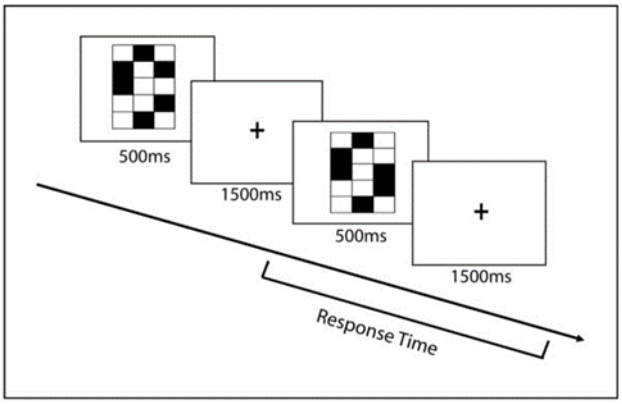

Figure 16. Control task: visual pattern span. A first checkerboard appeared on the screen for 500 ms, followed by a 2000-ms interval. Then a second checkerboard was presented for 500 ms. In the following 1500ms the subjects had to respond whether the two checkerboards the same or not by pressing one of two response keys.

Stimulation protocol

rTMS was carried out by means of a Magstim SuperRapid magnetic stimulator connected to four booster modules and a standard figure-of-eight shaped coil with an outer winding diameter of 70 mm (Magstim Company, Whitland, UK) that generates 2.2 T as a maximum output. Before the experiment, individual resting excitability thresholds of stimulation were determined by stimulating the right motor cortex and inducing a visible contractions evoked by a single TMS pulse in the contralateral first interosseus dorsalis muscle. The threshold was defined as the minimum intensity which induced a visible contraction in the tested muscle. The stimulation intensity used during the experiment was set at 90% of each subject's threshold. Participants wore a tightly fitting Lycra bathing cap on which the positions of Cz (vertex), and other locations from the International 10/20 EEG system were reproduced. The cap was positioned such that the Cz marking corresponded to the individual's measured Cz, thus ensuring that the position of the reference points was constant across subjects. In order to obtain an optimal online placement of the coil on specific anatomical structure the stereotaxic neuronavigation by the SofTaxic Evolution navigator system (E.M.S., Bologna, Italy) was used. This system consists of a graphic user interface and a 3D Fastrak digitizer (Polhemus Inc., Colchester, USA), and has three receivers and one stylus. Three receivers were placed on the subject's head, in order to rule out inaccuracy due to head movements. The stylus was used to register craniometrics landmarks (nasion, inion and two pre-auricular points) on the subject's head. The SofTaxic Navigator system, therefore, allowed the computation of an estimated volume of MRIs of the head, in order to guide the TMS coil positioning. The estimated MRIs were automatically computed by means of a warping procedure, operating on a generic MRI volume (template) on the basis of a set of about 50 points, digitized from the subject's scalp (Fogliata et al., 2007).

1 Hz rTMS trains (off-line, 90% of motor threshold, 600s) were applied on two different sites. The location of the stimulation sites was on average centred on Talairach co-ordinates (X= 39, Y= -41, Z=- 34; (Brodmann's area 9) (D'Esposito et al., 1998) and (X= 41, Y= - 99, Z= - 34; Brodmann's area 18) (Amunts et al., 2000). Subjects were divided in three groups depending on the stimulation condition:

Group 1: rTMS was delivered over the right dorsolateral prefrontal cortex (BA 9).

Group 2: rTMS was delivered over the right ventral occipito-temporal cortex (BA 18)

Group 3: rTMS was delivered over Cz.

For the vertex condition, the coil was tilted of 90° so that it was perpendicular to the floor. This condition reproduced the scalp sensation and the noise associated with the discharge of the coil, but because of the orientation of the coil, no stimulation reached the brain, acting as a sham condition.

Statistical analyses

A repeated measures Anova with group (frontal, occipito-temporal, sham) as between subjects variable and image (reversible, disambiguated, neutral) as within subjects variable was run on RTs of correct trials and on accuracy.

For the control task, a repeated measures Anova with group (frontal, occipito-temporal, sham) and session (S1 and S2) as within subjects variables was run on RTs of correct trials.

3.4.2 Results

Experimental task

Both the main effect of group and image were significant [F(2,27)=5.29; p= .011; η2= .28) and 2,27)=28.17; p< .0001; η2= .51)]; the interaction group x image was also significant [F(4,54)= 5.68; p= .001; η2= .29)] on RTs.

Post-hoc tests highlighted slower RTs for disambiguated and neutral images in the frontal group as compared to the occipito-temporal group (3583,2ms vs 2331,4ms and 3299,3ms vs 2227,2ms respectively; p= .014 and p= .016) and sham group (3583,2ms vs 2352,5ms and 3299,3ms vs 2072,5ms, respectively; p= .019 and p= .006) (see Table 4). No differences between the occipito-temporal and the sham group were found (see Figure 17).

In the case of accuracy (see Table 5), the main effect of image was significant [(F(2,27)= 53.43;p< .001; η2= .493)]. All groups showed greater accuracy for neutral images compared to reversible and disambiguated ones (p< .001). The effect of group was not significant [F(2,27)=.249; p= .781]. The interaction group x image was not significant [F(4,54)=1.17; p= .335; η2 = .080] (see Figure 18).

Control task

The main effect of session was significant [F(1,27)= 17.54; p< .001] but the effect of group was not [F(2,27)= 1.83; p= .18). The interaction group x session was not significant [F(2,27)= 1.17; p= .325; η2 = .080].

Table 4. Means and standard deviations for RTs in experimental task.

		M(n=10)	SD
reversible	Frontal	2345,4	535,8
	Occipital	2021,8	786,3
	Sham	1858,5	345,9
disambiguated	Frontal	3583,2	1157,5
	Occipital	2331,4	767,3
	Sham	2352,5	596,2
neutral	Frontal	3299,3	1274,8
	Occipital	2227,2	752,2
	Sham	2072,5	481,8

Table 5. Means and standard deviations for Accuracy in experimental task.

		M (n=10)	SD
reversibile	Frontal	,8588	,06323
	Occipital	,7735	,14412
	Sham	,8118	,05406
disambiguated	Frontal	,7765	,17217
	Occipital	,7941	,10917
	Sham	,8147	,14545
neutral	Frontal	,9429	,07027
	Occipital	,9381	,06846
	Sham	,9429	,07546

3.4.3 Discussion

In the present study, the role of the dorsolateral prefrontal cortex in perceptual reversal was investigated by means of rTMS. More precisely, the effect of rTMS delivered over the right dorsolateral prefrontal cortex and right ventral occipitotemporal cortex was assessed, while participants judged whether images were reversible or non-reversible. Results showed slower RTs only for non-reversible images in the frontal group as compared to the other two conditions (right ventral occipitotemporal cortex and sham stimulation). These results partly confirmed the hypothesis. Indeed, slower RTs were expected for the frontal group for both reversible and non-reversible images. It could be the case, in our experiment, that for reversible images the figure-ground switching required automatic and passive processes. Conversely, when non-reversible images was presented, subjects had to actively reverse the figure and the ground to find the alternative percept (that was not there), confirming that the right dorsolateral prefrontal cortex plays a prominent role for voluntary control over perceptual switches. This hyphotesis seems to be confirmed by an additional evidence: all groups showed longer RTs (although not statistically significant) and greater accuracy for neutral images compared to reversible and disambiguated ones. This result was found also in the second pilot study and could depend on the fact that subjects before judging the neutral stimuli repeatedly switched between the figure and the background to verify whether there was a second percept. The results of this study are in accordance with those of a previous study de Graaf et al. (2011). They found that the dorsolateral prefrontal cortex was causally relevant for voluntary control over perceptual switches. In contrast, no evidence was found for an active role of the frontal cortex in passive bistable vision. Our results are also in line with a previous lesion study (Windmann et al. 2006) and ERP (Pitts et al., 2007 and 2008) research and with exploration/attention-based theories of perceptual switching (Leopold and Logothetis 1999; Rees 2004; Slotnick and Yantis 2005; Pitts et al., 2007; Pitts et al., 2008; Sterzer et al. 2009), according to which frontal regions can prompt perceptual reconfiguration. It remains to be clarified why the same TMS protocol over the same region in the same participants did not have any effects on passive bistable vision. De Graaf et al. (2011) suggested that automatic top-down modulation involves a different (e.g., more ventral) frontal region or that automatic top-down modulation may involve the same regions but a different neural process from voluntary top-down modulation, a process that is not easily disrupted by TMS or with the current TMS protocol.

Our data suggest that the frontal regions do not start perceptual switching, which would seem to depend on bottom-up mechanisms. Therefore, automatic perceptual switches could be induced at lower levels in the visual system. In this scenario, frontal regions play a role key when voluntary control on reversal is required. This hypothesis is in line with Windmann et al. (2006). Windmann et al. (2006) found an interesting dissociation of voluntary control abilities in patients with frontal lobe damage. Their results indicated that although the patients showed normal switching rates, they were less able to induce as many perceptual switches as possible. Windmann et al. (2006) suggested that voluntary perceptual switching might require some form of attention-regulated ‘‘deactivation’’ or ‘‘destabilization’’ of the dominant pattern before the alternative pattern can be selected.

The idea that perceptual switching could involve different processes confirms the hybrid model proposed by Long and Toppino (2004), according to which both transient, localized sensory and global, long-lasting cognitive processes are required in the perceptual reversals. Therefore, no single process is likely to be the determining process in figural reversal.

However, the fact that subjects were asked “a judgment” could represent a limitation of this study. Therefore, a second experiment was conducted where no judgment was required and only spontaneous reversal was investigated. In addition, in the case of the present study it can not be excluded that the presentation of both, the ambiguous image and its disambiguated version, could play some role. Indeed, Long et al., (1992), investigating the effects of presentation of an unambiguous version of the reversible figure on viewing of the ambiguous figure found a positive-bias effect after a brief presentation of the unambiguous version, favoring the same perceptual response to the subsequently viewed ambiguous figure. In the present experiment, images were randomly presented and the disambiguated version did not preceed the ambiguous version; the bias effect was investigated in the third experiment.

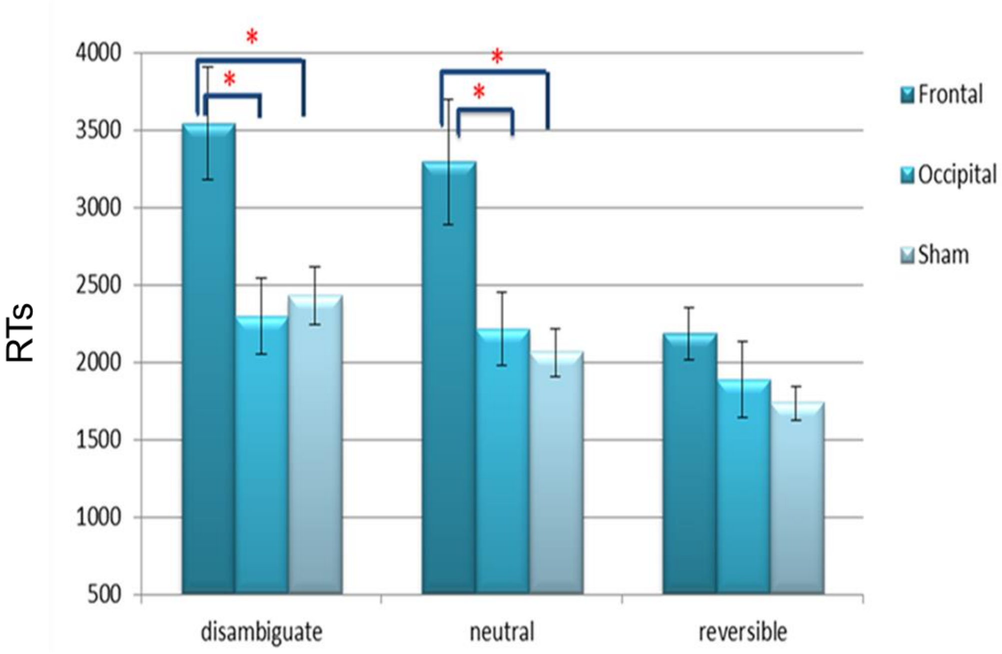

*Figure 14. RTs. *all p value < 0.05. The frontal group showed slower RTs for disambiguated and neutral images compared to the occipito-temporal group.*

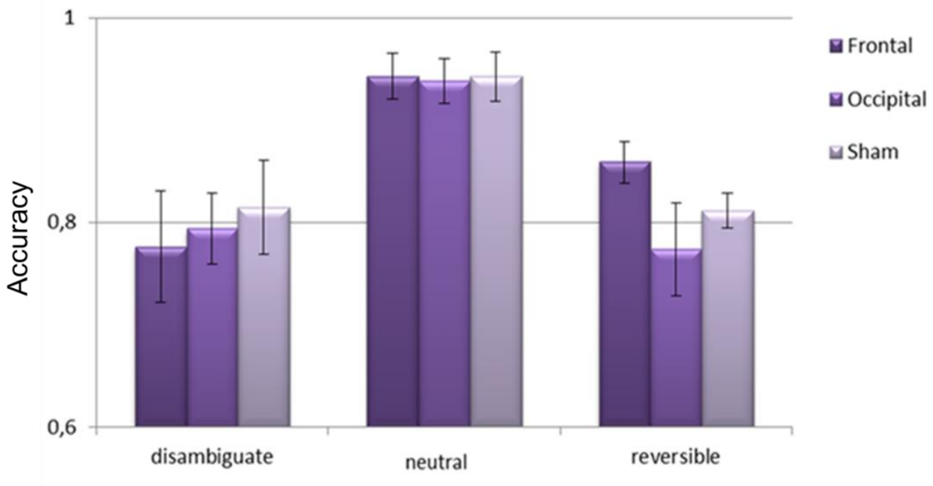

*Figure 15. Accuracy. * All group showed greater accuracy for neutral neutral images compared to reversible and disambiguated images (p< .001)*

4. The role of the right dorsolateral prefrontal cortex in active and passive perceptual switching: two rTMS studies

4.1 Introduction

Two studies were performed in an attempt to provide further information on the role of the dorsolateral prefrontal cortex in the figure-ground switching of reversible images and to investigate the adaptation effect (effect of presentation of an unambiguous version). In the previous study, it was found that the right dorsolateral prefrontal cortex plays a prominent role in voluntary control over perceptual switches but not in passive perceptual switching, which would seem to depend on bottom-up mechanisms. These results are in line with previous lesion (Windmann et al. 2006) and ERP (Pitts et al., 2007 and 2008) studies and with exploration/attention-based theories of perceptual switching (Leopold and Logothetis 1999; Rees 2004; Slotnick and Yantis 2005; Pitts et al., 2007; Pitts et al., 2008; Sterzer et al. 2009). However, in the case of the present study, results could have been affected by the fact that the task required “to judge” whether the stimuli were reversible or not and not only “to reverse” them. Therefore, a second experiment where no judgment was required and only spontaneous reversal was investigated was run. In addition, the presentationing both the ambiguous image and its disambiguated version could play some role. Indeed, Long et al. (1992), investigating the effect of presentation of an unambiguous version of the reversible figure on viewing the ambiguous figure, found a positive-bias effect after a brief (1-5s) presentation of the unambiguous version, favoring the same perceptual response to the subsequently viewed ambiguous figure (positive-bias). Conversely, participants, after a prolonged (from 60 to 150 seconds) inspection of one of the unambiguous versions, reported the alternative version of the presented ambiguous figure. The adaptation (or reverse-bias) effect is commonly classified as depending on sensory processes. These data are usually explained in the framework of the satiation theory, according to which the neural structures responsible for the percept compatible with the unambiguous version are fatigued and, therefore, an alternative version of the ambiguous figure is comprehended. Long and Moran (2007) found that adaptation is not only highly affected by presentation duration of the adapting stimulus, but is also highly localized; so, in order to obtain the effect, adaptation and test stimuli have to match in size. Long and Moran (2007) partially replicated and extended Long et al (1992)’s findings, by assessing the nature of the processes revealed by the application of the adaptation paradigm to reversible figures. In their study, they traced separately: (a) the relatively rapid recovery from retinally localized neural depression produced by an extended adaptation period, and (b) the more stable, global bias produced by cognitive priming. Specifically, Long and Moran (2007) run two experiments investigating the effects of prior exposure conditions on an observer's report of figural reversal. In experiment 1, observers were adapted over several minutes to an unambiguous version of a rotating Necker cube prior to the presentation of the standard ambiguous figure. Results indicated that adaptation produced an immediate bias to perceive the ambiguous figure in the opposite configuration (i.e. reverse bias) and to reduce reports of reversal over the test period. The introduction of a brief delay between the adaptation and test periods revealed that this bias is a highly transient effect and is only clearly evident when the adaptation and test figures are matched in size. In experiment 2, observers were primed with an unambiguous figure for a few seconds prior to the presentation of the standard ambiguous figure. In this case, the obtained bias strongly favored the observer's reporting the ambiguous figure to be in the same configuration as the adapting figure (positive bias); and neither introducing a delay period nor changing figure size had any effect. Long and Moran (2007) concluded that these experiments reveal the distinct roles of transient, retinally localized neural processes as well as more stable, global processes under specifiable conditions. Specifically, in experiment 1 was evident the involvement of transient adaptation effects in localized neural channels that serve to produce a reverse bias and to suppress reversals by temporarily lowering the apparent sensitivity of certain neural structures. These effects appear to dissipate rapidly and are localized to a significant degree to the area of the retina engaged by the adapting stimulus. Most evident in experiment 2 is the involvement of more global, less transient, cognitive processes that positively bias the system toward the configural interpretation of the reversible figure that matches the brief adapting figure. Consequently, Long and Moran (2007) argued that the their work reveals the striking ability of reversible figures to exhibit these two classes of processes under tightly specifiable conditions as the visual system faces the ambiguity problem of incomplete retinal information. Intaitė et al. (2013) explored the transience feature of the adaptation effect. They were interested in the possible outcomes of the adaptation effect, if there are several available interpretations for a subject to select from (i.e. in contrast to a single figure presentation task when two percepts simply interchange each other). Therefore, in this study (Intaité et al., 2013), the adapting stimulus was not shown before the test stimulus, but the two stimuli were presented simultaneously. In order to do that, they incorporated the adaptation and the multiple-figure presentation paradigms (Flügel, 1913; Babich and Standing, 1981; Toppino and Long, 1987). For this purpose, each figure (Rubin vase-faces; Necker cube; Bugelski & Alampay rat-man) was modified twice, so that one of the interpretations would dominate, but another one could still be conceivable. When that kind of design is used, the observer is capable to choose from more than one available perceptual interpretation. Intaité et al., (2013) hypothesized that the introduction of a bias to one of the presented figures should either significantly increase the possible randomness of perceptual changes or, alternatively, the changes would start to follow some sort of unifying pattern (e.g., observers would start to perceive both figures significantly more often in the biased interpretation). Intaité et al. (2013) found that observers tend to perceive two adjacent identical figures as reversing simultaneously, and the same percepts dominated both in the reversal rate and the duration of perception. In addition, the introduction of a bias had a different effect on different ambiguous figures. Effect of bias was most prominent for the Bugelski rat-man figure where both the ‘rat’ and ‘man’ biases suppressed the perception of the opposite interpretation of two simultaneously presented figures. The bias of the ‘up’ percept increased the frequency of its percept and shortened the duration of the ‘down’ percept for the Necker cube. The effect of a bias was least significant for the Rubin vase-faces figure where the bias of ‘vase’ decreased the duration of the ‘faces’ percept. The percepts of two figures presented simultaneously usually reversed synchronously. The introduction of a bias increased the frequency and duration of different percepts for the Bugelski rat-man and the Rubin vase-faces figures when one interpretation was perceived in one figure and another interpretation in the other figure. In the case of biased and neutral figures presented in pairs, modifications of interpretation either increased or decreased the frequency of a biased percept. These results show that both bottom-up and top-down perceptual processes influence the perception of ambiguous figures.

Therefore, these studies on the adaptation effect (Long et al., 1992; Long and Moran, 2007; Intaité et al. (2013) found that either a powerful positive bias or a powerful reverse bias can be readily produced by simply varying the duration for which the unambiguous figure is presented, and they demonstrated that the two effects exhibit very different relationships with either viewing conditions, suggesting distinct sensory and cognitive contributions in a theoretically consistent fashion.

Also in my previous study, results showed that sensory and cognitive processes can differently contribute to reverse. In order to clarify results of the first study, we run other two experimental tasks. The experimental task 1 aimed at investigating the role of the right dorsolateral prefrontal and the right ventral occipitotemporal cortices in spontaneous reversal. For this purpose, only reversible images were used.

Conversely, Experiment 2 was divided in two blocks. In one, participants were simply asked to indicate when the switch occurred and two percepts were visible (passive reversal). In the second, they had to actively reversal the figure-ground in order to perceive the second percept. Furthermore, by adapting the paradigm of Long et al. (1992), the effect of presentation of an unambiguous version before the reversible stimulus was studied. Indeed, in both blocks, half of reversible stimuli were preceded by a brief presentation of their disambiguated version. rTMS was used to investigate the role of the dorsolateral prefrontal cortex. According to the results of Long et al. (1992), the hypothesis was that the brief presentation of the disambiguated version would produce a positive-bias effect, eliciting shorter RTs. In addition, slower RTs was expected when rTMS was delivered on dorsolateral prefrontal cortex.

A pilot study was performed to select additional reversible images beyond those of the previous study.

4.2 Pilot study

The aim of the pilot study was to select images with the same degree of complexity. Only images that in 85% of trials were correctly reversed were selected to be used in experimental tasks.

4.2.1 Materials and methods

Subjects

Fifteen right-handed, healthy participants (five males, mean age= 24.92 years, SD= 2.97 y, range 21-31; mean educational level = 13.71 years, SD= 4.14, range 13-18) were enrolled for the pilot study. The experimental procedure was approved by the Ethical Committee University of Milano-Bicocca and each volunteer gave written informed consent to participation. All participants were naïve as to the experimental procedure, and the purpose of the study.

Stimuli

Ninety black-white images (6X9, 9X6, 9x9) were used: All images were reversible stimuli and belonged to the “multistability of meaning attribution” category. This category includes images to which two different meanings can be attributed (e.g. Rubin's vase). Image format was JPEG. The images from internet were modified by using GNU Image Manipulation Program (GIMP).

Procedure

Participants viewed 90 stimuli which subtended 5.6° (height) ×7.4° (width) of visual angle, randomly presented in the center of a screen 50 cm from the subject at eye level (fixation at centre) in a quiet, well lit room.. Each trial consisted of a fixation cross at the center of the screen for 1500 ms, followed by the appearance of the stimulus for 10s.The subject had to indicate the exact moment in which the figure-ground switching occurred by pressing (with the right hand) the space bar. After each stimulus, the subject was asked to briefly describe the two percepts in order to verify his/her accuracy.

Statistical analyses

For each image the percentage of correct responses was considered.

4.2.2 Results

Eighty out of 90 reversible images were correctly reversed at least in 85% of trials (mean percentage= 92.54, SD= 5.2) and were then used for the experimental task.

4.3 Experiment 1

4.3.1. Materials and methods

Subjects

Thirty healthy volunteers (6 M, mean age= 24.9 years, range 20-31; mean educational= 15.8 years, SD=1.9, range 13-18) who did not take part in the pilot experiment, participated in the study. Exclusion criteria were the same described in the previous study. The entire experimental procedure was approved by the Ethical Committee University of Milano-Bicocca and each volunteer gave written informed consent to participation. All participants were naïve as to the experimental procedure, and the purpose of the study.

Stimuli

Eighty black-white images (6X9, 9X6, 9x9) (selected as previously reported) were reversible stimuli that belonged to the "multistability of meaning attribution" category.

Experimental task

Participants viewed stimuli which subtended 5.6° (height) ×7.4° (width) of visual angle, presented in the center of a screen 50 cm from the subject at eye level (fixation at centre) in a quiet, well lit room.

The reversible stimulus apparead for 10000ms preceded by a fixation cross at the center of the screen for 1500 ms. Participants were instructed to look at them spontaneously and to indicate the exact moment in which the spontaneous perceptual reversal (the second percept was seen) occurred by pressing (with the right hand) the space bar on the keyboard. In order to verify accuracy, after each stimulus, participants were instructed to describe briefly the two percepts.

Several practice trials were administered, in order to familiarize with the procedure and the type of stimuli.

Control task

The control task was tha same of the previous experimental study.

Stimulation protocol

rTMS was carried out by means of the same magnetic stimulator of the first experiment. Before the experiment, individual resting excitability thresholds of stimulation were determined by stimulating the right motor cortex and inducing a visible contractions evoked by a single TMS pulse in the contralateral first interosseus dorsalis muscle. The stimulation intensity used during the experiment was set at 90% of each subject's motor threshold. In order to obtain an optimal online placement of the coil the stereotaxic neuronavigation by the SofTaxic Evolution navigator system was used (E.M.S., Bologna, Italy), as in the previous experiment.

Subjects were divided in three groups depending on the stimulation condition, as in the previous experiment:

Group 1 (10 subjects): rTMS delivered over the right dorsolateral prefrontal cortex (X= 39, Y= -41, Z=- 34; BA 9).

Group 2 (10 subjects): rTMS delivered over the right ventral occipito-temporal cortex (X= 41, Y= - 99, Z= - 34; BA 18)

Group 3 (10 subjects): rTMS delivered over Cz (as in the previous experiment).

Statistical analyses

A one-way Anova with group (frontal, occipito-temporal, sham) as independent variable was run on RTs of correct trials and on accuracy.

For the control task, a repeated measures Anova with group (frontal, occipito-temporal and sham) and session (S1 and S2) as within subjects variables was run on RTs of correct trials.

4.3.2 Results

Experimental task

No significant differences between groups were found for RTs (F(2,27)= 1.98; p= .184) and accuracy (F(2,27)= 1.27; p=.320) (table 6).

Table 6. Means and standard deviations for RTs and accuracy in experiment 1.

	M (RTs)	DS	M (accuracy)	DS
Frontal (10)	3081,19	787,05	,75	,05
Occipital (10)	2470,30	933,08	,80	,01
Sham (10)	3310,67	972,50	,74	,09

Control task

The main effect of session was significant [F(1,27)= 19.226; p< .001 ; η2= .416]. The effect of group was not significant [F(1,27)= .235; p= .633; η2 = .013].The interaction group x session was not significant [F(2, 27)= .608; p= .552; η2=.043)].

4.3.3 Discussion

In the present study, the role of the right dorsolateral prefrontal and right ventral occipitotemporal cortices in spontaneous reversal was investigated. Data showed no significant differences between groups. Therefore, the hypothesis of the previuos study, according to which frontal regions do not give rise to perceptual switching, seems to be confirmed. It is likely that when no action is required to reversal percepts, the switching between two possible alternatives is caused by a passive adaptation of local neural units during early stages of visual processing (Toppino and Long, 1987). These results seem in line with those of some ERPs studies that exclude the involvement of higher cognitive processes (Kornmeier and Bach, 2004, 2005). However, the present data are not sufficient to explain why in the previous study the frontal group showed slower RTs only when non-reversible images were presented. In order to compare the involvement of the frontal regions in passive and active reversal, a further experiment was run. For this purpose, in the last experimental task, rTMS was delivered only over the right dorsolateral prefrontal cortex. In addition, the bias effect of presentation of disambiguated stimuli was investigated.

4.4 Experiment 2

4.4.1 Materials and methods

Subjects

Twenty right-handed, healthy participants (nine males, mean age= 25.32 years, SD= 2.8, range 22-33; mean educational level = 16.59 years, SD= 1.62, range 13-18) who did not take part in the pilot experiment, participated in the study. Exclusion criteria were the same as in the previous study. The entire experimental procedure was approved by the Ethical Committee University of Milano-Bicocca and each volunteer gave written informed consent to participation. All participants were naïve as to the experimental procedure, and the purpose of the study.

Stimuli

120 black-white images (6X9, 9X6, 9x9) were used: 80 images (selected as previously reported) were reversible stimuli that belonged to the "multistability of meaning attribution" category and 40 images were reversible stimuli in a disambiguated version.

Experimental task

Participants viewed stimuli which subtended 5.6° (height) ×7.4° (width) of visual angle, presented in the center of a screen 50 cm from the subject at eye level (fixation at centre) in a quiet, well lit room.

The task was divided in two blocks. In each block, 60 stimuli were showed (40 reversible and 20 disambiguated stimuli). Each block included two conditions: non-bias and bias trials. Specifically, for non-bias trials the reversible stimulus apparead for 10000ms preceded by a fixation cross at the center of the screen for 1500 ms. For bias trials the fixation cross was followed by the appearence of the disambiguated stimulus for 5000ms. After the disambiguated stimulus, its reversible version apparead for 10s. The participants were differently instructed for the two blocks. In a block, when figures were presented, the participants were instructed to view them naturally, not to provoke perceptual reversals (passive condition). In other block, when figures were presented, the participants were instructed to provoke actively perceptual reversals (active condition). Both for passive and active condition the subject had to indicate the exact moment in which the perceptual reversals (the second percept was seen) occurred by pressing (with the right hand) the space bar on the keyboard. In order to verify the accuracy, after each stimulus, the participants were instructed to describe briefly the two percepts. The order of presentation of the two blocks was randomized between subjects.

Several practice trials were presented, in order to familiarize with the procedure and the type of stimuli.

Control task

The control task was tha same of the first two experimental tasks.

Stimulation protocol

rTMS was carried out by means of the same magnetic stimulator of the first experiment. Before the experiment, individual resting excitability thresholds of stimulation were determined by stimulating the right motor cortex and inducing a visible contractions evoked by a single TMS pulse in the contralateral first interosseus dorsalis muscle. The stimulation intensity used during the experiment was set at 90% of each subject’s motor threshold. In order to obtain an optimal online placement of the coil the stereotaxic neuronavigation by the SofTaxic Evolution navigator system was used (E.M.S., Bologna, Italy), as in the first experiment.

1 Hz rTMS trains (off-line, 90% of motor threshold, 900s) were applied on the dorsolateral prefrontal cortex (X= 39, Y= -41, Z=- 34; (Brodmann’s area 9)) (D’Esposito et al., 1998).

Participants were randomly divided in two groups depending on the stimulation condition:

Group 1 (10 subjects) rTMS delivered over the right dorsolateral prefrontal cortex (BA 9).

Group 2 (10 subjects): rTMS delivered over Cz (as in the first experiment).

Statistical analyses

A repeated measures Anova with group (frontal and sham) as between subjects variable and condition (PassiveNon-bias, PassiveBias, ActiveNon-bais, ActiveBias) as within subjects factors was run on RTs and Accuracy.

For the control task, a repeated measures Anova with group (frontal and sham) and session (S1 and S2) as within subjects variables was run on RTs of correct trials.

4.4.2 Results

Experimental task

The repeated measures ANOVA performed on RTs showed no significant main effect of Group (F(1, 18)= 1.246; p= .282; η2= .077) while the effect of condition was significant (F(3, 54)= 5.384; p= .003; η2= .264). There was also a significant group*condition interaction (F(3, 54)= 8.436; p < .001; η2= .360). At post-hoc analysis, the frontal group showed longer RTs in ActiveBias and ActiveNon-bias compared to both the PassiveBias (p= .045, p= .003; respectively) and PassiveNon-Bias (p= .024, p=.001; respectively) condition. Repeated measures ANOVA performed on accuracy showed no significant main effect of group (F(1, 18)= 1.416; p= .25; η2= .086) and of condition (F(3, 54)= 2.081; p= .116); η2= .306). Means and standard deviations of RTs and accuracy for all conditions are reported in Table 7 and 8, respectively.

Control task

The main effect of session was not significant [F(1,18)= .835; p= .373 ; η2= .044], as the effect of group [F(1, 18)= 1.715; p= .207; η2=.087). The interaction group x session was not significant [F(1,18)= .235; p= .633; η2 = .013]

Table 7. Means and standard deviations of RTs for all condition of the experiment 2.

Group	Condition	Mean	SD	Min	Max
frontal (10)					
	ActiveBias	3824,7	587,01	3178,19	4471,24
	AcitiveNon_bias	4073,13	641,63	33,73,80	4772,45
	PassiveBias	2950,86	747,42	2255,63	3646,07
	PassiveNon-bias	2856,16	749,39	2195,52	3516,81
sham (10)					
	ActiveBias	2951,22	1038,54	2341,67	3560,76
	ActiveNon_bias	2921,02	1120,03	2261,67	3580,35
	PassiveBias	3084,73	1052,13	2429,27	3740,19
	PassiveNon-bias	3027,38	974,49	2404,52	3650,24

Table 8. Means and standard deviations of accuracy for all condition of the experiment 2.

Group	Condition	Mean	SD	Min	Max
frontal (10)					
	ActiveBias	0,78	0,03	0,74	0,82
	ActiveNon-bias	0,82	0,06	0,77	0,88
	PassiveBias	0,84	0,04	0,79	0,90
	PassiveNon-bias	0,83	0,04	0,79	0,89
sham (10)					
	ActiveBias	0,86	0,06	0,82	0,90
	ActiveNon-bias	0,83	0,08	0,78	0,89
	PassiveBias	0,86	0,08	0,81	0,91
	PassiveNon-bias	0,86	0,08	0,81	0,91

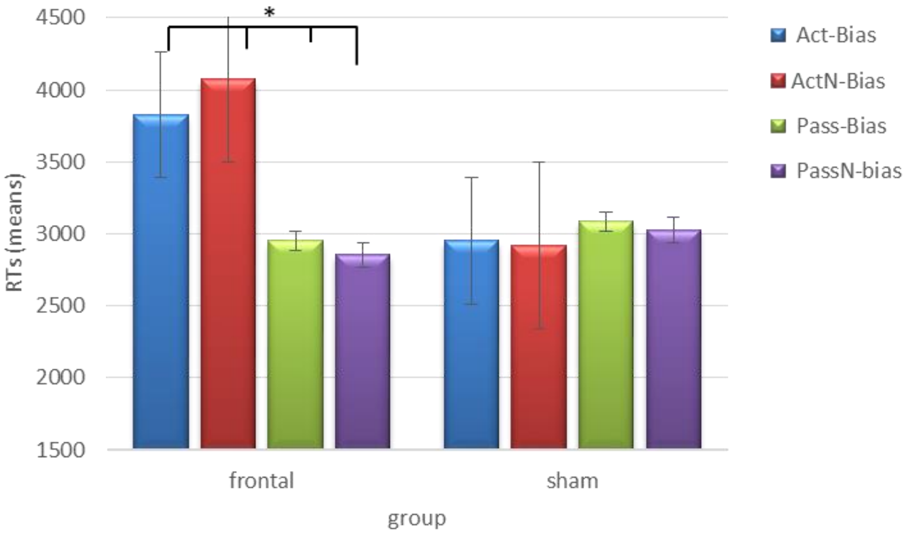

*Figure 16. Experiment 2. RTs. *all p value < 0.05. The frontal group showed slower RTs for active as compared to passive condition.*

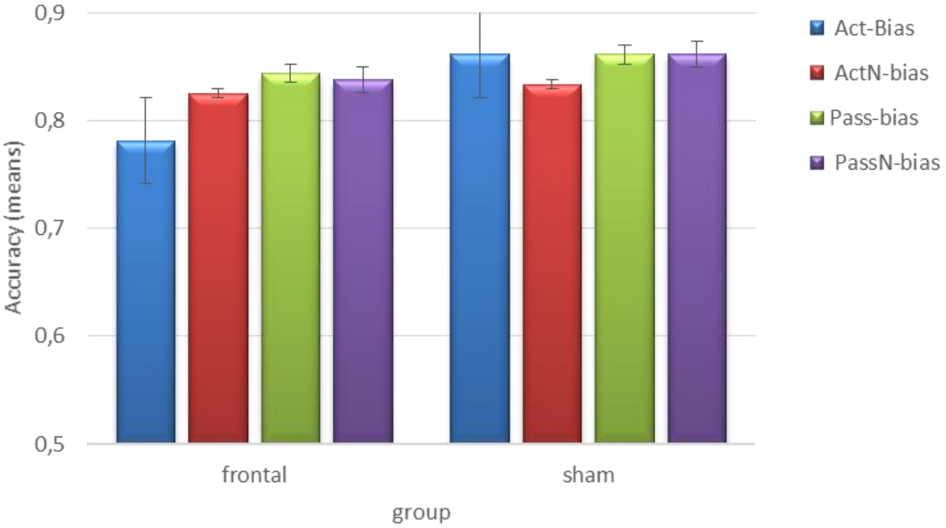

Figure 17. Experiment 2. Accuracy. No significant main effects of group and condition was found.

4.4.3 Discussion

Data from the present study showed that rTMS applied over the dorsolateral prefrontal cortex elicited longer RTs when an active control on perceptual reversal was required, regardless of whether the stimulus was preceded by its disambiguated version or not. This result seems confirm the hypothesis that the dorsolateral prefrontal cortex does not start the spontaneous reversal but it plays a key-role in voluntary control over perceptual switches. In other words, the frontal regions prompt perceptual switching when participants decide voluntarily to abandon the dominant percept in favor of the second percept. The results of this study are also in line with previous studies (Windmann et al. 2006; Pitts et al., 2007 and 2008; Leopold and Logothetis 1999; Rees 2004; Slotnick and Yantis 2005; Sterzer et al. 2009; de Graaf et al., 2011). Therefore, a top-down hypothesis alone is not sufficient to explain the process underlying the figural reversal but also sensory and automatic processes attend in switching. On the other hand, the low-level mechanisms seem to be underlying the passive reversal but it cannot explain because the rTMS applied over prefrontal cortex elicited longer RTs in active reversal. Therefore, the hybrid model proposed by Long and Toppino (2004) seems to be confirmed, since the dissociation between active and passive inversion. We found no bias effect of presentation of the unambiguous stimuli. This result is partly in line with Long et al. (1992). Indeed, they found that observers given a very brief period of adaptation (1 - 5 s) not only failed to exhibit a reverse-bias effect, but were more likely to see the same percept during the test period that they had been exposed to in the adaptation period. The absence of a bias effect can be explained by the variety of stimuli used. Indeed, Intaité et al. (2013) found that the introduction of a bias had a different effect on different ambiguous figures even if they belong to the same category, such as in the present experiment. Therefore, results of this study, besides confirming the role of the right dorsolateral prefrontal areas in perceptual inversions, allow excluding a bias effect of the disambiguated stimuli in the experimental task described in chapter 3.

5. Summary and general discussion

Over the past 150 years, multistable visual phenomena have drawn the attention of researchers who considered them a unique window for studying the underlying processes of visual perception. Research on multistable perception phenomena dates back to Necker’s initial paper (Necker, 1832). However, the neural processes underlying perceptual reversals remain unclear. What makes these stimuli particularly interesting is that an invariant stimulus pattern gives rise to (at least) two different perceptual interpretations and, therefore, allows dissociating perceptual from stimulus driven mechanisms. Different kinds of reversible (or ambiguous) figures have been developed and studied using psychophysical and neurophysiological methods. Well-known examples of such figures include the Necker cube, Boring's wife/mother-in-law figure, Jastrow's duck/ rabbit figure, Schroeder's staircase, Mach's card, Attneave's triangles, and many others (see Blake and Logothetis, 1992; Long and Toppino 2004 for a review of this literature). Bottom-up and top-down hypotheses were proposed to explain these visual phenomena. The former class of explanation places emphasis on essentially passive neural processes of satiation, also known as the localized fatiguing or adaptation of neural `channels'. According to satiation hypotheses, the cortical organization underlying the dominant percept form fatigues and is replaced with the neural activity within the alternate ‘switch’ cortical organization underlying the alternative percept. The second organization, in turn, now fatigues with further viewing until the organization underlying the first percept has sufficiently recovered and again dominates, eventually restoring the original percept; and a perceptual reversal is experienced by the observer (Long and Moran, 2007). Therefore, the bottom-up explanation assumes that perceptual reversal is primarily based on a rivalry between two competing perceptual interpretations at early processing levels, that is, between the retina and the corresponding receptive fields of the primary visual cortex (Blake et al., 2003). Evidences that are typically cited to support a sensory model are the fact that the reversal of figures depends on stimulus properties such as intensity (Lynn, 1961), figural completeness (Babich and Standing, 1981), and continuity of presentation (Leopold et al., 2002). Further results to support a bottom-up model are: the increasing number of reversals over time, the strong retinotopy of the reversal effect (Blake et al., 2003), the reverse bias and adaptation effects (Long and Olszweski, 1999), and the fact that independent reversals occur when simultaneously viewing multiple figures (Babich & Standing, 1981; Toppino and Long, 1987).

In contrast, the other class of explanations, namely top-down explanations, emphasizes the influence of higher cognitive processes. An evidence in favor of this explanation is the observation that the perceptual reversal requires a certain degree of volitional control (Leopold and Logothetis, 1999; Hol et al., 2003; Toppino, 2003; Slotnick and Yantis 2005). Further results that seem to support a cognitive model of figural reversal refer to the influence of attention effects (Hochberg and Peterson, 1987; Rock et al., 1994; Toppino, 2003), familiarity effects (Rock et al., 1994), learning and practice effects (Beer, 1989; Long et al., 1983), expectancy or set effects (Long et al., 1992), or the influence of mental workload (Reisberg, 1983; Reisberg & O'Shaughnessy, 1984). Electrophysiological and neuroimaging studies provide evidence somehow contradictory. Some ERPs studies seem to exclude the involvement of higher cognitive processes (Kornmeier and Bach, 2004, 2005), while other experiments found that perceptual reversals were influenced by early changes in spatial attention (Pitts et al., 2007, 2008, 2009; Qui et al., 2009). fMRI results indicate that the frontoparietal regions are implicated in perceptual switching

(Kleinschmidt et al. 1998; Lumer et al. 1998; Lumer and Rees 1999; Inui et al. 2000; Sterzer et al. 2002; Schoth et al. 2007; Zaretskaya et al. 2010), supporting a top-down hypothesis. An interesting explanation, known as hybrid model, was proposed by Long and Toppino (2004) to clarify these contradictory results. They suggest that the figural reversal depends on both sensory and cognitive processes.

Therefore, to date, the contribution that bottom-up and top-down processes give to perceptual reversal remains an open debate in the literature. In this thesis, three experimental tasks were run to investigate the role of cognitive processes in figural reversal. Specifically, the first study aimed at investigating the involvement of the right dorsolateral prefrontal cortex and the right occipito-temporal cortex in a perceptual reversal task. The involvement of the first structure would support a top-down hypothesis. The results showed that when rTMS was delivered over the right dorsolateral prefrontal cortex, participants were slower to judge stimuli as non-reversible images, but no differences were found for reversible images. This suggests that for reversible images the figure-ground switching requires automatic and passive processes. Conversely, when non-reversible images were presented, participants had to actively reverse the figure and the ground to find whether an alternative percept was available, confirming that the right dorsolateral prefrontal cortex plays a prominent role for voluntary control over perceptual switches. The evidence that all groups showed longer RTs (although not statistically significant) and greater accuracy for neutral images compared to reversible and disambiguated ones seems to support our hypothesis. Indeed, it is likely that participants before judging non-reversible stimuli repeatedly switched between the figure and the background to verify whether there was a second percept. This dissociation between passive and active figural reversal and the evidence that frontal regions play a key-role in voluntary control over figural switches are not new in literature. Indeed, de Graaf et al. (2011) studied not only passive bistable vision but also voluntarily controlled bistable vision, by means of TMS. They found that the dorsolateral prefrontal cortex was causally relevant for voluntary control over perceptual switches but not in passive bistable vision. Also clinical studies found a prominent role of frontal regions in active reversal. Indeed, patients with frontal lesions (Windmann et al., 2006) or with impaired cognitive flexibility (Trojano et al., 2010) seem to be less able to switch voluntarily between the dominant and the alternative percept.

A second study was then perfomed in order to clarify the results of the previous one. In this study, rTMS was delivered over the same sites of the previous experiment but only the spontaneous reversal was investigate. No differences were found between groups, supporting the hypothesis that frontal areas are not involved in starting the perceptual switching.

Since in the first two experimental tasks the dissociation between active and passive reversal was only hypothesized but not directly controlled, a third experiment was run. In addition, the bias effect of the unambiguous version of the reversible figure prior to the presentation of the standard ambiguous figure was investigated.

This experimental task involved two conditions: active and passive reversal. The frontal group showed longer RTs in the active condition compared to the passive one, confirming the hypothesis that frontal regions are not involved in passive reversal but only in active condition. Concerning the bias effect of presenting an unambiguous version of the reversible figure, no bias effect was found. This result could depend on the fact that in the present experiment a great number of stimuli was used. Indeed, Intaité et al. (2013) observed that the introduction of a bias had a different effect on different ambiguous figures, even if these belong to the same category (e.g. the effect of bias is most prominent for the Bugelski rat-man while it is least significant for the Rubin vase-faces figure). In the light of these results and of the fact that the stimuli were randomly presented, it is possible to exclude a bias effect of the disambiguated images in the first experimental task.

Two aspects characterize these three studies. The first is the use of TMS. The second is the high number of reversible images that were employed compared to previous studies. However, some data still need to be clarified. Our results support a critical role of the right dorsolateral prefrontal cortex in figural reversal when a voluntarily control is required. However, it is unclear which type of cognitive control is involved and which role cognitive control plays in initial reversal. Indeed, it is not possible to estabilish how participants induced the figural reversal. It would be interesting to investigate whether they inhibited the dominant perception in favor of the alternative one or moved the attention onto other elements of the figure. For this purpose, a useful technique would be the eye-tracker, a device for measuring eye positions and eye movements.

Without doubt, multistability is a complex phenomenon, and many different processes contribute to it. Therefore, an approach that includes the combination of different techniques in a single study is advisable. In addition, since multistability opens a window on the subjective experience of the perceiver -by using stimuli that are physically stable but lead to a rich and diverse phenomenology- the study of this topic can play a crucial role in understanding how perceptual awareness builds up. Also, it would be interesting to extend the study of multistability from vision to other sensory modalities. As emphasized by Schwartz et al. (2012) , “extending the study of multistability to sensory modalities other than vision is of interest for at least three reasons. Firstly, it provides a method for studying the neural bases of perceptual organization in those modalities. Secondly, the intrinsic characteristics of each sensory modality may extend the scope of the original visual multistability paradigm in important ways. For instance, in audition, the stimuli are by nature time-varying. Competition between perceptual organizations is thus not limited to space or motion direction, but must also involve the time dimension. Thirdly, and perhaps most importantly, the extension from vision to other modalities strengthens the hypothesis that multistability is a general property of perceptual systems”.

6. Conclusion

In sum, the results suggest that the figural reversal involves several processes both bottom-up and top-down, as proposed by Long and Toppino (2004) in their hybrid model. The level of involvement of sensory and cognitive processes seems to strongly depend on stimulus features and experimental condition. However, how the observers produce the inversion remains to be clarified and it could be a starting point for a future study.

In addition, we found that TMS proved to be a valid technique to investigate the neural processes underlying multistable visual phenomena. However, given the complexity of multistability that involves many different processes, the combination of various techniques in a single study would be the best solution.

7. References

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