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Cecchi, Ariel Sebastianos

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Cognitive Penetration, Perceptual Learning, and Neural Plasticity

ARIEL S. CECCHI

University of Geneva
University of Glasgow

Abstract

Cognitive penetration of perception, broadly understood, is the influence that the cognitive system has on a perceptual system (e.g., visual, auditory, haptic). The paper shows a form of cognitive penetration in the visual system (defined as early vision) which I call 'architectural'. Architectural cognitive penetration is the process whereby the behaviour or the structure of the perceptual system is influenced by the cognitive system, which consequently may have an impact on the content of the perceptual experience. I scrutinize a study in perceptual learning which provides empirical evidence that cognitive influences in the visual system produce neural reorganization in the primary visual cortex. The type of cognitive penetration can be synchronic and diachronic.

Keywords: Cognitive Penetration, Architectural Cognitive Penetration, Synchronic, Diachronic, Visual System, Early Vision, Perceptual Learning, Neural Plasticity.

1 Introduction

Cognitive penetration of perception, broadly understood, is the influence that the cognitive system has on a perceptual system (e.g., visual, auditory, haptic). Such cognitive influences may include not only knowledge, beliefs, intentions, expectations, and goals, but also desires, moods, feelings, and so on. (See Rowlands 2005; Raftopoulos 2009; Lyons 2011; Macpherson 2012; Siegel and Silins forthcoming; Lyons 2011; Siegel 2012; 2013; Stokes 2012.)

In this article, I defend a specific form of cognitive penetration in the visual system (defined as early vision) which I call 'architectural'. Architectural cognitive penetration is the process whereby the behaviour of the perceptual system is affected by the cognitive system. Cognitive influences can affect the architecture of the system either by guiding the function of the system – e.g., saccadic eye movements may be influenced by intentions (Wu 2013) – or by modulating its structure – e.g., cognitive influences may elicit neural reorganization in the visual cortex (Churchland 1988).[1] Architectural cognitive penetration has an indirect impact on the content of perceptual experience. The subject's cognitive background firstly influences the architecture of the visual system, which consequently may have an impact on the perceptual experience.

This type of penetration can be either synchronic or diachronic. Synchronic architectural cognitive penetration occurs when the cognitive influence and the perceptual act are simultaneous. Sensory stimuli are perceived at the same time the structure of the perceptual system is being altered by the cognitive system. Diachronic architectural cognitive penetration occurs when the cognitive influence is prior to the perceptual act. The perceptual system has been affected before, and perhaps a long time before, the sensory stimulus is perceived.

In this article, I argue that cognitive influences on attention affect the architecture of the perceptual system, producing both synchronic and diachronic forms of architectural cognitive penetration. I present empirical evidence indicating that the fulfilment of specific detection tasks in perceptual learning requires cognitive guidance of attention. Such cognitive influences affect the visual system at early stages of visual processing. The constant repetition of the same task due to perceptual learning eventually produces neural reorganization in the visual system.

Accordingly, the article is structured as follows. In section 2, I review the philosophical debate on cognitive penetration and neural plasticity. In section 3, following Pylyshyn, I give a minimal characterization of what can be considered as the visual system and cognitive functions. In section 4, I scrutinize the concepts of perceptual learning and neural plasticity. I introduce, in section 5, an empirical study on visual learning that I refer to throughout the following sections to show that it provides good evidence for architectural cognitive penetration. In a nutshell, the study indicates that cognitively guided attention, in conjunction with other perceptual learning conditions, affects the visual system at early stages of visual processing, producing neural changes in the brain. Section 6 is devoted to attention and its characteristics. I scrutinize cognitive control on attention (section 6.1), the kind of cognitive control necessary in perceptual learning (section 6.2), and ultimately, I examine the cognitive control on attention in the target study (section 6.3). In section 7, I analyse the nature of cognitive control in the target study and its relation with brain regions. Section 8 presents evidence supporting the claim that cognitively guided attention affects the visual system at very early stages of the visual processing.

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[1] In this article I examine architectural cognitive penetration in the visual system. Vision is a well studied field which provides very rich empirical data. However, there is ample evidence to extend this exposition to other sense modalities.

And finally, in section 9, I scrutinize synchronic and diachronic architectural cognitive penetration in the light of the results exposed.

2 Cognitive Penetration and Neural Plasticity

The concept of architectural cognitive penetration arises from the debate between Jerry Fodor and Paul Churchland in the 1980s. Fodor (1983) claims that perceptual systems are modular and informationally encapsulated. A perceptual system is informationally encapsulated when in order to process an input, its internal operations neither access information stored outside the system itself nor are influenced by information coming from other systems (Fodor 1983, 65-86; Fodor 2000, 62-64; Carruthers 2006, 5-7). More specifically, the visual system is informationally encapsulated if and only if its visual outputs result from the processing of information coming from its sensory organ (e.g., the retina), other structures proprietary of the system (e.g., visual cortical areas), and information stored in the system's database, and no influences from other systems (e.g., auditory, cognitive) intervene in the processing. Cognitive penetration in vision is, strictly speaking, non-encapsulation from the cognitive system. So, Fodor claims that the visual system is encapsulated and cognitively impenetrable.

By contrast, Churchland maintains that the visual system is not encapsulated. The neural structure of the brain is not rigid and static but plastic and dynamic. Visual cortical areas and their functions can be adapted to different perceptual conditions; such adaptation is possible thanks to neural reorganization in the visual system. The information stored in other systems, in particular in the cognitive system, penetrates the visual module by modifying its architecture. Therefore, contra Fodor, the visual system is cognitively penetrable.

This modulation is neither immediate nor simultaneous with the perceptual act, rather, it is produced by perceptual training. The kind of cognitive penetration Churchland is interested in is diachronic architectural cognitive penetration. Cognitive influences do not directly affect visual information retrieved from the visual scene, but rather the architecture of the visual system responsible for this processing.

Churchland supports his argument with the following examples. One supporting example is an inverting lens experiment (Churchland 1988, 174-175). For several days, participants in the experiment wore special lenses which had the effect of inverting the orientation of the visual scene (the world appeared literally upside down). Half of the subjects wore the lenses constantly while the other half wore them only occasionally. With little more than a week of practice the participants in the first group adapted their behaviour to the new configuration of the world and were able to interact normally with the environment and familiar objects. They managed "to recoordinate their vision with the rest of their sensory and motor systems" (Churchland 1988, 174). By contrast, the participants in the second group still had serious problems in dealing with everyday activities. (See Kottenhoff 1957, for a summary of this experiment.)

Churchland concludes that constantly wearing the inverting lenses changed the neural organization of the visual system so that it could be adapted to the new environmental conditions. He argues that the inverting lens example presents good evidence against motor and perceptual encapsulation, or, in other words, that neural plasticity in the brain appears to be elicited by *motor* and *cross-modal penetration*. He writes:

> Cases like these are important, for they reflect the plasticity of some very deep 'assumptions' implicit in visual processing, such as the specific orientation of the visual world *relative to one's other sense modalities and to one's motor systems*. If assumptions as deep as these can be reshaped in a week or two, then our perception begins to look very plastic and very penetrable indeed." (Churchland 1988, 175; my italics.)

As a second supporting example, he claims that the Müller-Lyer illusion (but also other similarly persistent illusions such as Ponzo and Hering illusions) could have been "an incidental consequence of a long period of perceptual training on certain typical kinds of perceptual problems" (Churchland 1988, 174). The presumed neural plasticity in this new example would not have been produced by other sense modalities or the motor system, but instead by the subject's cognitive equipment. Neural plasticity producing the Müller-Lyer illusion would be the result of *cognitive penetration* of the visual system. He writes:

> The illusion exists in the first place only because the relevant processing module is *the well-trained victim of some substantial prior education* – that is, *of some penetration by cognitive activity*. The Ponzo and the Hering illusions may have a similar origin. (Churchland 1988, 174; my italics.)

Presumably, being exposed to a slightly different environment during a long period of training would change the neural behaviour of the visual system so that the perceptual illusion would disappear:

> If the Müller-Lyer illusion is an incidental consequence of a long period of perceptual training on certain typical kinds of perceptual problems, then presumably a long period of training in an environment of a quite different perceptual character would produce a subject free from that particular illusion. (Churchland 1988, 174)

In reply, Fodor argues that neural plasticity in the brain appears to be the rule rather than the exception, but it does not mean that neural reorganization is elicited by cognitive penetration. If some mechanisms in the visual system are engaged in the adaptation to new environmental conditions, then such changes in neural response are evoked on "specific ecological grounds" (Fodor 1988, 193). All Churchland's examples show, he argues, is that there is neural plasticity in the visual system and that it has been produced by the adaptation of the visual system to environmental changes. For instance, in the inverting lens experiment the system could have effectuated some visuo-motor calibrations (Fodor 1988, 193). Whether this adaptation is due to penetration is something that Churchland does not demonstrate. In consequence, neural plasticity cannot be considered as the result of motor, cross-modal, or cognitive penetration. Therefore, encapsulation need not be rejected nor penetration accepted.

Even though Churchland's examples do not provide good reasons to support any form of penetration in the visual system, in this paper I present an empirical study which shows that there is architectural cognitive penetration. With this goal in mind, in the following section I explain what could be understood by 'visual' and 'cognitive' systems.

3 Visual System

Visual perception is sometimes defined as a very early stage of visual processing called "early vision" (Pylyshyn 1999, 342) or simply "perception" (Raftopoulos 2009, 51). All subsequent higher visual processes requiring memory belong to what is known as "cognition" (Pylyshyn 1999, 344) or "observation" (Raftopoulos 2009, 51). Early vision is impervious to cognitive influences – that is, encapsulated from cognition, or cognitively impenetrable (Fodor and Pylyshyn 1981; Fodor 1983; 2000; Pylyshyn 1984; 1999; 2003; Raftopoulos 2001b;a; 2005b; 2009).

The visual system (i.e., early vision) encodes primitive properties such as luminance, motion, binocular disparity (stereoscopic vision: depth and relief), colour, edge polarity, contour, shape, spatial relations, position, orientation, size, texture (Raftopoulos 2009, 51) but also occlusion and surfaces, i.e., three-dimensional objects (Pylyshyn 2003, 143, 146-147; 1999, 343).[2] The outputs delivered by early vision are complex and primitive representations of objects expressible in the vocabulary of geometry (Pylyshyn 2003, 133-134) which are sufficient to identify objects that match with categories stored in memory (Pylyshyn 1999, 361).

Visual perception does not require access to memory in order to compute

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[2] This involves the 3-dimensional model of objects in Marr's (1982).

perceptual inputs (Pylyshyn 1999, 361; 2003, 134-136): “the early-vision system could encode any property whose identification does not require accessing general *memory*” (Pylyshyn 2003, 136; my italics). Thus, a necessary condition for being a visual output is to be computed independently of any access to memory. The visual processing becomes cognitive when the visual output is recognized and categorized. Cognitive processes depend on the subject’s cognitive background, and are, by definition, cognitively penetrable. (See Pylyshyn 1984, 134-135; Raftopoulos 2001a, 427; 2009, 77, 80.)

Early vision is functionally defined.[3] Pylyshyn (1999, 342 and n. 2) characterizes the visual system by the sort of functional (psychophysical) properties it computes rather than by its neurophysiology. A neuroanatomical definition of early vision is difficult to offer because “[t]he neuroanatomical locus of early vision [...] is not known with any precision” (Pylyshyn 1999, 344). On the one hand, not every stimulation on the retina is processed by the visual system, some of this information is encoded for other systems.[4] On the other hand, visual inputs cannot be restricted to sensory stimulation on the retina; the visual system also treats information from other modalities.[5]

Although Pylyshyn tries to avoid a neuroanatomical definition of the visual system, the need to differentiate the visual system from cognitive factors (such as long-term memory) compels Pylyshyn to provide a minimal neuroanatomical description of the visual system. He claims that the visual system itself is “roughly identified with the visual cortex, as mapped out, say, by Felleman and Van Essen 1991” (Pylyshyn 1999, 347; 2003, 67-68).

Felleman and Van Essen (1991) give what nowadays can be considered as a “standard” neurophysiological definition of the visuo-motor system. The definition includes the visual cortex, central and posterior parietal areas, and the inferior temporal cortex. This description basically equates to Milner and Goodale (2006)’s dorsal and ventral streams: while the former projects from the primary visual cortex to posterior-parietal areas, the latter culminates in the inferotemporal cortex. In addition, Felleman and Van Essen (1991)’s description of the visual system given in terms of visuo-motor functions, which means that the visual system is not only responsible for the processing of visual stimuli on the retina, but also for the allocation of attention, eye movements, and other visual functions (see also Fodor 1983, 67 and Wu 2013,

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[3] I thank Santiago Echeverri who drew my attention to this aspect and motivated the following discussion.

[4] For example, a few retinal projections culminate in the superior colliculus (SC) responsible for head and eye movements, others project to the pretectum which regulates pupillary light reflex, whereas others end up in the optic tract controlling circadian rhythms. See Goodale and Milner 2005, 312; Purves et al. 2004, 263; Tovée 2008, 74.

[5] For instance, the vestibular system seems to affect perception of orientation, and proprioceptive signals from the eyes and head appear to influence visual location (Pylyshyn 1999, 361).

19-20). Therefore, frontal cortical areas responsible for eye guidance and movement (i.e., the frontal eye field (FEF) and the dorsolateral prefrontal cortex (DLPFC)), and non-cortical areas responsible for allocation of visual attention and eye movements (i.e., the superior colliculus (SC)) belong to the visuo-motor system as well. Eventually, Pylyshyn seems to provide a neuroanatomico-functional definition of the visuo-motor system.

As Pylyshyn does with the visual system, it is worthwhile to provide a succinct neuroanatomico-functional characterization of the cognitive system. The cognitive system is responsible for two essential faculties regarding visual perception: executive functions guiding the performance of visual tasks, and the categorization and recognition of visual items. These two faculties rely on memory.

The performance of a visual task depends on working memory. Working memory is the ability to retain and manipulate information (about past and future actions) for the prospective execution of a task (Fuster 2008, 185; Deco and Rolls 2008, 247). This mnemonic ability, as well as other cognitive executive functions (e.g., attention, planning, decision-making), is intimately associated with frontal cortical areas, to wit, the prefrontal cortex (PFC) (Fuster 2008, 178-192). Visual recognition and categorization depend on long-term memory, which collects and stores detailed representations of visual items useful for their identification. Long-term memory depends on the inferotemporal cortex, and middle temporal areas (Deco and Rolls 2008, 271-273).

To sum up, the PFC is mainly correlated with cognitive processing (such as executive functions), while the IT cortex is related to visual feature processing. However, working memory and long-term memory are interdependent. The performance of visual tasks demanding the recognition and categorization of an object is intimately linked to the interaction between the PFC and the IT cortex. (See Deco and Rolls 2008, 280; also Echeverri forthcoming.)

Although the computation of visual properties begins in the visual system, the perceptual processing goes on and becomes rapidly affected by cognition. Signals coming from higher cortical areas (such as the PFC and non-visual temporal areas) influence the visual cortex shortly after the stimulus presentation. According to Raftopoulos (2009, ch. 2), visual perception is a process which lasts 100 or 120 milliseconds post-stimulus onset. Typically, the primary visual cortex (the earliest cortical area responsible for visual processing) becomes activated 40 ms after stimulus presentation, and during the next 60-80 ms the visual processing seems to be unaffected by re-entrant pathways in the visual system. In this time period of processing the visual system is considered as encapsulated and impenetrable by cognition (Fodor 1983, 64-86; Pylyshyn 1999, 344; Raftopoulos 2009, 3). After this interval, cognition penetrates vision – that is, signals from higher cortical areas pervade the visual cortex, influencing the visual processing.

Therefore, the visual system is cognitively impenetrable only if cognitive influences do not affect the visual system before 100 ms after stimulus presentation. In other words, the visual system is encapsulated only if signals from higher brain areas (such as those responsible for memory) do not pervade the visual processing in the time span of early vision.[6]

To summarize, the visual system is defined in neuroanatomico-functional terms. The visual processing in early vision culminates at about 100 milliseconds after stimulus onset. All subsequent computation responsible for the categorization and recognition of visual objects belongs to cognition. The visual system is cognitively encapsulated when the visual processing is not affected by cognitive influences (such as working and long-term memories) in the time span of early vision.

The objective in the rest of this paper is to present compelling evidence in favour of architectural cognitive penetration in the visual system. In other words, I scrutinize a study in perceptual learning in which the primary visual cortex is influenced by cognitive signals from higher cortical areas (associated with memory) during the time period of early vision. As a consequence of the plastic condition of the brain, this influence results in neural changes in the primary visual cortex. Such architectural changes have an impact on the content of the subject's perceptual experience. In the following section, I examine the concepts of perceptual learning and neural plasticity.

4 Perceptual Learning and Neural Plasticity

Perceptual learning is defined as the unconscious improvement (or deterioration) in stimulus discrimination resulting from the performance of some perceptual task requiring an intensive practice. Repeating the same perceptual activity several times can result in faster detection and improved discrimination of perceptual inputs, which leads to a more efficient response to future stimuli perceived by the organism. Such an improvement results in neural changes thanks to the plastic condition of the brain. (See Gilbert and Sigman 2007, 688; Bartolucci and Smith 2011, 3898.)

Neural plasticity is the ability of the brain to adapt its structural organization to different situations arising from developmental, environmental, or traumatic circumstances. Such capacity has been observed in both infant and adult humans (Röder and Rösler 2004, 722) for whom cortical areas remain malleable throughout life (Crist et al. 2001, 519). Development and aging are characterised by changes in the organization of brain structures, e.g., in infant development. Intense practice as a consequence of environmental conditions also elicits neural reorganization in the brain (Crist et al. 2001, 519; Schwartz

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[6] This is a necessary but not sufficient condition for cognitive penetration. See section 6.

et al. 2002, 17137). An example could be observed in the inverting lens experiment. Moreover, brain damage caused by traumatic events can produce a restructuring of functional brain regions. For example, in neural reassignment after amputation of one finger, neurons in the somatosensory cortex which were previously associated with the amputated phalange become associated with the adjacent fingers. (See Röder and Rösler 2004, 723, for further details.)

Neural plasticity can be classified according to the kind of reorganization it generates: *physiological* plasticity is distinguished from *anatomical* plasticity. Physiological plasticity designates changes in the response properties of neurons (e.g., firing thresholds, disinhibition or potentiation of previously existing neural connections, and the like), whereas anatomical plasticity denotes changes in the structure of the neuron (e.g., number and form of synapses, size of cell somata and dentritic trees, and so on).

Physiological and anatomical changes are interdependent; during an initial learning phase, the firing rates of neurons change, e.g., by enhancing or inhibiting neural response of existing connections. Later, in a consolidation phase, structural modification strengthens the initial physiological changes by changing the architecture of the cells. This classification of neural changes is closely related to the elapsed time since the evoking event. Rapid changes, those occurring within seconds to hours, most likely during the learning phase, cause physiological modulations. Slow changes, those occurring over days and months, most likely presented in the consolidation phase, engender anatomical changes. (See Röder and Rösler 2004, 721.)

Understanding the transition from physiological to anatomical reorganization demands an explanation of ‘consolidation’. Perceptual learning is intimately connected with memory. In perceptual discrimination, for instance, not only does the subject need to remember how to perform the task, but her brain does also. The former sort of memory belongs to declarative memories – i.e., memories that a person can call to mind (for instance, the capital of France) –; the latter are non-declarative memories – i.e., memories normally used without conscious recollection (for example, how to ride a bicycle) (Stickgold 2005, 1272).

Information resulting from motor, perceptual, or cognitive activities in everyday life requires some processes which integrate them into memory. While the initial encoding of a memory occurs in a few milliseconds, its long-term maintenance requires processes that continue to modify it over hours to years; these processes are known as ‘memory consolidation’. Consolidation designates both the stabilization of memories – such as the fixation of information in the brain – and the enhancement of this information – such as the improvement of performance in the absence of further practice (Stickgold and Walker 2007, 333).

Memory consolidation depends on plastic effects which convert information into a long-lasting integrated memory (Stickgold 2005, 1272). Consolidation processes are automatic, occurring without intent or awareness of the subject (Walker and Stickgold 2004, 126; Stickgold 2005, 1272; Stickgold and Walker 2007, 332-333, 341). Additionally, they can take place during wakefulness, sleep, or both, depending on the learning conditions (Stickgold 2005, 1273). When the learning task is *explicit*, that is, when subjects are informed at the beginning of the training that there is a repeating pattern to be detected (e.g., the orientation of an object), consolidation is sleep-dependent – i.e., stabilization and improvement only occur across sleep. During sleep there is an offline reactivation of the trained brain areas which plays a critical role in consolidation (Wamsley and Stickgold 2010, 1011). By contrast, when the learning task is *implicit*, that is, when participants are not informed that there is a recurrent pattern but only told that it is a reaction time test (e.g., to detect flashing lights), and if they do not become aware of the repeating pattern during the training (e.g., the display of the lights presents some regularities), improvement in performance occurs across wakefulness, but also during sleep (Stickgold 2005, 1275; Stickgold and Walker 2007, 335). In sleep-dependent consolidation, the first night of sleep after the training stabilizes and improves performance. Consolidation can continue for at least 48-96 hours following successive nights of sleep without additional training (Schwartz et al. 2002, 17137; Stickgold 2005, 1274). No improvement is observed through wakefulness in the subsequent days. Strikingly, sleep deprivation the first night after the training prevents normal consolidation of memory: even when a first night awake is followed by two nights of recovering sleep, no consolidation is observed three days later (Stickgold 2005, 1274).

To summarize, perceptual learning tasks elicit two forms of neural reorganization. Physiological neural changes occur within seconds to hours during or after the performance of a repetitive visual task. In contrast, anatomical neural changes occur over days and months and depend on consolidation.

In the following section, I introduce an empirical study which provides significant evidence for neural modulation evoked by architectural cognitive penetration. In this study, subjects' intentions and aims with regard to the fulfilment of a visual task penetrate the visual system producing neural reorganization. Cognitive influences observed during the performance of the task initially produce physiological neural changes and later, after consolidation, anatomical modifications. Subsequent sections are devoted to defending this claim.

5 Perceptual Learning Study

In what follows, I introduce an empirical study in visual perceptual learning (Schwartz et al. 2002) which shows that the visual system can acquire new skills in visual detection by intensive training.[7] The improvement in detection occurred in the primary visual cortex (also called striate cortex or area V1) and intimately depended on cognitive influences on the visual system.

In the experiment, participants performed a double-detection task: they simultaneously reported a central and a peripheral object displayed on a screen for only a few milliseconds. The experiment consisted of two different sessions with an interval of 24 hours between them. The first session was the training; subjects learned to perform the double-detection task. The second session (24 hours later) was the test; subjects' performance on the same task was tested. I refer to this study as the 'target study' or 'double-task experiment'.

The task consisted in an intensive monocular training requiring subjects to report, simultaneously, both the identity of an element appearing in the centre of the visual field and the orientation of an object located in the periphery.[8] The central object was a letter (randomly rotated L or T). The peripheral target was composed of three adjacent diagonal lines (forming either a horizontal or a vertical array) displayed at various positions within the upper-left quadrant of the visual field.[9] Both central and peripheral objects appeared against a homogeneous background of horizontal bars.[10]

Eye movements were restricted to the fixation of the central letter whereas the discrimination of the peripheral lines' orientation required the allocation of voluntary covert spatial attention. The learning task was represented by the peripheral array; the objective of the training was to improve performance in detection of the array's orientation (Schwartz et al. 2002, 17138).

Participants in the experiment were divided into two groups. One group of subjects trained the left eye whereas the other trained the right. For all the subjects (regardless of whether they trained the right or left eye), all visual targets were displayed at various positions in the upper-left visual quadrant so that only the lower-right part of retinotopic map was affected during the learning.[11]

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[7] The study was realized for the first time by Karni and Sagi (1991). However, while the experiment scrutinized in this paper employed brain imagining techniques, theirs did not.

[8] Monocular training exercises only one eye. When we look straight at the fixation point (the centre of gaze) there is a portion of the visual field that can be seen by both eyes; this region is labelled the binocular visual field (Bear et al. 2007, 312). Monocular vision is used to avoid the overlapping of visual information elicited by binocular vision.

[9] A quadrant is one of the four portions resulting from dividing the visual field by a horizontal and a vertical line passing through the fixation point (Bear et al. 2007, 312).

[10] The purpose of the background is to ensure an homogeneous and global electric activation in the primary visual cortex (Schwartz et al. 2005, 771).

[11] Visual information captured by the retina is represented in the primary visual cortex on

In the first session (training), subjects underwent a total of 1,760 trials, each lasting between 700 and 1100 milliseconds, plus the time to give a response and to receive a feedback about its accuracy. In each trial, the central and peripheral targets were displayed together for 16 ms. Participants were asked to report the identity of the central letter and the orientation of the array.

Performance in participants' visual detection was measured by the number of responses correctly reporting both the central letter and the orientation of the peripheral array. Furthermore, functional magnetic resonance imaging (fMRI) techniques were used all through the study to measure neural activity in the trained regions of the retinotopic map.

During the training, subjects gradually improved their capacity to detect the orientation of the peripheral object (Schwartz et al. 2002, 17137). During the test session, performance in the detection of the peripheral element's orientation for the trained and untrained eyes was tested. The results indicate a significant improvement in peripheral target detection for the trained but not the untrained eye. In contrast, performance in the detection of the central letter did not show any significant improvement (Schwartz et al. 2002, 17139).[12]

Neural activity in the visual cortex elicited by the trained eye was monitored and compared to the untrained eye and to the same eye before the training (Schwartz 2007, 28). In the trained visual areas, visual detection improved with practice alongside progressive changes in neural behaviour.

Due to the highly demanding conditions of the learning task (see section 6.3), its completion necessitated cognitively guided attention influencing the visual system at early stages of the visual processing. Functional MRI results indicate that higher brain areas were recruited for the fulfilment of the task. Top-down signals were necessary to stimulate neural activity in the lower-right region of V1 and facilitate detection. The constant and repetitive stimulation of neurons in the striate cortex due to cognitive influences was partially respon-

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a topographic neural map, called the 'retinotopic map'. Metaphorically, the visual system can be compared to a camera whose lens is composed of small light sensors connected to pixels on a monitor. When the light reaches the lens, the light sensors activated send an electrical signal to pixels on the monitor, reproducing the image projected on the lens. Analogously, there is a roughly point-by-point anatomical connection between locations on the retina in the eye (i.e., the lens of the camera) and regions of electrical activity in the primary visual cortex (i.e., the monitor). Neurons near each other in the visual cortex receive signals from nearby areas on the retina, reproducing a topographic map of the visual scene. (See De Weerd 2010, 1075-1077). In addition, visual information coming from the scene has a cruciform projection onto this map: it is inverted from top to bottom and from left to right. The visual inputs detected in the upper-left visual quadrant are therefore projected onto the lower-right part of the primary visual cortex (i.e., the lower bank of the right calcarine sulcus) (Schwartz et al. 2002, 17139-17140).

[12] Detection at fixation was equally good in all conditions either for the trained or the untrained eye. It seems that the visual system is specialized in foveal detection.

sible for improving performance by causing physiological neural modulations.

To sum up, the perceptual learning task in the target study produced a rapid improvement in visual detection. This progress occurred as a result of cognitive influences on the visual system facilitating visual detection: electrical activity from higher brain areas affected early stages of the visual processing. The constant repetition of the detection task produced gradual neural modulations in the trained region of the primary visual cortex, improving performance.

During the test session, 24 hours after the intensive training and a night of sleep, the same detection task was tested. Functional MRI data for the trained eye reveal an increase of neural activity in the trained region (the lower-right region of the striate cortex).[13] This increment was observed neither for the untrained eye nor for the same eye before the training (Schwartz et al. 2002, 17139). In addition, fMRI measures suggest that neural activity observed in the trained region for the trained eye was independent of either attentional influences from higher brain areas or neural networks activated during the learning (Schwartz 2007, 28). Instead, neural responses appeared to occur before any top-down influences on the trained region of V1 were observed. However, the execution of the same task for the untrained eye did recruit higher brain areas associated with perceptual learning and attention.

These results lead Schwartz et al. (2002, 17140) to conclude that training resulted in neural changes in V1. That is, a day later, the primary visual cortex had *learned* to detect the peripheral item. The consequence of the learning was observed in anatomical neural changes occurring by means of consolidation.[14]

The problem with this conclusion is that neural activity in the striate cortex during the test session might result from local top-down attentional feedbacks occurring at short delays rather than arise from independent neural reorganization (Schwartz et al. 2002, 17140; Pourtois et al. 2008, 55; Bartolucci and Smith 2011, 3898). As was observed in other studies, the improvements in perceptual learning may be caused by top-down influences from later visual processing stages (Pourtois et al. 2008, 55) or fronto-parietal attentional networks (Schwartz et al. 2005, 774-775) undetectable by fMRI techniques.[15] As such, neural activity in V1 during the test session could have been subject to top-down influences.

However, a replication of this study using high-density electroencephalog-

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[13] Such activity corresponds precisely to the retinotopic projection of the peripheral item's spatial location (i.e., the upper-left visual quadrant).

[14] Notice that the detection task involved non-declarative memory and explicit learning (subjects were aware of the repeating pattern) two conditions which demand sleep-dependent consolidation.

[15] Because the target study employed fMRI, this alternative explanation of improvement is not blocked. While brain imaging techniques such as fMRI have excellent spatial resolution, they do not have sufficient temporal resolution to establish the exact latency of top-down influences into V1.

raphy (EEG) confirms the original results (Pourtois et al. 2008).[16] During the test session, subjects' peripheral detection for the trained eye highly improved: neural activity in V1 elicited by the peripheral object was observed as early as 44 ms post-stimulus onset, indicating a peak of activation at 85 ms (Pourtois et al. 2008, 58-59). Furthermore, during this interval, no top-down influences due to learning requirements or attentional effects on the primary visual cortex were detected (Pourtois et al. 2008, 59-60). By contrast, when the untrained eye was tested, top-down influences from higher brain areas were necessary for V1 to enhance neural activity in the relevant retinotopic region and facilitate peripheral detection. The replication of the study definitely confirms that neural reorganization only occurred for the trained eye at the trained location. (See Pourtois et al. 2008, 60; also Ahissar and Hochstein 1993, 5718-5720.)

To summarize, participants in the target study performed a central and a peripheral detection task: to report both the identity of a central letter and the orientation of the peripheral object. The learning component of the task was represented by the peripheral detection which required voluntary covert spatial attention. During the learning session, cognitive influences on attention were necessary all through the training to detect the peripheral array: cognitively guided attention enhanced neural activity in the region of the primary visual cortex corresponding to the peripheral element's spatial location. The constant and repetitive stimulation of V1 neurons during the learning session produced an improvement in the detection of the peripheral target. Such top-down influences produced gradual physiological neural modulations in the visual cortex, increasing the performance in visual detection. Such improvement in peripheral detection performance was also observed for the trained eye during the test session. However, this time, the detection of the peripheral target was accomplished without top-down influences on the primary visual cortex. One day after the training, thanks to consolidation, the visual system presented (anatomical) neural reorganization at the trained retinotopic region. In other words, the visual system *learned* to detect the peripheral object. On the contrary, the detection of the peripheral element for the untrained eye required constant top-down influences.

In the following sections, I consider this empirical study in depth. I begin with an exposition of attention and its different aspects (section 6), I explain cognitive control (section 6.1), the sort of cognitive control involved in perceptual learning (section 6.2), and finally, I scrutinize cognitive control on attention in the target study (section 6.3).

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[16] Unlike fMRI, EEG has a high temporal resolution (to the detriment of spatial resolution) of about 2 milliseconds which offers very detailed information on the time span of visual processing (Pourtois et al. 2008, 56; McDowell et al. 2008, 255; Rauss et al. 2011, 1241).

6 Attention

The physical world presents the subject with far more environmental information than her perceptual system is able to effectively process. Some inputs are relevant for the subject's current behaviour while others are not. Selecting the right information is essential in order to produce optimal cognitive and behavioural responses.

Attention is a mechanism that selects the information that is relevant for our aims while filtering out the irrelevant. For example, the words printed on this page are relevant to the task of reading, however perceptual information about the page number, the coffee mug, the pen, and other objects neighbouring the page are not. Attention selects the words and filters out perceptual inputs that are not currently important. Without attention there would not be selection, and without selection the visual system would process a myriad of irrelevant inputs, making any cognitive or behavioural task very difficult to perform.

In what follows, I consider some characteristics of attention which are important for our purposes: the type, the allocation, the guidance, and the selective character of attention. First of all, there are three types of attention, each of them defined according to the sort of information selected from the visual scene: object-centred attention (objects), feature-centred attention (features), and spatial attention (spatial regions). Each type of attention depends on specific neural networks.

Second, attention can be allocated in two distinct ways. *Overt* attention is deployed when the observer moves her eyes to some spatial location, object, or feature, and the focus of attention coincides with the direction of gaze. *Covert* attention is allocated when the subject fixates on some region or object in the visual scene despite directing the focus of attention somewhere other than the direction of gaze. Covert attention is possible because of the observer's ability to attend to a location without accompanying eye movements. (See, e.g., Styles 2005, 75; 2006, 43.)

Third, there are two general influences guiding visual selection. Attention can be controlled by bottom-up sources (i.e., stimuli driven) when it is captured by the saliency of the sensory stimuli in the visual scene. And it can also be guided by top-down influences (i.e., cognitively driven) following the observer's behavioural goals. (See, e.g., Desimone and Duncan 1995.)

Finally, there are two aspects of the selective character of attention that must be distinguished: the *focus* (i.e., the location where attention is directed) and the *gating* of attention (i.e., the sort of stimuli selected from the focus).

The focus of attention is frequently discussed in philosophy (e.g., Pylyshyn 1999, 344, 358; Siegel 2012, 205-206; Macpherson 2012, 29; Stokes 2013, 650; Stokes and Bergeron forthcoming). Changing the focus of attention to the right rather than the left of the visual scene will make different stimuli impact on the retina. This selective dimension refers to an extrinsic feature of attentional mechanisms: attention acts as a spotlight which highlights part of the visual scene, making some visual information *accessible* to the observer.

Shifts of attentional focus are not considered as cases of cognitive penetration (Fodor 1988, 190-192; Pylyshyn 1999, 344; Raftopoulos 2005b, 81; 2009, 277-290; Siegel 2012, 205-206; Macpherson 2012, 29; Stokes 2013, 650, 655).[17] According to Pylyshyn (1999, 353) and Raftopoulos (2001a, 438-439), the allocation of attention is *prior* to the operation of early vision. That is, the focus of attention is a pre-perceptual stage which makes the visual stimuli accessible for further processing.

Although the allocation of attention determines the stimuli in the visual scene that will be accessible (e.g., the right rather than the left side of the room), not all the stimuli falling under the spotlight are selected for further processing. The properties which will be eventually selected are those representing the relevant information for the organism's goals (e.g., the subject's intentions) (Schwartz et al. 2002, 17137; Gilbert and Sigman 2007, 689; Wu 2008, 1009-1017). Attention functions then as a gate-keeper which picks out the information from the spotlight that is pertinent for the subject's current goals and makes it *accessed* to the organism. This is an intrinsic and more sophisticated dimension of attention called the "gating" of attention (Karni and Sagi 1991, 4970; Karni and Sagi 1995, 8-9; Pylyshyn 1999, 345, 359-361; Raftopoulos 2001a, 444; 2009, 303-304; Gilbert and Sigman 2007, 688-689)[18].

In a nutshell, while the focus of attention refers to the capacity of the selective mechanism to highlight relevant regions of the visual scene, the gating of attention refers to the capacity of this mechanism to select the relevant information from the spotlight. Both attentional focus and gating can be stimulus- or goal-driven. However, although the focus of attention may be voluntarily guided, the gating exclusively depends on the system's capacity to compute the needs of the organism (e.g., the subject's goals). Succinctly, whereas the focus of attention regulates the direction and size of the spotlight, the gating regulates the specificity of this focus (which features will be selected).

Let's now scrutinize the target study in the light of the above characteristics of attention. Subjects were required to fix the direction of gaze on a central target while voluntarily allocating visual attention to the upper-left region of the visual field to detect a peripheral target. In short, the perceptual task required subjects to deploy *cognitively driven covert spatial attention.* In the next sections, I scrutinize the role of attentional gating and argue that, in

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[17] See Wu (2013) for an account of cognitive penetration in the allocation of attention.

[18] Wu 2008 distinguishes between the focus of attention (2008, 1006-1017) and attentional parsing (2008, 1017-1021). However, it is unclear to me whether the parsing refers to what is normally known as the attentional gating or whether it is another characteristic of the attentional focus.

the target study, the selection of the relevant properties from the attentional spotlight strictly depended on cognitive influences in early vision. That is, architectural cognitive penetration depends on cognitive influences affecting the gating of attention.

Nevertheless, according to Pylyshyn (1984; 1999; 2003) and Raftopoulos (2001a;b; 2005b; 2009), the gating of attention does not threaten cognitive impenetrability of perception in perceptual learning.[19] Either the gating is produced by stimulus-driven attention (i.e., selection is independent of top-down influences), or cognitively driven attention influences the visual system at a post-perceptual stage (Pylyshyn 1999, 359-360; Raftopoulos 2001a, 443-444; 2005a, 76; 2009, 303-304). However, Raftopoulos (2009) recognizes that cognitively guided attention facilitates the gating of visual properties by pervading early vision, but claims that this influence does not undermine cognitive impenetrability of perception. The following are three reasons given by Raftopoulos to support his claim. Firstly, the earliest cognitive influence on the visual system occurs at about 70 ms after stimulus presentation; nevertheless this modulation is first observed in the extra striate cortex and later in V1 (Raftopoulos 2009, e.g., 79-80, 88). Secondly, the role of cognitively guided attention is to facilitate visual selection, but it is not at the origin of the visual selection: the relevant stimuli are already bottom-up retrieved (Raftopoulos 2009, e.g., 87). And thirdly, the attentional gating does not affect the content of the perceptual experience: because the perceptual content is already bottom-up determined, attention only eases the visual processing (Raftopoulos 2009, e.g., 84).[20]

I devote the rest of this paper to showing that, contrary to Pylyshyn's and Raftopoulos' view, cognitively guided attention does affect early vision by enabling the selection of the relevant visual properties in perceptual learning. In the next section I scrutinize cognitive control on attention.

6.1 Load Theory of Attention

Attention can be guided by both the perceptual (stimulus-driven) and the cognitive (goal-driven) systems (Lavie et al. 2004, 339, 351-352).[21] Selection of the relevant stimulus from the visual field (e.g., the words on this page) can be successful either under perceptual control alone or under perceptual and cognitive control together. The efficacy of perceptual mechanisms guiding attention in selecting the relevant information depends on the perceptual system's capacity. The visual system has a limited processing faculty and cannot

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[19] I am in debt to Jack Lyons for pointing out to me Pylyshyn's and Raftopoulos' view.

[20] There are many other reasons given by Raftopoulos, here I have mentioned only the most relevant to the aim of this paper.

[21] The subsequent explanation corresponds to what is known as the "load theory of attention" (Lavie and Tsal 1994; Lavie 1995; 2005; 2010).

process all stimuli affecting the retina. Instead, visual information is processed until the visual capacity is exhausted. When the amount of indispensable perceptual information necessary for the subject's cognitive or behavioural aims consumes the full perceptual capacity of the system – i.e., in situations of *high perceptual load* – irrelevant inputs are ignored because no capacity is left to process them. However, when the appropriate information does not engage the system's full resource – i.e., a case of *low perceptual load* – the spare capacity allows the processing of irrelevant inputs unnecessary for the fulfilment of the subject's aims.

In cases of low perceptual load, cognitive control on attention is necessary both to select the necessary visual information and to reduce or eliminate the processing of unnecessary inputs. Selection will be successful depending on the cognitive load required for the task. Under *low cognitive load* (e.g., to identify a letter) cognitive capacities are sufficient to select the relevant information but there might not be enough to filter out irrelevant information. On the contrary, under high cognitive load (e.g., to identify a letter, its orientation and colour) cognitive capacities will select the relevant while ignoring unnecessary stimuli.[22]

Attention selects the relevant information from the visual scene by enhancing neural activity in the visual cortex corresponding to relevant stimuli (Schwartz et al. 2005), or inhibiting or suppressing the processing of irrelevant inputs (Lavie and Tsal 1994; Lavie 2005). Relevant information appears to be selected under both high and low cognitive load conditions. However, while under low cognitive load unattended or irrelevant inputs still evoke neural activity, under high load the activity elicited by irrelevant inputs is reduced or eliminated (Schwartz 2007, 30-31). Therefore, cognitive control on attention plays an essential role in visual selection: it regulates neural activity responsible for visual processing.[23]

To summarize, attention can be guided by both the perceptual and cognitive systems. Attentional selection is successful when the detection of the stimuli exhausts the full capacity of the perceptual system (high perceptual load). Nevertheless, under low perceptual load, attention requires cognitive control to select the relevant stimuli and inhibit or suppress the processing of unnecessary inputs.

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[22] Observe that in Lavie's terms "high" and "low" cognitive load refer to the load on the cognitive system. That is, when the cognitive system is under high cognitive load no spare capacities will be available for attentional control. However, the way these terms are used in the present exposition refers to the cognitive load required by the perceptual task. That is, I am concerned with the cognitive load allocated to the spare cognitive resource available for attentional control.

[23] Notice that this account of attention is compatible with, and complementary to, the biased competition model theorized by Desimone and Duncan (1995) and the model of attentional selection endorsed by Wu (2008).

To account for architectural cognitive penetration in the visual system, the perceptual task in the target study must involve some form of cognitive control on attention. If attentional selection is successful solely in virtue of perceptual control (i.e, a case of high perceptual load), the visual detection task would not involve any cognitive guidance. However, this is not the case; the accomplishment of the double-detection task in the target study demands a high cognitive load on attention. In the next section, I consider the sort of cognitive control required in perceptual learning, and later (section 6.3), I scrutinize the target study in the light of these results.

6.2 Cognitive Control on Attention in Perceptual Learning

In this section I review other empirical studies to demonstrate that successful learning in the target study necessarily requires both *voluntary covert spatial* attention and a very specific *cognitive task-related control* on attention.[24] The former aspect concerns the focus whereas the latter refers to the gating of attention.

The target study consisted in a double-detection task: a central identification at fixation simultaneously with a peripheral detection requiring covert spatial attention. In what follows, I introduce a series of single-task studies necessary to elucidate the role of cognitive control in perceptual learning. Although all the subsequent experiments demanded central fixation, some of them required only central detection without peripheral task – call this a 'central-task experiment' –, and the others demanded peripheral detection without any central task – call this sort of study 'peripheral-task experiment'.

There is good evidence that spatial attention is necessary for peripheral detection leaning. An experiment in which peripheral distractors were displayed was tested (Crist et al. 2001). All subjects were to do was to maintain fixation at the centre of the screen while a small flashing bar was briefly presented in the peripheral visual field. (Apart from central fixation, strictly speaking this study did not require any central- or peripheral-detection task.) The experiment represents a form of implicit learning which does not requires subject's awareness. The aim of this study was to test whether the visual system could improve performance in peripheral detection without explicit vigilance.

After a few weeks of training, neural activity in the trained and untrained visual cortical hemispheres was measured. The results do not show any substantial improvement in peripheral target detection as a consequence of the passive training: neural activity elicited by the flashing bars was almost iden-

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[24] I am thankful to Fiona Macpherson for comments on a first draft of the paper which helped me to write this section, and to Sophie Schwartz for an explanation of scientific aspects discussed here.

tical in both hemispheres of the primary visual cortex. (See Crist et al. 2001, 519-520.) The findings suggest that peripheral detection does not improve with the passive stimulation of cortical visual areas. The allocation of *spatial attention* is a necessary condition for perceptual learning.

In the type of learning tasks scrutinized in this article, spatial attention also needs to be covertly allocated. In the following central-task experiment (Schwartz et al. 2005; Rauss et al. 2009)[25], participants were required to report a central T-shaped item that varied in colour (six different colours) and orientation (vertical or horizontal) while distractors were presented in the periphery.[26] The task demanded the allocation of attention exclusively on the central task under easy and difficult conditions. Under easy circumstances (low cognitive load of attention) the targets were red Ts irrespective of their orientation; during the difficult conditions (high cognitive load of attention) the targets were any upright yellow or upside-down green Ts (Schwartz et al. 2005, 772).

The results of the central-task experiment demonstrate that the training was successful: subjects improved performance in central detection as a consequence of neural reorganization in the primary visual cortex. Functional MRI data reveal that under high cognitive load central detection was successful while distractors were ignored. From a neurophysiological perspective, there was a substantial increase of neural activity corresponding to the detection of the central letter and an inhibition of activity with regard to distractors. Under low cognitive load, however, although the central task was successfully achieved, neural activity triggered by distractors increased (Schwartz et al. 2005, 782; Schwartz 2007, 32). In sum, the peripheral stimuli were ignored under high cognitive load but still processed under low load.

Though changes in cognitive load enhanced and inhibited neural activity elicited by distractors, no learning in peripheral detection was observed. That is, even under low cognitive load conditions (i.e., a situation in which irrelevant peripheral stimuli were detected), the primary visual cortex did not exhibit any neural reorganization resulting from peripheral detection. In short, the visual system did not learn to perceive peripheral items. This suggests that perceptual learning for peripheral detection requires the deployment of *covert* spatial attention.

The first experiment presented above provides good evidence to support the claim that perceptual learning cannot be successful without spatial attention. The second study shows that spatial attention must be covertly allocated. Furthermore, the target study required subjects to allocate covert spatial attention

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[25] The same central task was tested in both studies, however, while Schwartz et al. (2005) adopted fMRI techniques to assess brain activity, Rauss et al. (2009) employed EEG. Here, I focus the discussion on the fMRI data; in section 8 I scrutinize EEG results.

[26] A distractor is an irrelevant item presented in the visual scene making the identification of the relevant object more difficult.

in a *voluntary* fashion. Therefore, the aspects scrutinized so far show that in the target study improvement in peripheral detection necessarily depends on voluntary covert spatial attention. Notice that these features correspond to the focus of attention, i.e., the allocation of the spotlight. I would like to turn now to specific characteristics concerning the gating of attention, i.e., the stimuli that will be eventually selected from the spotlight. This aspect intrinsically depends on cognitive requirements.

Peripheral detection in perceptual learning necessarily implies *top-down task-related control* on attention. A peripheral-task experiment was designed to determine the role of top-down effects on attention (Ahissar and Hochstein 1993). The aim of the experiment was to test whether voluntary covert spatial attention is sufficient to improve peripheral detection or whether, on the contrary, task-related conditions play any role in perceptual learning.

The study consisted in a monocular central fixation with a peripheral detection task. The fixation point was surrounded by four rectangular boards (one for each quadrant) composed of homogeneous oblique lines. The orientation of the boards changed in each trial (i.e., they were horizontally oriented in one hemifield and vertically oriented in the other).[27] Moreover, in two of these four boards (either the two at the bottom or the two at the top) the internal composition changed: one line was differently oriented with respect to the others. Briefly, whereas the orientation of boards changed from left to right, the internal composition changed with respect to the upper and the lower visual fields. In each trial the whole pattern was shown for 16 milliseconds.

There were two different peripheral detection tasks. For half of the participants, the trained task was a *global identification*: the aim was solely to report the orientation of the rectangular boards in either the left or the right hemifield, regardless of their internal composition. For the other half of participants, the task was a *local detection*: the goal was to report if there was an "odd" element (i.e., a bar differently oriented) within the top or bottom boards, regardless of the orientations of the boards. (See Ahissar and Hochstein 1993, 5719.)

During the test session both groups of participants were tested in their respective trained tasks. The findings indicate a substantial improvement in performance. Furthermore, each group was also tested on the alternative, and untrained task. This second test aimed to verify whether the improvement observed in the trained task transferred to the untrained one (Ahissar and Hochstein 1993, 5719-5720). If the group trained in global recognition performed equally well during the (untrained) local recognition task, and vice versa, it would suggest that the skills acquired during the training were independent of any task instruction. In this case, all that would be required in perceptual learning is the deployment of voluntary covert spatial attention

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[27] The two quadrants on the left and the two on the right comprise respectively the left and the right hemifields.

(Ahissar and Hochstein 1993, 5719-5720).

The results attest that subjects trained in one task did not perform well in the untrained one.[28] During the experiment, despite the fact that both tasks used exactly the same visual pattern (four rectangular boards composed of small oblique lines) and that relevant and irrelevant stimuli overlapped (the odd elements formed part of the boards), the performance only improved for the trained task (Ahissar and Hochstein 1993, 5718; Schwartz 2007, 34-37).

The study evidences that voluntary covert spatial attention is necessary but not sufficient to improve peripheral detection: the attentional focus does not act as a "spatial window" which makes all the stimuli available (Ahissar and Hochstein 1993, 5720-5721). *Cognitive* control on attention attributable to specific task demands is also required. Despite the fact that subjects were looking at the same visual pattern and the same information was accessible for both groups from the attentional spotlight, the stimuli accessed (selected) strictly depended on the gating of attention. Therefore, attentional selection was conditioned by "top-down task-depending influences" (Ahissar and Hochstein 1993, 5718).

From a neurophysiological point of view, the improvement in performance from one task did not transfer to the other because each task required the detection of different stimulus properties, either local orientation or global shape (Ahissar and Hochstein 1993, 5718). Cells in the primary visual cortex are highly specialized in location, orientation, size, and monocular discrimination (Karni and Sagi 1991, 4966, 4969; Ahissar and Hochstein 1993, 5718; Crist et al. 2001, 519; Schwartz et al. 2002, 17137, 17139; Schwartz 2007, 28). In contrast, neurons in higher levels of the visual system are sensitive to more complex stimuli. As a consequence, the local detection task may have trained V1 neurons specialized in orientation, and the training in global identification may have modulated extrastriate visual cortical areas such as V2 and V3 (Ahissar and Hochstein 1993, 5720).

Finally, a peripheral-task experiment which exhibits a critical cognitive task-related control on attention was tested by Kelly et al. (2008). In this study, target and distractors shared the same internal properties and, occasionally, the same location in the visual field. The task required subjects to fixate centrally, but allocate voluntary covert spatial attention to different peripheral regions of the visual scene as cued. Subjects were instructed to report the target when it appeared at the attended location, and to ignore irrelevant stimuli. Distractors appeared either at the attended or unattended locations.

The complexity of the experiment lied in the fact that target and distractors

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[28] A small improvement in local detection performance for subjects trained in global identification was observed. The reason might be that during the training in global identification some local detection is automatically learned without spatial attention (Ahissar and Hochstein 1993, 5720-5721).

shared the same properties (all of them were Gabor stimuli), to wit, luminance and orientation. The relevant stimuli were distinguishable from irrelevant ones solely with regard to contrasts in luminance and different orientations. Therefore, a high cognitive load on attention was required to discriminate targets from distractors at the attended location.

The training evidenced a substantial improvement in peripheral detection. Electroencephalographic (EEG) data obtained during the performance of the task show that electrical signals from higher cortical areas affected the primary visual cortex by enhancing and inhibiting neural activity in the same subsets of neurons depending on whether the stimulus was or not a target. In other words, neural activity was enhanced in the same neurons when the item matched the task's instruction and inhibited when it did not (Kelly et al. 2008, 2635). The improvement obtained after the learning would not have been possible without specific top-down control on attention determined by the task conditions.

In conclusion, empirical data demonstrate that improvement in peripheral detection strictly depends on task requirements. The active participation of the observer is necessary to improve performance in perceptual learning (Schwartz et al. 2002, 17137). Following the task's instructions results in cognitive task-related control on attention necessary to select the relevant stimuli properties (e.g., location, orientation, size, colour, and the like) (Ahissar and Hochstein 1993, 5722; Schwartz et al. 2002, 17137, 17142; Rauss et al. 2011, 1245; and also Chun and Wolfe 2001, 284). Cognitive task-related feedbacks affect attention to enhance the subsets of neurons processing the relevant stimuli (Gilbert and Sigman 2007, 688-689; also Crist et al. 2001, 524). The result of this stimulation is observed as an improvement in visual detection for the trained visual properties and the trained region (Ahissar and Hochstein 1993, 5718).

To summarize, perceptual learning for peripheral detection requires two aspects of attention: the focus and the gating. Firstly, endogenous (voluntary) covert spatial attention acts as a spotlight making the highlighted information *accessible*. And secondly, under cognitive task-related control, attention makes the relevant stimuli from the spotlight *accessed*. Neither passive peripheral stimulation nor covert spatial attention alone improves performance. The relevant information is successfully selected thanks to the active participation of the observer during the training. Following the instructions of the task generates the cognitive task-related control on attention necessary to select the relevant properties.

In the next section, I examine the kind of cognitive load and cognitive control on attention required by the target study.

6.3 Cognitive Control on Attention in the Target Study

The target study demanded a low perceptual load together with a high cognitive load on attention. The detection of the central letter was a simple task, so that its detection demanded a low perceptual load. Higher perceptual load would have been necessary if more items had to be selected at fixation. Likewise, the detection of the peripheral object represented little difficulty. The array of three lines was against a homogeneous background of horizontal lines so that detecting its orientation required filtering out the backdrop. A higher perceptual load would have been demanded if more peripheral object's features had to be detected (e.g., orientation and colour). (See, e.g., Lavie 2005, 75-76.) In sum, given that the double-detection task in the target study did not engage subjects' full perceptual capacity, the selection of the appropriate stimuli among distractors necessitated cognitive control on attention.

Let's now examine cognitive load in the target study. Cognitive control on attention varied in two respects: distribution and degree of load. With regard to distribution, notice that cognitive load was exclusively demanded at the central fixation in the central-task study (Schwartz et al. 2005) and at the periphery of the visual field in the peripheral-task studies (Ahissar and Hochstein 1993; Kelly et al. 2008), but it was distributed between both tasks (central and peripheral) in the target study.

Concerning the degree of load, cognitive load was low in the central task of the target study: it only required the detection of a letter (either T or L) regardless of its orientation and colour. Likewise, the cognitive load in the peripheral task was low. It was lower than in the peripheral-task study realized by Kelly et al. (2008) (which required the detection of location, orientation and contrast luminance) but similar to the local detection task realized by Ahissar and Hochstein (1993) (only neurons sensitive to location and orientation were engaged). If higher cognitive exigencies were demanded for the both tasks there would not have been enough cognitive resources available to perform visual detection.

Though low cognitive load in both tasks suggests a moderate cumulative cognitive load, there is in addition a fundamental aspect in the study that must be remarked: *time*.[29] The pattern containing the letter and the oriented item was shown for a few milliseconds (16 ms). The task was therefore more demanding than it appeared because the selection had to be done very fast. Therefore, the combination of a moderate cognitive load in double detection and the very brief time of presentation implies a high overall cognitive load in the target study.

Peripheral detection in the target study depended on the gating of atten-

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[29] Thanks to Sophie Schwartz who drew my attention to this aspect.

tion. The double-detection task involved high cognitive load on task-related attentional control. High cognitive demands on attention provided the necessary resources to stimulate the subset of neurons sensitive to the target properties (position and orientation) and inhibit neurons sensitive to distractor properties. Neither the internal composition of the target (formed of three lines) nor the background (composed by small horizontal bars) were selected and then trained (Karni and Sagi 1991, 4966; Schwartz et al. 2002, 17141; Pourtois et al. 2008, 60). The constant and repetitive enhancement and inhibition of neural activity during training modulated neural behaviour in the primary visual cortex. These effects were local: neural plasticity occurred in the region of the retinotopic map which corresponds to the location of the target in the visual field (Karni and Sagi 1991, 4966, 4969; 1995, 9; Schwartz et al. 2002, 17140-17141; Pourtois et al. 2008, 60).[30]

To summarize, the evidence scrutinized indicates that in the target study the cognitive effects on attention during the learning session were responsible for neural reorganization in the primary visual cortex. However, that is not enough to defend architectural cognitive penetration in the visual system. Two further aspects need to be explained: first, the origin of top-down control on attention in the target study, and second, whether these influences effectively alter visual processing within the time period of early vision. This is the aim of the next two sections.

7 Cognitive Control and the Brain

Functional imaging techniques used in the target study collected information concerning neural activity in the whole brain. The results indicate that during the performance of the task the primary visual cortex (namely its lower-right portion) received top-down influences originating from distant higher brain areas.

One problem regarding top-down task-related control is the ambiguity of the concept of ‘top-down’. The primary visual cortex is the earliest area responsible for visual processing so that the label ‘top-down’ frequently refers to any re-entrant signal coming from any other brain area. A successful explanation of cognitive penetration in the visual system based on neuroscientific studies necessitates an elucidation of which top-down influences are cognitive and which may count as top-down perceptual, motor, or any other type of influence.

Four distinct top-down influences can be distinguished: intra-modal, cross-modal, motor, and cognitive. Higher influences within the visual system (e.g.,

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[30] For instance, if the target is displaced a few degrees of visual angle from its original location during the training, the task has to be relearned (Karni and Sagi 1991, 4967-4968; Karni and Sagi 1995, 5).

signals coming from extrastriate visual areas, e.g., V2 or V3, into the striate cortex) may be best considered as lateral or horizontal (visual) influences (Fodor 1983, 77-78; Pylyshyn 1999, 347; Raftopoulos 2009, 274). They constitute *intra-modal penetrability.* Similarly, top-down influences from other sense modalities (e.g., auditory system) are cross-modal influences (e.g., Pylyshyn 2003, 126-130). They may be contemplated as *cross-modal penetrability.* Top-down electrical signals into the visual system coming from the motor cortex may be identified as motor influences and considered as *motor penetrability.* However, none of these forms of penetrability results from cognitive influences. *Cognitive penetrability* requires the identification of cognitive areas in the brain.

In section 3, it has been explained that Pylyshyn gives a neuroanatomico-functional definition of the visual system and argues that early vision is cognitively encapsulated. Cognition involves higher faculties such as long-term memory and executive functions (e.g., working memory and attention). Each of these faculties is roughly identified with some region in the cortex: long-term memory lies on the inferotemporal (IT) cortex, working memory mainly correlates with the prefrontal cortex (PFC), and spatial attention depends on fronto-parietal networks (Schwartz et al. 2005, 774-775). This brief description, already exposed in section 3, gives us some grounds to examine top-down cognitive influences.

Five higher brain areas were recruited in the target study during the performance of the double-detection task: the left frontal lobe (mainly, the PFC), the left posterior intraparietal sulcus and the right inferior parietal lobule (both located in the intraparietal lobe), and the left and right amygdala (Schwartz et al. 2002, 17139-17140).

Intraparietal areas are partially identified with the somatosensory associative and motor cortices; accordingly, it is judicious to consider them as perceptual or motor, or at least, as non-cognitive.[31] Contrasting with this, the prefrontal cortex (PFC) realizes cognitive functions. On the one hand, it is responsible for maintaining task-processing priorities (i.e., working memory), and on the other hand, while associated with parietal areas, it controls attentional selection (Lavie et al. 2004, 341; Schwartz et al. 2002, 17140; Schwartz et al. 2005, 770). The amygdala also appears to have a cognitive role: it increases learning (enhances and reinforces the processing of the relevant visual stimuli) by strengthening the motivational aspects in attention (Schwartz et al. 2002, 17142; Vuilleumier and Driver 2007).

Therefore, two higher brain areas, to wit, the prefrontal cortex and the amygdala, can be considered as responsible for *cognitive task-related control* on attention. Whereas fronto-parietal networks monitor spatial attention, the

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[31] I do not exclude the possibility that these areas may play a cognitive role on attentional control, but I intend to avoid controversy.

PFC and the amygdala are responsible for cognitive guidance of attention.

In the next section, I show that cognitive influences affect the primary visual cortex within the time period of early vision.

8 Cognitively Guided Attention Influences Early Vision

Let's examine now the time period of visual processing in two detection tasks presented in section 6.2: the central-detection task in the study realized by Rauss et al. (2009) and the peripheral-detection task tested by Kelly et al. (2008). Because both studies monitored brain activity using EEG, they provide very detailed information for examining the time span of cognitive influences on the visual system.

During the central-task experiment (Rauss et al. 2009), subjects were required to report a central T-shaped object with different colours and orientations while distractors were displayed in the peripheral visual field. The study monitored top-down effects on the visual system due to changes in cognitive load. The task required subjects to report a single feature (i.e., the colour) under low cognitive load, and a feature conjunction (i.e., colour and orientation) under high load (Rauss et al. 2009, 1724). Top-down feedbacks in the primary visual cortex were monitored in two intervals: in the first 60 ms and from 60 to 100 ms after stimulus onset.

EEG results obtained during the training session indicate that cognitively guided attention affected the primary visual cortex at very early stages of the visual processing. Re-entrant feedbacks were manifestly observed in the time-window going from 60 to 100 ms under both load conditions. Although overall top-down influences were stronger in the second interval, they were also observed before 60 ms. In addition, cognitive influences were stronger under high rather than low cognitive load (Rauss et al. 2009, 1729).

Early influences on the visual system were also detected in Kelly et al. (2008)'s peripheral-detection task. Subjects were required to report the target at the attended location and to ignore distractors regardless of whether they appeared at the cued or uncued location. The study evidences that the degree of cognitive control on attention was proportional to the complexity of the discrimination task: the more demanding the task the stronger the engagement of higher brain areas. But, again, under all cognitive conditions the same higher brain areas were recruited (Kelly et al. 2008, 2635). Interestingly, EEG data point out that neural activity in the primary visual cortex was affected by cognitively guided attention as early as 57 ms after stimulus onset (Kelly et al. 2008, 2632).

To sum up, EEG data obtained in the central- and peripheral-detection tasks indicate, firstly, that attention influenced the primary visual cortex at very short delays of the visual processing – from 57 to 100 milliseconds after stimulus onset (Rauss et al. 2009, 1729; Kelly et al. 2008, 2632) and even before this interval (Rauss et al. 2009, 1729) – and secondly, that the effects depended on the complexity of the task, rather than on changes in cognitive load. These findings provide compelling reasons to maintain that in the target study cognitively guided attention most likely influenced earlier stages of the visual processing.[32]

Remember that Raftopoulos defines visual perception as a process lasting between 100 or 120 milliseconds after stimulus presentation, which, moreover, is cognitively encapsulated (see section 3). This claim contrasts with the evidence examined in this section: in the target study, early vision is in fact cognitively penetrated throughout the training session. Perceptual learning thus requires architectural cognitive penetration to be successful. The results demonstrate that early vision is cognitively penetrable. In the last section, I analyse architectural cognitive penetration in detail.

9 Architectural Cognitive Penetration

Architectural cognitive penetration designates the influence that the cognitive system directly exerts on the architecture of a perceptual system. Architectural changes in the visual system consequently have an indirect impact on the content of the perceptual experience.[33] It is due to architectural modulations that changes in perceptual content occur. Architectural cognitive penetration is synchronic when cognitive influences are simultaneous with the perceptual act and it is diachronic when cognitive effects precede perception.

In the target study, the perceptual task demanded the identification of a central letter simultaneously with the detection of a peripheral item's orientation. The peripheral detection represented the learning task. Due to the highly demanding experimental conditions the selection of the object's orientation necessitated both the allocation of spatial attention (focus) and the selection of the relevant properties from this focus (gating).

During the training session cognitively guided attention influenced the visual system within the time span of early vision. Attentional mechanisms selected the appropriate object properties by stimulating the neurons in the

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[32] To my knowledge there are no EEG data for the learning session in the target study, or, at least, they are not available. That prevents us from directly concluding that cognitively driven attention affected early vision *during* the training session.

[33] Notice that this is not always the case, some architectural changes may solely speed up the visual processing, increase performance by creating new neural connections, and so on, while the perceptual experience remains the same before and after the training. See, e.g., Raftopoulos 2001a, 438; 2009, 87.

primary visual cortex which encoded the relevant properties. This top-down modulation occurs at the very beginning of the visual processing, most likely on the order of 60 ms after stimulus presentation, and probably before. Taking into consideration, on the one hand, that the activation of V1 starts at about 40 ms after stimulus presentation (Raftopoulos 2009, 293; also Rauss et al. 2011, 1238-1240), and on the other hand, that cognitively driven attention affects V1 at about 60 ms after stimulus onset, it appears that only the first 10-20 ms of visual processing are the result of a predominantly bottom-up processing (Foxe and Simpson 2002, 146). Thus, cognitive influences on V1 are essential for the selection of the appropriate stimuli.

Moreover, top-down attentional selection occurred *synchronically*, i.e., every time the participant was presented with the visual pattern. Consequently, during the training session, the constant and synchronic stimulation of striate visual areas by cognitively guided attention resulted in physiological neural changes in the visual system.

Therefore, structural modulations occurring in the visual system due to cognitively guided attention are the result of *synchronic architectural cognitive penetration*. Firstly, the visual processing was influenced by cognitively guided attention. Secondly, there is good evidence that attention regulated visual selection in early vision. Thirdly, cognitive influences modulated the architecture of the visual system. And finally, architectural changes were synchronically, although gradually, produced in every trial all along the training session.

Notice that these findings contrast with Raftopoulos' (and also Pylyshyn's) claim mentioned in section 6: first, that the earliest cognitive influences in the visual system are observed at later delays in extrastriate visual areas; and second, that attention only facilitates visual selection, but it is not at the origin of the selective process. However, the analysis of visual processing in perceptual learning I have presented in this paper refutes these two claims. The target study clearly indicates that cognitively guided attention does affect the primary visual cortex at the very beginning of the visual processing and is in fact at the origin of visual selection.

Empirical data obtained during the test session confirm that the visual system had improved performance in peripheral detection. First of all, no top-down cognitive influences were required for the selection of the relevant object properties during the accomplishment of the peripheral-detection task. And second, the learning was followed by an improvement in detection with respect to the training session. The increase in performance was the result of anatomical neural reorganization occurring after consolidation when neural changes became stabilized. Therefore, the visual system learned to perform the task.

The successful detection of the peripheral object during the test session was possible thanks to *diachronic architectural cognitive penetration*. The consolidation of cognitively induced architectural modulations enabled the visual system to perform the peripheral-detection task without synchronic cognitive intervention. At that point, the cognitive influences that modified the architecture of the visual system were diachronically produced.

In conclusion, while synchronic architectural cognitive penetration solely depends on specific aspects of the training task, diachronic architectural cognitive penetration depends on both perceptual training and consolidation. Thus, the synchronic form of penetration and consolidation seem to be necessary conditions for diachronic architectural cognitive penetration. Observe that although the link between cognitive influences and anatomical neural plasticity is indirect, the account of diachronic architectural cognitive penetration is not undermined (see Wu 2013, 661-664, for an analysis of the compatibility of indirect cognitive influences with cognitive penetration).

There is an important aspect to consider here: cognitive penetration is typically characterized with respect to the cognitive impact on the resulting perceptual experience (Rowlands 2005, 15; Raftopoulos 2009, 119; Siegel 2013, 699; Macpherson 2012, 28; Stokes 2013, 650; Stokes and Bergeron forthcoming). If neural modulations elicited as a result of cognitive influences do not have any effect on the perceptual content, there would not be cognitive penetration (Raftopoulos 2009, 84). However, this is not the case for architectural cognitive penetration: the stimulus properties are retrieved thanks to cognitive influences. That is, neural changes do not only speed up the visual processing of some properties resulting in a more vivid, rich, or accurate perceptual experience. Instead, cognitive effects influencing the architecture of the visual system determine the content of the subject's perceptual states (e.g., global or local orientation, size, colour, luminance, and the like).

Again, this consequence refutes Raftotopoulos' claim that cognitive influences in perceptual learning do not have an impact on perceptual content (see section 6). In fact, cognitively guided attention in perceptual learning does influence perceptual experiences: perceptual content is strictly determined as a function of the task's instructions.

I would like to scrutinize a further remark regarding architectural cognitive penetration and perceptual learning: cognitive guidance on attention is necessary but not sufficient to produce neural reorganization in the striate cortex. Perceptual learning depends on several brain functions such as control of dual-task coordination, working memory, attention, and other neural networks engaged in learning processes (e.g., Schwartz et al. 2002, 17137; Lavie et al. 2004, 341). It is thanks to the conjunction of all of these functions that neural behaviour in the visual system changes (i.e., perceptual learning is successful). For example, performing only five trials in the target study will not produce any neural change in the primary visual cortex; it is after several repetitions that some neural adaptation is observed. Attentional networks engaged in the first five trials will be identical to those recruited in the rest of the training. The difference lies in the fact that several repetitions are required to increase cognitive control on attention and keep subject's alertness, coordination, and other functions stimulated. Consequently, although cognitive control on attention is necessary for visual selection and to engender neural reorganization, other essential functions which depend on neural networks involved in perceptual learning are required.[34]

In conclusion, in this paper I have scrutinized a form of cognitive penetration which I call 'architectural' and which can occur synchronically or diachronically. I have introduced an empirical study which shows that neural changes in the visual system are produced first by synchronic architectural cognitive penetration, and a day later, became the result of diachronic architectural cognitive penetration. Notice that, in contrast with Churchland, I have provided solid reasons and compelling examples to demonstrate that neural reorganization in the visual system is genuinely produced by cognitive penetration.[*]

References

Ahissar, M. and S. Hochstein 1993, "Attentional Control of Early Perceptual Learning", *Proceedings of the National Academy of Sciences* 90, pp. 5718–5722.

Bartolucci, M. and A. T. Smith 2011, "Attentional Modulation in Visual Cortex Is Modified During Perceptual Learning", *Neuropsychologia* 49, pp. 3898–3907.

Bear, M., B. W. Connors, and M. A. Paradiso 2007, *Neuroscience: Exploring the Brain* (3rd ed.), Philadelphia: Lippincott Williams & Wilkins.

Carruthers, P. 2006, *The Architecture of the Mind. Massive Modularity and the Flexibility of Thought*, Oxford: Clarendon Press.

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[34] The aim of this paper is to show that cognitively guided attention is a necessary condition for architectural cognitive penetration, what the sufficient conditions are is an empirical question exceeding the scope of this paper.

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Chun, M. M. and J. M. Wolfe 2001, "Visual Attention", in E. B. Goldstein (ed.), *Oxford: Blackwell Handbook of Sensation and Perception*, Blackwell Publishing Ltd.

Churchland, P. M. 1988, "Perceptual Plasticity and Theoretical Neutrality: A Reply to Jerry Fodor", *Philosophy of Science* 55, pp. 167–187.

Crist, R. E., W. L. Li, and C. D. Gilbert 2001, "Learning to See: Experience and Attention in Primary Visual Cortex", *Nature* 4, pp. 519–525.

De Weerd, P. 2010, "Visual Filling In and Completion", in E. B. Goldstein (ed.), *Encyclopedia of Perception*, pp. 1075–1077, Thousand Oaks: SAGE.

Deco, G. and E. T. Rolls 2008, "Neural Mechanisms of Visual Memory: A Neurocomputational Perspective", in S. J. Luck and A. Hollingworth (eds.), *Visual Memory*, Chapter 8, Oxford: Oxford University Press.

Desimone, R. and J. Duncan 1995, "Neural Mechanisms of Selective Visual Attention", *Annual Review Neuroscience* 18, pp. 193–222.

Echeverri, S. forthcoming, "Indexing the World? Visual Tracking, Modularity, and the Perception–Cognition Interface", *The British Journal for the Philosophy of Science*.

Felleman, D. J. and D. C. Van Essen 1991, "Distributed Hierarchical Processing in the Primate Cerebral Cortex", *Cerebral Cortex* 1, pp. 1–47.

Fodor, J. A. 1983, *The Modularity of Mind*, Cambridge, MA: MIT Press.

Fodor, J. A. 1988, "A Reply to Churchland's 'Perceptual Plasticity and Theoretical Neutrality'", *Philosophy of Science* 55, pp. 188–198.

Fodor, J. A. 2000, *The Mind Doesn't Work That Way: The Scope and Limits of Computational Psychology*, Cambridge, MA: MIT Press.

Fodor, J. A. and Z. W. Pylyshyn 1981, "How Direct Is Visual Perception? Some Reflections on Gibson's 'Ecological Approach'", *Cognition* 9, pp. 139–96.

Foxe, J. J. and G. V. Simpson 2002, "Flow of Activation from V1 to Frontal Cortex in Humans. A Framework for Defining 'Early' Visual Processing", *Experimental Brain Research* 142, pp. 139–150.

Fuster, J. M. 2008, *The Prefrontal Cortex* (4th ed.), London: Academic Press.

Gilbert, C. D. and M. Sigman 2007, "Brain States: Top-Down Influences in Sensory Processing", *Neuron* 54, pp. 677–696.

Goldstein, E. B. 2010, *Encyclopedia of Perception*, Volume 1 & 2, Thousand Oaks: SAGE.

Goodale, M. A. and A. D. Milner 2005, *Sight Unseen: An Exploration of Conscious and Unconscious Vision*, Oxford: Oxford University Press.

Karni, A. and D. Sagi 1991, "Where Practice Makes Perfect in Texture Discrimination: Evidence for Primary Visual Cortex Plasticity", *PNAS, Proceedings of the National Academy of Sciences* 88, pp. 4966–4970.

Karni, A. and D. Sagi 1995, "A Memory System in the Adult Visual Cortex", in B. Julesz and I. Kovacs (eds.), *Maturational Windows and Adult Cortical Plasticity*, pp. 1–15, Reading MA: Addison-Wesley.

Kelly, S. P., M. Gomez-Ramirez, and J. J. Foxe 2008, "Spatial Attention Modulates Initial Afferent Activity in Human Primary Visual Cortex", *Cerebral cortex* 18, pp. 2629–2636.

KOTTENHOFF, H. 1957, "Situational and Personal Influences on Space Perception with Experimental Spectacles", *Acta Psychologica* 13, pp. 79–97.

LAVIE, N. 1995, "Perceptual Load as a Necessary Condition for Selective Attention", *Journal of Experimental Psychology: Human Perception and Performance* 21, pp. 451–468.

LAVIE, N. 2005, "Distracted and Confused?: Selective Attention Under Load", *Trends in Cognitive Sciences* 9, pp. 75–82.

LAVIE, N. 2010, "Attention, Distraction, and Cognitive Control Under Load", *Current Directions in Psychological Science* 19, pp. 143–148.

LAVIE, N., A. H., J. W. DE FOCKERT, AND E. VIDING 2004, "Load Theory of Selective Attention and Cognitive Control", *Journal of Experimental Psychology: General* 133, pp. 339–354.

LAVIE, N. AND Y. TSAL 1994, "Perceptual Load as a Major Determinant of the Locus of Selection in Visual Attention", *Perception & Psychophysics* 56, pp. 183–197.

LYONS, J. 2011, "Circularity, Reliability, and the Cognitive Penetrability of Perception", *Philosophical Issues* 21, pp. 289–311.

MACPHERSON, F. 2012, "Cognitive Penetration of Colour Experience: Rethinking the Issue in Light of an Indirect Mechanism", *Philosophy and Phenomenological Research* 84, pp. 24–62.

MARR, D. 1982, *Vision: A Computational Investigation into Human Representation and Processing of Visual Information*, San Francisco: Freeman.

MCDOWELL, J. E., K. A. DYCKMAN, B. P. AUSTIN, AND B. A. CLEMENTZ 2008, "Neurophysiology and Neuroanatomy of Reflexive and Volitional Saccades: Evidence from Studies of Humans", *Brain and Cognition* 68, pp. 255–270.

MILNER, A. D. AND M. A. GOODALE 2006, *The visual brain in action* (2nd ed.), Oxford Psychology Series, Oxford: Oxford University Press.

POURTOIS, G., K. S. RAUSS, P. VUILLEUMIER, AND S. SCHWARTZ 2008, "Effects of Perceptual Learning on Primary Visual Cortex Activity in Humans", *Vision research* 48, pp. 55–62.

PURVES, D., G. J. AUGUSTINE, D. FITZPATRICK, W. C. HALL, A.-S. LAMANTIA, J. O. MCNAMARA, AND S. M. WILLIAMS 2004, *Neuroscience* (3rd ed.), Sunderland, Massachusetts: Sinauer Associates, Inc.

PYLYSHYN, Z. W. 1984, *Computation and Cognition: Toward a Foundation for Cognitive Science*, Cambridge, Massachusetts: MIT Press.

PYLYSHYN, Z. W. 1999, "Is Vision Continuous with Cognition? The Case for Cognitive Impenetrability of Visual Perception", *Behavioral Brain Sciences* 22, pp. 341–423.

PYLYSHYN, Z. W. 2003, *Seeing and Visualizing: It's Not What You Think*, Cambridge, Massachusetts: MIT Press.

RAFTOPOULOS, A. 2001a, "Is Perception Informationally Encapsulated? The Issue of the Theory-Ladenness of Perception", *Cognitive Science* 25, pp. 423–451.

RAFTOPOULOS, A. 2001b, "Reentrant Neural Pathways and the Theory-Ladenness of Perception, *Philosophy of Science* 3, pp. 187–199.

RAFTOPOULOS, A. 2005a, *Cognitive Penetrability of Perception: Attention, Strate-*

gies and Bottom-Up Constraints, Hauppauge, NY: Nova Science.

Raftopoulos, A. 2005b, "Perceptual Systems and a Viable Form of Realism", in A. Raftopoulos (ed.), *Cognitive Penetrability of Perception: Attention, Strategies and Bottom-Up Constraints*, Chapter 5, Hauppauge, NY: Nova Science.

Raftopoulos, A. 2009, *Cognition and Perception: How Do Psychology and Neural Science Inform Philosophy?*, Cambridge, MA: MIT Press.

Rauss, K., S. Schwartz, and G. Pourtois 2011, "Top-Down Effects on Early Visual Processing in Humans: A Predictive Coding Framework", *Neuroscience and Biobehavioral Reviews* 35, pp. 1237–1253.

Rauss, K. S., G. Pourtois, P. Vuilleumier, and S. Schwartz 2009, "Attentional Load Modifies Early Activity in Human Primary Visual Cortex", *Human brain mapping* 30, pp. 1723–1733.

Rowlands, M. 2005, "The Cognitive Penetrability of Perception", in A. Raftopoulos (ed.), *Cognitive Penetrability of Perception: Attention, Strategies and Bottom-Up Constraints*, Chapter 2, Hauppauge, NY: Nova Science.

Röder, B. and F. Rösler 2004, "Compensatory Plasticity as a Consequence of Sensory Loss", in G. Calvert, C. Spence, and B. Stein (eds.), *The Handbook of Multisensory Processes*, Cambridge, MA: MIT Press.

Schwartz, S. 2007, "Functional MRI Evidence for Neural Plasticity at Early Stages of Visual Processing in Humans", in N. Osaka, I. Rentschler, and I. Biederman (eds.), *Object Recognition, Attention, and Action*, pp. 27–40, Tokyo: Springer.

Schwartz, S., P. Maquet, and C. Frith 2002, "Neural Correlates of Perceptual Learning: A Functional MRI Study of Visual Texture Discrimination", *Proceedings of the National Academy of Sciences* 99, pp. 17137–17142.

Schwartz, S., P. Vuilleumier, C. Hutton, A. Maravita, R. J. Dolan, and J. Driver 2005, "Attentional Load and Sensory Competition in Human Vision: Modulation of fMRI Responses by Load at Fixation During Task-Irrelevant Stimulation in the Peripheral Visual Field", *Cerebral cortex* 15, pp. 770–786.

Siegel, S. 2012, "Cognitive Penetrability and Perceptual Justification", *Noûs* 46, pp. 201–222.

Siegel, S. 2013, "The Epistemic Impact of the Etiology of Experience", *Philosophical Studies* 162, pp. 697–722.

Siegel, S. and N. Silins forthcoming, "The Epistemology of Perception", in M. Matthen (ed.), *Oxford Handbook of Philosophy of Perception*, Oxford: Oxford University Press.

Stickgold, R. 2005, "Sleep-Dependent Memory Consolidation", *Nature* 437, pp. 1272–1278.

Stickgold, R. and M. P. Walker 2007, "Sleep-Dependent Memory Consolidation and Reconsolidation", *Sleep Medicine* 8, pp. 331–343.

Stokes, D. 2012, "Perceiving and Desiring: A New Look at the Cognitive Penetrability of Experience", *Philosophical Studies* 158, pp. 477—492.

Stokes, D. 2013, "Cognitive Penetrability of Perception", *Philosophy Compass* 8, pp. 646—663.

Stokes, D. and V. Bergeron forthcoming, "Modular Architectures and Informational Encapsulation: A Dilemma".

Styles, E. A. 2005, *Attention, Perception, and Memory : An Integrated Introduction*, Hove: Psychology Press.

Styles, E. A. 2006, *The Psychology of Attention* (2nd ed.), Hove: Psychology Press.

Tovée, M. J. 2008, *An Introduction to the Visual System* (2nd ed.), Cambridge: Cambridge University Press.

Vuilleumier, P. and J. Driver 2007, "Modulation of Visual Processing by Attention and Emotion: Windows on Causal Interactions Between Human Brain Regions", *Philosophical Transactions of the Royal Society B* 362, pp. 837–855.

Walker, M. P. and R. Stickgold 2004, "Sleep-Dependent Learning and Memory Consolidation", *Neuron* 44, pp. 121–133.

Wamsley, E. J. and R. Stickgold 2010, "Dreaming and Offline Memory Processing", *Current Biology* 20, pp. 1010–1013.

Wu, W. 2008, "Visual Attention, Conceptual Content, and Doing It Right", *Mind* 117, pp. 1003–1033.

Wu, W. 2013, "Visual Spatial Constancy and Modularity: Does Intention Penetrate Vision?", *Philosophical Studies* 165, pp. 647–669.