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Involvement of the parietal cortex in perceptual learning (Eureka effect): An interference approach using rTMS

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ABSTRACT

The neural mechanisms underlying perceptual learning are still under investigation. Eureka effect is a form of rapid, long-lasting perceptual learning by which a degraded image, which appears meaningless when first seen, becomes recognizable after a single exposure to its undegraded version. We used online interference by focal 10-Hz repetitive transcranial magnetic stimulation (rTMS) to evaluate whether the parietal cortex (PC) is involved in Eureka effect, as suggested by neuroimaging data. RTMS of the PC did not affect recognition of degraded pictures when displayed 2 s after the presentation of their undegraded version (learning phase). However, rTMS delivered over either right or left intraparietal sulcus *simultaneously* to the undegraded image presentation, disrupted identification of the degraded version of the same pictures when displayed 30 min after the learning phase. In contrast, recognition of degraded images was unaffected by rTMS over the vertex or by sham rTMS, or when rTMS of either PC was delivered 2 s *after* the presentation of the undegraded image. Findings strongly support the hypothesis that both PC at the level of the intraparietal sulcus play a pivotal role in the Eureka effect particularly in consolidation processes, and contribute to elucidate the neural network underlying rapid perceptual learning.

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1. Introduction

Perceptual learning is the practice-induced improvement in the ability to perform specific perceptual tasks (Ahissar & Hochstein, 2004; Fahle & Poggio, 2002; Fiorentini & Berardi, 1980; Gibson, 1969). It may require a number of trials repetition depending on the difficulty of training condition. However, experimental evidence demonstrated that even a single exposure to a stimulus, if adequately informative, may induce rapid changes in perception (Ahissar & Hochstein, 1997; Dolan et al., 1997). This form of one-shot learning has been defined Eureka effect (Ahissar & Hochstein, 1997) and occurs when an ambiguous image, which appears meaningless when seen for the first time, becomes recognizable after a single exposure to an unambiguous version of the same image (Dolan et al., 1997; Tovee, Rolls, & Ramachandran, 1996). The neural mechanism by which this rapid, strong and long-lasting phenomenon facilitates image recognition are still debated (Ahissar & Hochstein, 1997, 2004). Recordings from single neurones in macaque monkeys showed that the anterior part of the superior temporal sulcus and in the inferior temporal cortex are engaged in visual perceptual learning (Tovee et al., 1996). In humans, functional neuroimaging data showed a bilateral activation of medial and lateral parietal regions, as well as of inferotemporal areas, during the Eureka effect (Dolan et al., 1997). However, functional activation of a brain area does not necessarily mean that it plays a causal role in a certain task. Hence, whether or not the parietal cortex is crucial in rapid perceptual learning is still a matter of investigation.

Transcranial magnetic stimulation (TMS) allows to induce a transient disruption of the neural network responsible for a given cognitive task (Pascual-Leone, Walsh, & Rothwell, 2000). Hence, here we used online interference by focal repetitive TMS (rTMS) to investigate the role of the parietal cortex (PC) at the level of the intraparietal sulcus in the neural processes underlying the Eureka effect. In separate experiments, we evaluated whether rTMS delivered to either the right or left lateral PC in coincidence with the exposure to the unambiguous version of the pictures (learning phase) affected immediate or delayed recognition of the ambiguous images. In addition, the effects of sham stimulation, of rTMS

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of a control site (vertex), and of rTMS of the PC applied *after* the learning phase were also tested.

2. Materials and methods

2.1. Subjects

Thirty-three right-handed healthy volunteers (18 women; mean age 24.2 years, range 19–30 years) with normal or corrected-to-normal vision and no history of implanted metal devices or neurological disease gave their written informed consent. The study was performed according to the Declaration of Helsinki and the local ethics committee approved the use of rTMS. The subjects were asked to report adverse effects experienced during or after rTMS. All participants were naive to the purposes of the study, and information about the experimental hypothesis was provided only after the experimental tests were completed. As the study consisted of three different experiments in which the same visual stimuli were employed, 11 volunteers participated in each experiments and each subject took part in only one experiment.

2.2. TMS procedures

Single-pulse TMS and rTMS were delivered using a Magstim Rapid stimulator with a biphasic current waveform (Magstim Co., UK), connected to an eight-shaped coil (external diameter of each loop, 9 cm) placed tangentially to the scalp, with the handle pointing backwards and 45° away from the midline. Prior to the experimental session, the resting motor threshold (RMT) was measured from either the right and left first dorsal interosseous (FDI) muscle by delivering single magnetic pulses to the hand area of the contralateral primary motor cortex, according to the International Federation of Clinical Neurophysiology Committee recommendations (Rossini et al., 1994). RTMS was delivered at 10-Hz using an intensity of 90% RMT of the contralateral FDI. The duration of the rTMS trains was 500 ms in experiments 1 and 2 and 2 s in experiment 3. These rTMS parameters were in accordance with published international safety recommendations (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). For 10-Hz sham rTMS, a specially designed eight-shaped coil that produces no magnetic field but mimics the acoustic artifact of real stimulation (Magstim Co., UK) was used.

For focal stimulation of the right and left PC, the centre of the junction of the coil was placed over P4 and P3 positions of the 10–20 EEG International System, respectively (Rossi et al., 2006). In each subject, P4 and P3 were localized by a neuronavigational system (SofTaxic, E.M.S., Bologna, Italy) using digitized skull landmarks (nasion, inion, and two preauricular points) and about 50 scalp points provided by a Polaris Vicra optical tracker (Northern Digital, Canada). Coordinates in Talairach space of cortical sites underlying P4 (40, −62, 40) and P3 (−43, −64, 39) were approximately estimated by the optically tracked neuronavigator on the basis of a MRI-constructed stereotaxic template and corresponded to the right and left intraparietal sulcus, respectively. Moreover, rTMS was also applied over the vertex (Cz of the 10–20 EEG International System).

2.3. Visual stimuli and experimental protocol

Seventy gray-scale images representing objects and animals were binarized using the Adobe Photoshop 6.0 software. The binarization process converts the gray-level image to a two-tone (black and white) image (Fig. 1A). These pictures were preliminary shown to another group of 20 young healthy volunteers (age range 22–27 years) in order to select 41 consecutive images that were correctly identified by <15% of subjects when seen for the first time. Such relatively low identification rate was arbitrarily chosen to allow a clear Eureka effect to be detected. This subset of images was used for the Eureka protocol in each experiment. Participants were seated in a comfortable chair 57 cm away from a 17-in. monitor (resolution: 1024 × 768 pixels; refresh frequency: 85 Hz) on which the images were displayed.

Three blocks of 11 visual stimuli were created and presented to each subject (Fig. 1A). For each block, 8 binarized images were displayed before the presentation of the undegraded version of the same picture (coherent sequences) to elicit the Eureka effect in the learning phase (Ahissar & Hochstein, 2004; Dolan et al., 1997). Three non-coherent sequences in which the undegraded and the binarized pictures were different were intermingled to avoid an automatic response (Fig. 1A). Binarized and gray-level images were displayed for 2 s and 500 ms, respectively. Then, the binarized images were displayed again 2 s after the presentation of the gray-level images and subjects were requested to press a button with the right index finger as soon as the presumed identification of the binarized images occurred (immediate response, see Fig. 1A). They were asked to name the stimulus and were given feedback on the correctness of the response. Finally, 30 min after the learning phase, all the coherent sequences of pictures displayed in the three blocks during the learning phase and 8 novel pictures (distractors) were presented for 2 s in the binarized version and subjects were request to repeat the identification task (delayed response, see Fig. 1A). Prior to experiment, a training session with a different set of pictures was performed in order to allow the subject to practice with the procedure.

In each experiment, the perceptual task was performed in three different experimental conditions and one block of visual stimuli was presented in each condition. The order of picture sequences of in each block of visual stimuli, the order of experimental conditions, and the coupling between blocks and experimental conditions were randomized and counterbalanced across subjects.

In experiment 1, we evaluated whether rTMS delivered to the right lateral PC simultaneously to the presentation of the undegraded images (learning phase, see Fig. 1B) influenced the Eureka effect. This condition was compared with one in which subjects received sham rTMS over the same scalp site (sham condition) during the learning phase and with the baseline (no rTMS condition, see Fig. 1B).

Experiment 2 was tailored to test whether rTMS of the left lateral PC also modified the Eureka effect compared to the baseline condition (no rTMS). A third experimental condition in which rTMS was applied over the vertex was included. This control condition provided information complementary to sham rTMS used in experiment 1 by testing for nonspecific effects of real rTMS. Sham stimulation of the lateral PC and real rTMS of a control site (vertex) were included in separate experiments in order to limit the number of visual stimuli to be detected from each participant in each experiment. As in experiment 1, rTMS was simultaneous to the presentation of the undegraded images (Fig. 1B).

As TMS allow us to interfere with the brain function with a temporal resolution in the ms range (Pascual-Leone et al., 2000), experiment 3 aimed to provide a first insight into the timing of rTMS-induced modulation of the Eureka effect. Differently from experiments 1 and 2, real rTMS of either the right or left PC and sham rTMS of the right PC were delivered 2 s after the presentation of the gray-level pictures, during the presentation of binarized images (Fig. 1B).

2.4. Data analysis and statistics

The percentage of binarized pictures identified was seen for the first time (before presentation of the undegraded images) was entered in mixed analyses of variance (ANOVA) with group (subjects participating in experiments 1, 2, and 3) as between-subjects factor and sequence (coherent and non-coherent sequences) as within-subject factor.

In each experimental condition, the Eureka effect was evaluated from the coherent sequences of images, after discarding of trials in which the binarized image was identified before presentation of its undegraded version. When the recognition task was performed 2 s after the presentation of the undegraded images (immediate response), the primary measure used to quantify the performance was the percentage of pictures correctly identified (accuracy). For the delayed response (30 min after the learning phase), accuracy of degraded image recognition was expressed as a percentage of pictures already identified during the immediate response. In either the immediate and delayed responses, the mean response time (RT) from the onset of binarized image presentation was also measured from trials in which the degraded image was recognized.

In each experiment, the dependent variables (accuracy and RT) measured in either the immediate and delayed responses were entered in separate one-way repeated-measures ANOVA with EXPERIMENTAL CONDITION (3 levels) as within-subject factor. Post hoc tests were performed using the Tukey's test. Significance was set at $p < 0.05$.

3. Results

When each block of eleven degraded (binarized) images was seen for the first time (before presentation of the undegraded pictures, see Fig. 1A), the percentages of correct identifications (mean ± SE) in experiments 1, 2, and 3 were: 5.3 ± 2.0% and 7.2 ± 2.0%; 2.7 ± 1.6% and 6.1 ± 2.3%; 4.0 ± 2.3% and 1.0 ± 1.0% for coherent and non-coherent sequences, respectively (range between a minimum of 0% to a maximum of 20% across subjects). Although this baseline performance was particularly low in the group of subjects participating in experiment 3, mixed ANOVA showed no significant difference across the experiments ($F_{2,30} = 1.930$, $p = 0.163$), or between coherent and non-coherent sequences ($F_{1,30} = 1.204$, $p = 0.281$), or interaction between experiment and sequence ($F_{2,30} = 0.850$, $p = 0.438$). In contrast, when the recognition of previously unidentified pictures was performed 2 s after the presentation of their associated grey-scale images ("immediate response" 2 s after the learning phase, see Fig. 1A) in absence of any stimulation ('no rTMS' condition of experiments 1 and 2), the mean accuracy of degraded image identification was extremely high (mean ± SE = 97.7 ± 1.5% and 95.5 ± 2.7%, respectively, see Fig. 2A and B). When the two-tone (black and white) images correctly identified 2 s after the undegraded picture presentation were shown again 30 min after the learning phase ("delayed response", see Fig. 1A), the accuracy of recognition was still quite high (mean ± SE = 73.8 ± 4.0% and 75.2 ± 5.8%, respec-

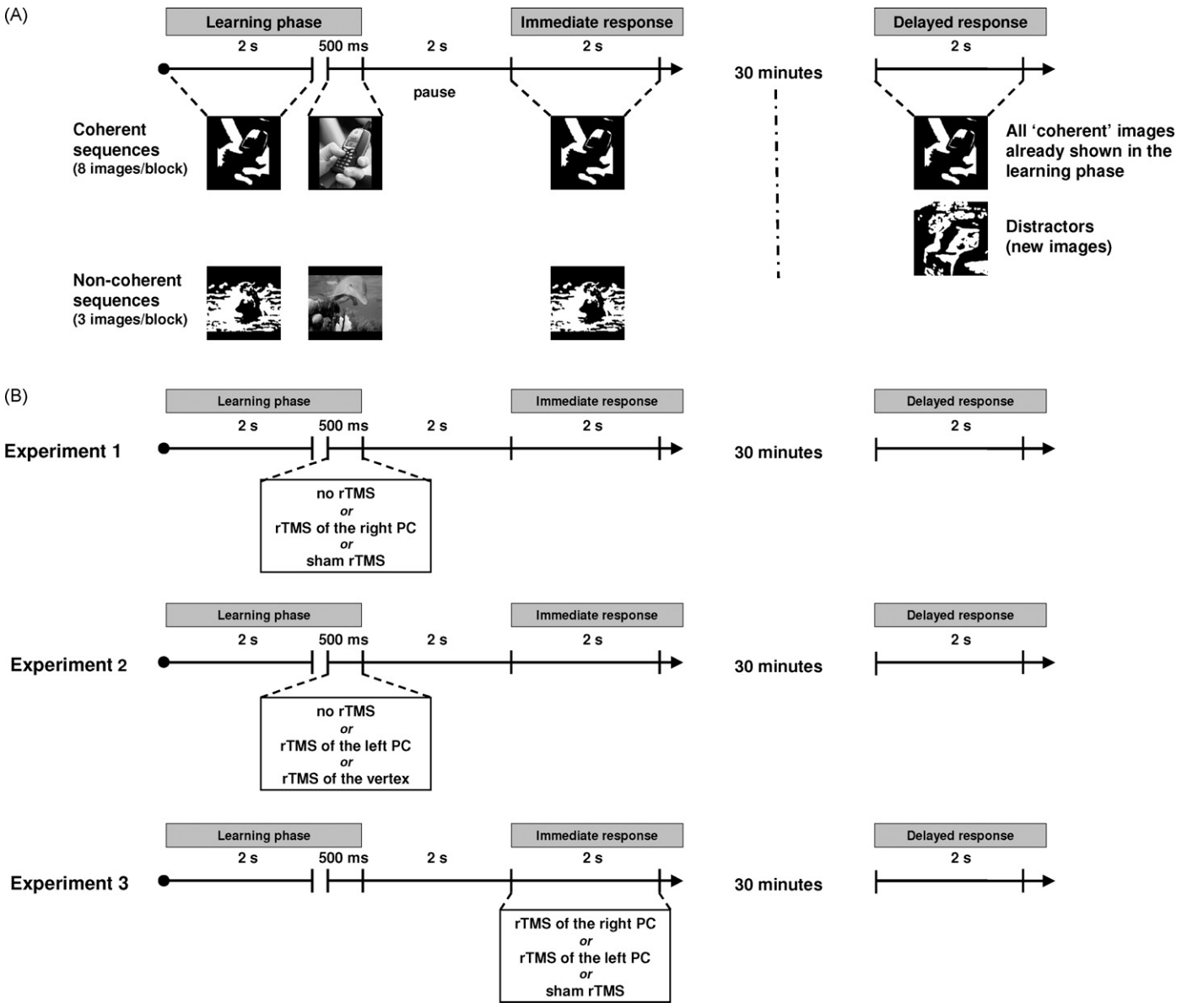

Fig. 1. Procedure for experiments 1, 2, and 3. (A) Timeline of the whole perceptual task used in experiment 1, experiment 2, and experiment 3. In the learning phase, one example of coherent sequence and one example of non-coherent sequence of stimuli are given. (B) Time of interventions in the different experiments. In experiments 1 and 2, rTMS or sham stimulation were delivered simultaneously to the presentation of the undegraded images, whereas in experiment 3, rTMS or sham stimulation were delivered 2 s after the exposure to the gray-scale pictures, during the presentation of binarized images.

tively, see Fig. 2A and B). As to the non-coherent sequences, all binarized images which were not identified when seen for the first time, remained unrecognized when displayed after the exposition to different undegraded pictures. Hence, the Eureka effect was specifically seen with coherent sequences. Again, during the delayed recognition task, the percentage of correct identifications of the novel pictures (distractors) was very low (mean ± SE of all experiments: 6.8 ± 1.7%).

In experiment 1, when the recognition task was performed 2 s after the learning phase, the mean percentage of pictures correctly identified in real rTMS of the right PC and sham stimulation conditions was 94.3 and 95.7%, respectively (Fig. 2A). Repeated-measures ANOVA did not reveal significant differences ($F_{2,20} = 0.581$, $p = 0.568$) across the three experimental conditions (real rTMS, sham stimulation, and no rTMS conditions). In contrast, ANOVA showed a significant effect of experimental condition on the accuracy of the identification task executed 30 min after the learning phase ($F_{2,20} = 5.526$, $p = 0.012$). The Tukey's post hoc test revealed that real rTMS of the right PC reduced the mean percentage of binarized images correctly identified in the post-learning phase (58.9%) with respect to baseline and sham conditions (73.8 and 73.9%, respectively, p = 0.024 for both conditions; see Fig. 2A).

In experiment 2, when the identification task was performed 2 s after the learning phase, repeated-measures ANOVA showed no significant effect of experimental condition on the accuracy ($F_{2,20} = 0.279$, $p = 0.759$; Fig. 2B). In contrast, when the recognition of degraded images was performed 30 min after the learning phase, ANOVA revealed a significant difference in accuracy across experimental conditions ($F_{2,20} = 5.762$, $p = 0.011$). The Tukey's post hoc test showed that rTMS of the left PC reduced mean percentage of binarized images correctly identified in the post-learning phase (60.9%) with respect to baseline and rTMS over the vertex conditions (75.2 and 73.0%, respectively; $p = 0.013$ and 0.038, respectively; see Fig. 2B).

In experiment 3, repeated-measures ANOVA showed no significant accuracy difference across the three experimental conditions

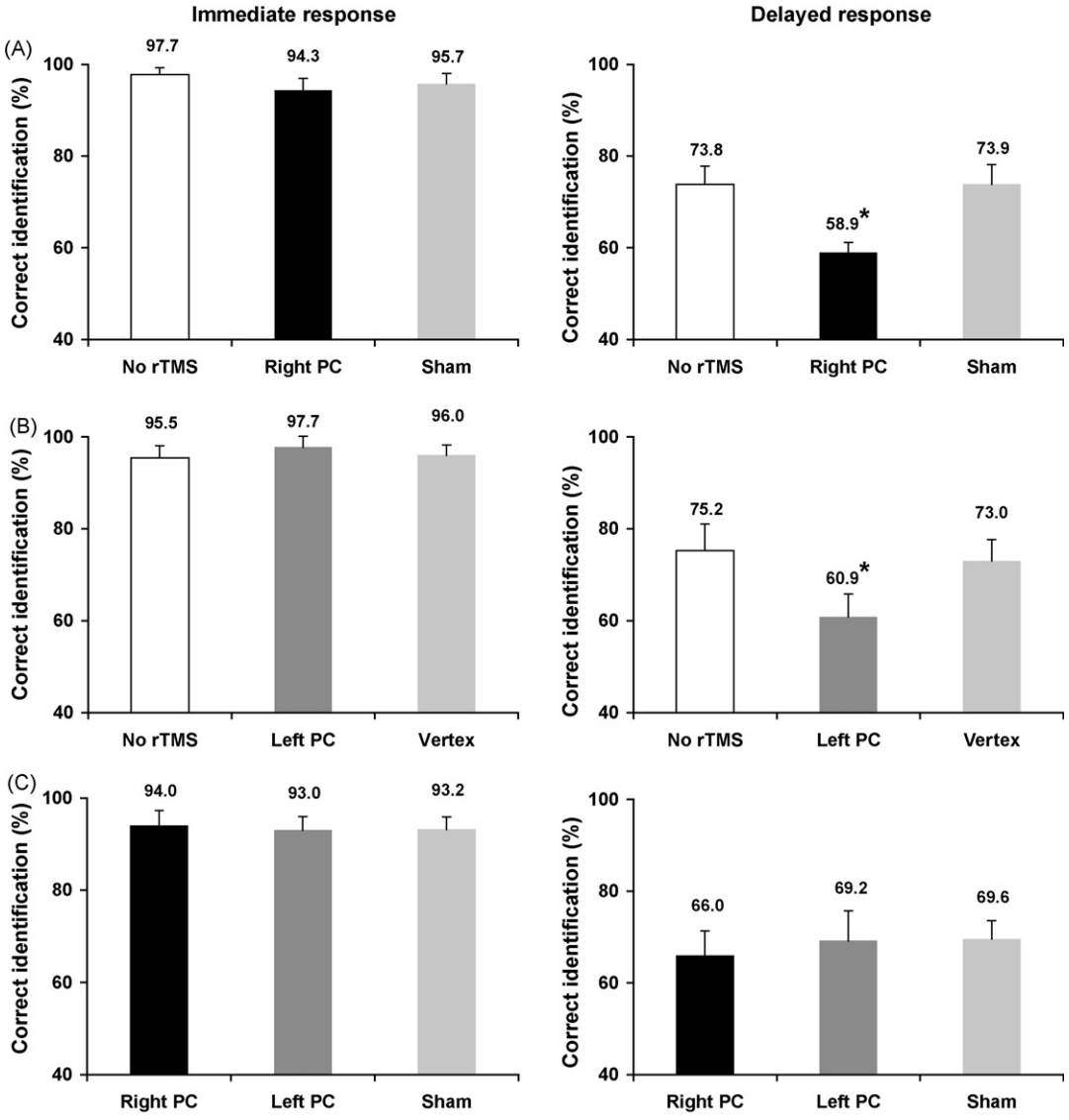

Fig. 2. Graphs Illustrating the Results from experiments 1, 2, and 3. Mean percentage accuracy of the binarized picture recognition task performed 2 s (immediate response) and 30 min (delayed response) after the exposure to the undegraded version of the same image in each experimental condition (learning phase). Error bars indicate the standard error of the mean. Asterisks denote significant post hoc comparisons ($p < 0.05$). (A) Experiment 1. When delivered simultaneously to the undegraded image presentation, rTMS of the right PC significantly reduced the correctness of binarized image identification 30 min after the learning phase with respect to baseline (no rTMS) and sham stimulation conditions. (B) Experiment 2. RTMS of the left PC delivered during the undegraded image presentation significantly worsened binarized image recognition 30 min after the learning phase as compared to baseline (no rTMS) and sham stimulation conditions. (C) Experiment 3. When delivered 2 s after the exposure to undegraded images (i.e. during the binarized picture presentation) rTMS of either PC did not modify the accuracy of the recognition tasks compared to sham stimulation.

($F = 0.037$, $p = 0.963$ and $F = 0.207$, $p = 0.815$ for immediate and delayed responses, respectively; see Fig. 2C).

For all experiments, the mean response times (RT) of the successful recognition tasks are shown in Table S1 (available online). Neither 2 s nor 30 min after the undegraded picture presentation, repeated-measures ANOVA showed a significant effect of experimental condition on the RT (experiment 1: $F_{2,20} = 0.352$, $p = 0.707$ and $F_{2,20} = 1.842$, $p = 0.184$, respectively; experiment 2: $F = 0.295$, $p = 0.748$ and $F = 1.475$, $p = 0.253$, respectively; experiment 3: $F = 2.169$, $p = 0.140$ and $F = 1.567$, $p = 0.239$, respectively).

4. Discussion

The main novel finding of the present study is that transient disruption of the right or left PC by high-frequency rTMS applied at the intraparietal sulcus during the presentation of the non degraded image reduces the probability to identify the degraded images when the recognition task was performed 30 min after the learning phase of the Eureka protocol. This effect requires real stimulation of the PC because it was not observed with sham stimulation. In addition, this finding cannot be accounted for by a nonspecific effect of rTMS because real rTMS over the vertex did not significantly affect the performance. Finally, rTMS of the PC does not influence the recognition of degraded pictures when the identification task is performed 2 s after the unambiguous image presentation. Hence, the present data strongly suggest that both the right and left PC at the level of the intraparietal sulcus contribute to the neural network that is responsible for the Eureka effect and that their role is mainly crucial for the *persistence* of the effects of this rapid perceptual learning on perception. As no interference with the recognition tasks was seen when rTMS of either PC was applied 2 s after the presentation of the non degraded pictures (i.e. during the presentation of binarized images), it is

likely that the PC are mainly engaged during the learning phase of the protocol. Further investigation will be necessary to fully characterize the time course of the rTMS-induced modulation of the Eureka effect with respect to the presentation of unambiguous and degraded pictures by changing the temporal sequence of the trial.

The Eureka effect can be reasonably accounted for in the context of the reverse hierarchy theory of perceptual learning (Ahissar & Hochstein, 1997, 2004) and is thought to be guided from top-down attentional mechanisms (Ahissar & Hochstein, 2004). An interaction between different neural systems including the network responsible for processing stimulus attributes and those involved in spatial attention, feature binding, visual imagery, and memory processes has been hypothesized (Ahissar & Hochstein, 2004; Dolan et al., 1997). Recordings from single neurones in the anterior part of the superior temporal sulcus and in the inferior temporal cortex of macaque monkeys showed an increased firing to ambiguous images of faces after that the unambiguous versions of the same images were displayed (Tovee et al., 1996). These findings likely reflected a neural substrate of rapid perceptual learning. The hypothesis that also the PC is involved in the neural processes underlying the Eureka effect was mainly based on functional neuroimaging data (Dolan et al., 1997). Using positron emission tomography, these authors observed an increased activity in lateral and medial parietal regions when degraded images, which appeared meaningless when seen for the first time, were identified after the presentation of their undegraded version in the explicit learning phase. In addition, recent fMRI data suggest that lateral PC is engaged during the top-down facilitation produced by verbal priming when subjects performed a recognition task of degraded visual objects (Eger et al., 2007). As neuroimaging data are intrinsically correlational, we have dealt with this issue using a causal approach by rTMS-induced disruption of the lateral PC during the Eureka protocol. We decided to stimulated the lateral PC because it is more easily stimulated than medial cortical areas. Hence, our rTMS data expand the knowledge of the neural network underlying perceptual learning in humans, proving evidence that the both PC at the level of the intraparietal sulcus have a causative role in the Eureka effect.

The PC is considered to be engaged in memory related imagery processes (Cabeza et al., 2003; Fletcher et al., 1995; Mottaghy et al., 1999; Wheeler & Buckner, 2004). However, no effect on post-learning performance was obtained by delivering rTMS of the intraparietal sulcus during the presentation of the binarized pictures *after* the explicit learning phase, when processes related to memory of the undegraded images might have been active. In addition, using an episodic memory paradigm not involving active manipulation of the stimuli, Rossi et al. (2006) found that rTMS of either intraparietal sulcus did not interfere with the encoding/retrieval performance of visuospatial material. This would make unlikely the possibility that the impairment of the recognition task we selectively observed in the late post-learning phase of the Eureka protocol (i.e. half an hour after delivering rTMS at the intraparietal sulcus *during* the explicit learning phase) depends on an interference with memory recall processes and favours the view that our data reflect the involvement of the PC at the level of the intraparietal sulcus in processes specifically related to perceptual learning. The ultimate mechanisms by which this involvement occurs are still to be clarified. One hypothesis is that it may depend on the role of lateral PC is thought to exert in attentive processes and visual feature binding (Corbetta, Shulman, Miezin, & Petersen, 1995; Friedman-Hill, Robertson, & Treisman, 1995; Shafritz, Gore, & Marois, 2002). Namely, the partial disruption of such functions produced by focal rTMS of either intraparietal sulcus may be sufficient to disturb the learning process lessening the attentional components and feature binding processing. This would lead to a less effective learning process, sufficient to allow immediate recognition of the degraded image, but insufficient to produce a long lasting effect on perception. This hypothesis is corroborated by recent rTMS data showing an involvement of the right PC in a wide variety of visual search tasks such as visual conjunction of features (Esterman, Verstynen, & Robertson, 2007; Muggleton, Cowey, & Walsh, 2008; Walsh, Ashbridge, & Cowey, 1998), attentional capture (Hodsoll, Mevorach, & Humphreys, 2009), and feature-based search (Oliveri, Zhaoping, Mangano, Turriziani, Smirni, & Cipolotti, 2009). The fact that we found a disruptive effect when rTMS was applied to either the right or left intraparietal sulcus raises the possibility that the bilateral engagement of the lateral PC is peculiarly related to the visual perceptual learning task used in the present study. Alternatively, the role of the lateral PC in perceptual learning could be selectively related to the consolidation processes of the perceptual learning trace, which enable delayed image recognition, but which are not necessary for the immediate picture recognition. We expect that future rTMS studies will further refine the understanding of the neural basis of the different phases of the Eureka effects by providing effective and topographically specific interference with the degraded picture recognition task performed *immediately* after priming.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2010.02.031.

References

Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, *387*, 401–406.
Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Science*, *8*, 457–464.
Cabeza, R., Dolcos, F., Prince, S. E., Rice, H. J., Weissman, D. H., & Nyberg, L. (2003). Attention-related activity during episodic memory retrieval: A crossfunction fMRI study. *Neuropsychologia*, *41*, 390–399.
Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805.
Dolan, R. J., Fink, G. R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R. S., et al. (1997). How the brain learns to see objects and faces in an impoverished context. *Nature*, *389*, 596–599.
Eger, E., Henson, R. N., Driver, J., & Dolan, R. J. (2007). Mechanisms of top-down facilitation in perception of visual objects studied by FMRI. *Cerebral Cortex*, *17*, 2123–2133.
Esterman, M., Verstynen, T., & Robertson, L. C. (2007). Attenuating illusory binding with TMS of the right parietal cortex. *Neuroimage*, *35*, 1247–1255.
Fahle, M., & Poggio, T. (2002). *Perceptual learning*. Cambridge: MIT Press.
Fiorentini, A., & Berardi, N. (1980). Perceptual learning is specific for orientation and spatial frequency. *Nature*, *287*, 43–44.
Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S., & Dolan, R. J. (1995). The mind's eye—activation of the precuneus in memory related imagery. *Neuroimage*, *2*, 196–200.
Friedman-Hill, S. R., Robertson, L. C., & Treisman, A. (1995). Parietal contributions to visual feature binding: Evidence from a patient with bilateral lesions. *Science*, *269*, 853–855.
Gibson, E. (1969). *Principles of perceptual learning and development*. New York: Appleton Century Crofts Press.
Hodsoll, J., Mevorach, C., & Humphreys, G. W. (2009). Driven to less distraction: rTMS of the right parietal cortex reduces attentional capture in visual search. *Cerebral Cortex*, *19*, 106–114.
Mottaghy, F. M., Shah, N. J., Krause, B. J., Schmidt, D., Halsband, U., Jäncke, L., et al. (1999). Neuronal correlates of encoding and retrieval in episodic memory during a paired-word association learning task: A functional magnetic resonance imaging study. *Experimental Brain Research*, *128*, 332–342.
Muggleton, N. G., Cowey, A., & Walsh, V. (2008). The role of the angular gyrus in visual conjunction search investigated using signal detection analysis and transcranial magnetic stimulation. *Neuropsychologia*, *46*, 2198–2202.
Oliveri, M., Zhaoping, L., Mangano, G. R., Turriziani, P., Smirni, D., & Cipolotti, L. (2009). Facilitation of bottom-up feature detection following rTMS-interference of the right parietal cortex. *Neuropsychologia* [Epub ahead of print]

Pascual-Leone, A., Walsh, V., & Rothwell, J. (2000). Transcranial magnetic stimulation in cognitive neuroscience—virtual lesion, chronometry, and functional connectivity. *Current Opinion in Neurobiology*, *10*, 232–237.

Rossi, S., Hallett, M., Rossini, P. M., Pascual-Leone, A., & The Safety of TMS Consensus Group. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, *120*, 2008–2039.

Rossi, S., Pasqualetti, P., Zito, G., Vecchio, F., Cappa, S. F., Miniussi, C., et al. (2006). Prefrontal and parietal cortex in human episodic memory: An interference study by repetitive transcranial magnetic stimulation. *European Journal of Neuroscience*, *23*, 793–800.

Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., et al. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: Basic principles and procedures for routine clinical application. Report of an IFCN Committee. *Electroencephalography and Clinical Neurophysiology*, *91*, 79–92.

Shafritz, K. M., Gore, J. C., & Marois, R. (2002). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 10917–10922.

Tovee, M. J., Rolls, E. T., & Ramachandran, V. S. (1996). Rapid visual learning in neurones of the primate temporal visual cortex. *Neuroreport*, *7*, 2757–2760.

Walsh, V., Ashbridge, E., & Cowey, A. (1998). Cortical plasticity in perceptual learning demonstrated by transcranial magnetic stimulation. *Neuropsychologia*, *36*, 45–49.

Wheeler, M. E., & Buckner, R. L. (2004). Functional–anatomic correlates of remembering and knowing. *Neuroimage*, *21*, 1337–1349.