

Does the Emotional Modulation of Visual Experience Entail the Cognitive Penetrability or Emotional Penetrability of Early Vision?

Athanassios Raftopoulos (raftop@ucy.ac.cy)
Department of Psychology
University of Cyprus
P.O. Box 20537
Nicosia 1678, Cyprus

Abstract

I argue that emotive states affect perceptual processing either directly or indirectly with latencies that fall within late vision and not early vision. These effects differ from the effects of, and are subserved by different neuronal mechanisms than those that subserved, attentional effects on perception, although the two sorts of effects may interact. It follows that the emotive effects found in perception do not entail either the cognitive penetrability of early vision or its emotional penetrability.

Introduction

Discussions on the cognitive impenetrability (CI) of perception almost exclusively concern attentional modulation of perceptual processing. Pylyshyn (1999) argues that attention does not modulate a stage of visual processing, namely, early vision, which is CI. Late vision, in contradistinction, is cognitively penetrated (CP). Raftopoulos (2009) reaches the same conclusion based on neuroscientific evidence on the timing of attention. However, even if attention does not signify the CP of early vision, other influences might modulate early visual processing. Since emotional states affect perception, is early vision penetrated by emotional states? Siegel (2006) and Stokes (2012) have argued that affective states affect the phenomenology of perception. A second interesting question is whether emotional effects are independent of attention, or whether they should be interpreted as attentional phenomena in which emotional stimuli are more attended. (Brown et al. 2010)

Philosophers usually discuss about the CP of perception as if perception were a unified stage. If they find reason to believe that some perceptual states are CP, they conclude that perception is CP. However, perception is not a homogeneous, undifferentiated process. It consists of two main stages, namely early vision and late vision, of which only the former may be CI. Siegel (2006, 501) acknowledges that it is likely that visual perception has an informationally encapsulated part that is CI and another part that is influenced by cognitive processing. These two visual parts represent different properties of the environment. For example, object membership to some category, which according to Siegel is part of the content of perception, may be represented in the CP

stage of perception. Since perception has two stages, any adequate discussion about CP should make clear to which stage the claim concerning CP purports to apply, and, similarly, any claim concerning the penetration of perception by emotional influences should make clear to which stage of visual processing it purports to apply.

Affective states modulate perceptual processing and affect the allocation of processing resources to incoming sensory stimuli. In this sense, they function as attention does and for this reason, the difference between attentional and emotional mechanisms notwithstanding, many researchers talk of 'emotional attention'. (Vuilleumier 2005) Emotional states can affect perceptual processing both directly or indirectly.

The indirect effects occur when signals from brain areas like the OFC (orbitofrontal cortex), and the amygdala that process the emotional aspects of stimuli are transmitted to parietal and frontal areas and affect the semantic processing of the stimulus that takes place there, as when the valence of a stimulus speeds up or inhibits object recognition. In this case, the emotional processes co-determine the allocation of cognitively driven attention and, thus, affect indirectly perceptual processing through attentional effects; emotional effects modulate attention and, thereby, perception. (Phelps 2006) Since, I assume that the earliest effects of cognitively driven attention modulate perceptual processing at 150 ms after stimulus onset the earliest, and that early vision lasts for up to 80-120 ms, I take it that the indirect emotional influences on perceptual processing through attentional allocation do not threaten the CI of early vision.

There are also direct emotional effects on perceptual processing through top-down transmission of signals from either the OFC or the amygdala to the visual processing areas, signals that are distinct from those generated in parietal and frontal areas. Should this be the case, early vision despite its CI, would be emotionally penetrated (EP). There is, for example, evidence that irrespective of whether or not a face cue directs covert attention, the fear face cue enhances contrast sensitivity. (Phelps and LeDoux 2005) There is also evidence for modulation of the P1 waveform at 120 ms after stimulus onset by emotional stimuli, a latency that precludes this modulation being the result of top-down cognitive signals

but can be accounted for by signals from the amygdala affecting directly visual processing.

In this paper, I argue that emotive states do not affect directly early vision but only late vision. In the first section, I discuss early and late vision, as well as CP and EP. In the second section, I discuss the timing of emotional effects to determine whether they affect perceptual processing and, to the extent that the answer is affirmative, which stage of perceptual processing. Given that early vision lasts for 120ms, to affect early vision affective effects must be registered within 120 ms. If they occur later than that and while perceptual processing still lasts, they affect late vision. I conclude that direct emotional effects are found in late vision but not in early vision. Thus, early vision is not EP.

2. Visual Stages, CP, and EP

I assume that perception consists of two stages; early vision and late vision. The former is CI, while the latter is CP as far as cognitive effects that are mediated by cognitively driven attention are concerned. Thus, I assume that cognitively driven attention does not affect directly early vision.

Early vision includes both a feed forward sweep (FFS) of signal transmission in which signals are transmitted bottom-up and which lasts, in visual areas for about 100 ms, and a stage at which lateral and recurrent connections between neurons allow recurrent processing. This sort of recurrent processing—Lamme (2003) calls it *local recurrent processing* (LRP)—occurs at 80-120 ms, is restricted within visual areas, and does not involve signals from cognitive centers. The unconscious FFS extracts high-level information that could lead to categorization, determines the classical receptive field of neurons and their basic tuning properties, and results in some initial feature detection. The representations formed at this stage are restricted to including information regarding the transducible features of objects, that is, information about spatio-temporal properties, surface properties, viewer-centered shape, color, texture, orientation, motion, and affordances, in addition to the representations of objects as bounded, solid entities that persist in space and time. Parts of this stage's contents are at the personal level. By being restricted within the visual system and by not involving signals from the cognitive areas of the brain, FFS and LRP are CI.

During early vision no cognitively-driven attentional effects exist. Neurophysiological evidence for this comes from various findings (discussed in Raftopoulos 2009, ch. 2) that strongly suggest that the first signs of cognitively driven attentional effects on visual areas up to V4 occur at about 150 ms. Thus, early vision is a pre-attentional stage of visual processing that is CI in the sense that its formation is not directly affected by signals from cognitive centers. It is in defining what 'directly' means that considerations about attention enter the picture and make necessary some explication of what 'pre-attentional' means.

First, my claim does not entail that there is no selection during early vision. There are non-attentional selection

mechanisms that filter information before it reaches awareness. These mechanisms are not considered to be attentional because they occur very early and do not involve higher brain areas associated with attentional mechanisms (prefrontal cortex, parietal cortex, etc.)

Second, 'pre-attentional' should be construed in relation to cognitively driven attention that affects perceptual processing directly, the claim being that early vision involves processes that are not affected directly by this sort of attention. Cognitively driven attention is opposed both to exogenous or stimulus-driven attention, and to the effects of either spatial or feature/object cueing before stimulus onset. The latter do not affect in a top-down manner visual processing but just rig up the feedforward sweep. This phenomenon is referred to as the *attentional modulation of spontaneous activity*. For example, attending to a location at which the stimulus will appear may enhance the base-line activation, that is, the spontaneous firing rates, of the neuronal assemblies tuned to the attended location in specialized extrastriate areas. The same phenomenon is found with respect to feature/object-centered attention.

Late vision is affected by cognitive effects and, thus, involves higher cognitive areas of the brain (memory etc); late vision involves the global neuronal workspace. (Dehaene et al. 2006) Such effects start at about 150 ms when information concerning the gist of a visual scene, retrieved on the basis of low spatial frequency (LSF) information in the parietal cortex in about 130 ms, reenters the extrastriate cortex and facilitates the processing of the high spatial frequency information (HSF) leading to faster scene and object identification. (Kihara and Takeda 2010; Peyrin et al. 2010)

Let me explain what I mean by CP and CI of early vision. CP=The CP of early vision is the nomological possibility that cognitive states can causally affect in a top-down, direct, on-line way (that is, while the viewer has in her visual field and attends to the same location or stimulus, or is prepared to attend to the same stimulus when it appears) early vision, in a way that changes the visual contents that are or would be experienced by a viewer or viewers with similar perceptual systems, under the same external viewing conditions.

The reference to direct on-line effects purports to insulate a process that is indirectly affected by cognitive inferences from being construed as CP. The indirect effects include both cognitively driven spatial and feature/object based attention, and the preparedness to attend that covers cases in which the viewer expects a certain object or feature to appear either at a certain cued location or somewhere in her visual field. The former cases are post-early vision effects. The later cases constitute a rigging-up of the FFS and are not instances of CP, which is supposed to affect perception on-line. The term of causality ensures that any relation between contents occurs as a result of the causal influences of cognitive states on perceptual states and contents and is not a matter of coincidence. Finally, the specification of 'top-down' ensures that the operational constraints, which are at play in perception

to solve the various problems of underdetermination both of the distal objects from the retinal image and of the percept from the retinal image do not constitute cases of CP because by being hardwired in the perceptual system, they cannot be cognitive effects. (Raftopoulos 2009)

A similar definition applies to EP.

EP=The EP of early vision is the nomological possibility that affective states can causally affect in a top-down, on-line way (that is, while the viewer has in her visual field the same stimulus or is prepared for the appearance of the same stimulus) early vision, in a way that changes the visual contents that are or would be experienced by a viewer or viewers with similar perceptual systems, under the same external viewing conditions.

Note that there are some differences from the definition of CP owing to the fact that, as we shall see, it is likely that emotional stimuli can be processed and experienced even when they are outside the focus of attention. As in the case of CP, the preparedness purports to cover cases in which a cue regarding the valence of an upcoming stimulus may influence the base-line activation of the neurons encoding the stimulus.

2. Timing Emotional Effects

When the brain receives information, it generates a hypothesis based on the input and what it knows from the past to guide recognition and action. In addition to what it knows, it uses affective representations, that is, prior experiences of how the input had influenced internal bodily sensations. In determining the meaning of the incoming stimulus, the brain employs representations of the affective impact of the stimulus to form affective predictions. These predictions are made within ms and do not occur as a separate step after the object is identified; rather they assist in object identification. There is substantial evidence that the OFC, which is the centerpiece of the neuronal workspace that realizes affective responses, plays an important role in forming the predictions that support object recognition. (Barr 2009)

Activation of the OFC owing to bottom-up signals is observed between 80-130 ms. (Bar 2009) This activity is driven by LSF information and, hence, magnocellular visual input. A second wave of activity in the OFC is registered at 200 to 450 ms, probably reflecting the refinement and elaboration of the initial hypothesis. There is evidence that the brain uses LSF information to make an initial prediction about the gist of a visual scene or object, that is, to form a hypothesis regarding the class to which the scene/object belongs. This hypothesis is tested and details are filled using HSF information in the visual brain and information from visual working memory. (Johnson and Olshausen 2005; Kihara and Takeda 2010; Peyrin et al. 2010)

Barrett and Bar (2009) argue that the medial OFC directs the body to prepare a physical response to the input, while the lateral parts of OFC are integrating the sensory feedback from the bodily states with sensory cues. The medial OFC has

reciprocal connections to the lateral parietal areas in the dorsal system, where it receives LSF information transmitted through magnocellular pathways. Using LSF information, the medial OFC extracts the affective context in which the object has been experienced in the past and this information is relayed to the dorsal system where it contributes to the determination of the sketchy gist of the scene or object. The lateral OFC, in its turn, has reciprocal connections with inferior temporal areas of the ventral stream, whence it receives HSF information through parvocellular pathways (the pathways that carry detailed information about a visual scene in the ventral system). Its role is to integrate sensory with affective information to create a specific representation of the scene or object, which eventually leads to conscious experience. Note that owing to the time delay of the information transmitted through parvocellular pathways compared to the information transmitted through magnocellular pathways, information arrives faster at the medial OFC than at the lateral OFC. (Ashley et al. 2003)

Emotional stimuli, owing to their intrinsic significance, have a competitive advantage relative to neutral stimuli and are more likely to win the biased competition among stimuli for further processing. However, affecting the biased competition among stimuli is what attentional effects do too and, so, the question arises as to the relation between emotional and attentional influences on visual processing. Evidence shows that both attention to non-emotional stimuli and emotional stimuli *per se* can boost neural responses (Vuilleumier et al. 2004; Shupp et al. 2003). This suggests that the net result of both attentional and motivational modulation of the visual cortex is very similar. Since emotional effects, like attentional effects, enhance perceptual processing, they are sometimes referred to as 'emotional attention'. (Vuilleumier 2005) However, the neuronal pathways responsible for attentional and emotional effects are likely different, since, among other things, differences in size and duration of the time courses of semantic and emotional processing and their influences on the visual cortex have been observed. (Attar et al. 2010; Vuilleumier 2005; Vuilleumier and Driver 2007) Another reason for being skeptical of the view that the same mechanism underlies attentional and emotional effects is that there is mixed evidence concerning whether unattended emotional stimuli (fearful faces) are processed. Williams et al. 2005 argue that although differential amygdala responses to fearful versus happy facial expressions are tuned by mechanisms of attention, the amygdala gives preference to potentially threatening stimuli under conditions of inattention. Moreover, the influence of selective attention on amygdala activity depends on the valence of the facial expression. Bishop et al. 2007, on the other hand, argue that affective modulation of the BOLD signals occurs only when the task demands low attention.

Studies in humans (Olofsson et al. 2008; Vuilleumier and Driver 2007) show that emotional vs. neutral faces processing produces a higher amplitude of VEP (visual evoked potentials)

and an enhancement of the P1 ERP component at about 120 ms. P1 originates in extrastriate areas and is considered to be the hallmark of the effects of exogenous spatial attention on visual processing, that is, the effects of the automatic orienting response to a location where sudden stimulation has occurred. This entails that the emotion-related modulation of the visual cortex arises prior to the processing stages associated with fine-grained face perception indexed by the N170 component for face recognition. This reinforces the view that emotional affects are prior to, and help in determining, the categorization of the stimuli, and that they can collaborate with attentional effects by enhancing the processing of spatially relevant and emotionally significant stimuli. The early latency precludes this modulation being the result of top-down cognitive signals. Neither can the modulation be accounted for by signals from the amygdala because the amygdala in humans processes the emotional content of facial expressions at 140-170 ms after stimulus onset (Conty et al. 2012), or at 200 ms (Pessoa & Adolphs 2010). Despite its early latency, the P1's modulation by emotion occurs when early vision is almost over (120 ms).

The N170 is also modulated by emotional content and this modulation occurs at about the same time that amygdala start processing the emotional content of face expressions. (Conty et al. 2012) EEG studies that manipulate attentional and emotional facial expressions orthogonally (Holmes et al. 2003) show that emotional effects start modulating face processing at the fusiform gyrus closely following the N170 face specific component. Thus, the emotional modulation of the extrastriate cortex takes place prior to task-related attentional selection and prior to the full processing of faces in the cortex. This is also an indication that emotional effects enhance or inhibit the processes that lead to object recognition.

ERP results on affective processing show also an early posterior negativity (EPN) at about 200-300 ms for arousing vs. neutral pictures, which involves both fronto-central and temporo-occipital sites and which is thought to index 'motivated attention'. The motivated attention selects affectively arousing stimuli for further processing on the basis of perceptual features. Furthermore, other findings show that the affective amplitude modulation persists for a prolonged period of time, which entails that emotionally arousing stimuli receive enhanced encoding even when they had to be ignored by being task irrelevant. (Olofsson et al. 2008) Around the same time (200-300 ms), stimulus valence has been shown to elicit a decreased N2 negativity (unpleasant compared to pleasant stimuli). Since at 200-300 ms latencies stimulus discrimination and response selection are thought to occur, affective visual stimuli may influence neural activation before response stages. (Carretie et al. 2004)

The negativity biases of ERP waveforms at these latencies may reflect rapid activity by amygdala processing of aversive information and the transmission of this information to fronto-parietal areas where it modulates the allocation of attention so that unpleasant stimuli may receive priority processing. Or,

they may reflect the functioning of an early selective attention mechanism that does not depend on valence categorization but on motivational relevance and which facilitates processing of stimuli with high motivational relevance. (Shupp et al. 2004)

Emotional effects are found at long latencies as well (>300ms), probably reflecting the impact of emotional signals to the processing of sensory information in fronto-parietal areas. Both P3 and the following positive slow wave relate to the elevated ERP positivity caused by the emotional modulation of P3 and of the slow wave, and by the valence value and arousal level of the stimulus (valence influences P3b but not P3a, while arousal influences both).

In general, valence effects are found predominantly for early and middle-range ERP components, probably reflecting the role of emotional intrinsic value of the stimulus for stimulus selection. Arousal effects, that is, a positive shift in the ERP waveforms, are found for middle-range and late components and constitute the primary affective influence at these latencies (Olofsson et al. 2008). They probably reflect the allocation of processing resources to the selected stimuli.

The discrepancies found in studies comparing emotional with attentional effects are probably caused by the fact that in the various experiments there were different manipulations of the kind of attention involved (spatial vs. object-based attention). In ERP studies when non-spatial attentional manipulations were applied (pictures of fearful faces and houses were superimposed so that spatial attention could be controlled and object-based attention could be manipulated) a sustained positivity in response to fearful faces emerged at about 160 ms in the fusiform gyrus, which was not affected by attentional manipulations. (Santos et al. 2008) Similar results suggesting that emotion-related modulation occurs even when emotional stimuli were not task relevant have been found with SSVEP studies. (Muller et al. 2008)

To disentangle this issue, Attar et al. (2010) examined not the time course of emotional processing of stimuli *per se* but its effects on attentional resource allocation in a primary task with respect to which the emotional stimuli functioned as distractors. Their findings suggest that highly arousing emotional pictures consume much more processing resources than neutral pictures over a prolonged period of time, which means that emotional distractors receive prioritized processing despite severe resource limitations. This effect, however, is of relatively small size when compared to the effects of general picture processing on task-related activity, where irrelevant whole pictures without any emotional value that act as distractors have a detrimental effect on task related activity. More importantly for this paper, however, Attar et al (2010) found, at the behavioral level, significant decreases in target detection rates when emotional compared to neutral pictures were concurrently presented in the background. At the neuronal level, the effect was accompanied by a stronger decrease of SSVEP amplitudes directed to a primary task for emotional relative to neutral pictures. The earliest onset for the affective deflective amplitude was at 270 ms. According to

our knowledge about the neural sites at which SSVEP signals are generated, the deflection observed stems from sources in early visual areas. (Andersen et al. 2012) Attar's et al (2010) work also shows that the presence of a challenging primary task that limits the availability of processing resources does not eliminate the observed emotion-induced reduction of SSVEP amplitudes, which suggests that the effects of emotional distractors are not contingent on top-down attentional control. Note that the SSVEP findings accord well to the findings on the timing of the emotional effects on visual processing found in the various ERP studies discussed above.

The discussion thus far shows both attentional and emotional effects on visual processing from brain areas other than the visual cortex. However, the brain regions and neural pathways involved in emotional and attentional influences seem to be different. For example, amygdala is involved in emotional modulation of perceptual processing, whereas the FEF and other parietal regions are involved in the modulation of perceptual processing by spatial attention. Amygdala is well poised to modulate perception because it receives sensory inputs from all modalities and sends signals to many cortical and subcortical regions that can potentially influence perception. Amygdala is sensitive both to coarse LSF information that travels fast in the brain and to slow HSF information. This way an initial appraisal of emotional significance based on a limited amount of information may proceed quicker than the elaborate and time consuming processing associated with conscious awareness of a stimulus.

This may explain why ERPs to fearful expressions in face selective neurons in monkeys are registered very early (50-100 ms after the initial selective activity), while the fine encoding of faces that relies on the slower traveling HSF information starts at 170ms as indexed by the specifically related to face-processing N170.

Concerning the relation between affective and attentional effects, one can make the following general remarks. The amygdala responds to fearful expressions independent of attentional modulation. The amygdala can reinforce the representation of fearful faces in fusiform cortex, an influence that is disrupted when the amygdala is damaged. (Vuilleumier et al. 2004) Recordings of face-selective neurons in monkeys (Sugase et al. 1999) suggest that the amygdala modulates perceptual processing 50-100 ms after the initial face-selective activity. Since the monkey amygdala neurons respond to threatening face expressions between 120-250 ms (Pessoa & Adolphs 2010), the earliest modulation of face selective neurons by amygdala signals starts at about 170 ms, in accordance with Holmes et al (2008) findings. The amygdala activity probably reflects coarse-grained global processing of the input, while the affective modulation of face processing reflects affective information contributing to a more fine-grained representation of faces at later latencies with a delay of 50 ms compared to global processing.

Emotional enhancement of the responses of neurons in visual areas of the brain can operate even when attention is

impaired owing to parietal damage in spatial neglect. fMRI studies with patients show enhanced fusiform activity for fearful faces compared to neutral faces even when the faces were neglected. (Vuilleumier et al. 2004) fMRI studies show that amygdala feedback to the fusiform area influences visual cortex additively to the modulation of the same area by attention (in this case attention and emotion cooperate). Thus, even though emotional states produce activations analogous to those of attention, the fact that they enhance the representation of emotionally task-irrelevant stimuli means that these effects are probably realized by different neural pathways.

Emotional and attentional effects can also compete. Emotional modulation of distractors enhances the responses of the neurons encoding them. This increases the competition with the targets by reducing the responses of the neurons encoding them. Emotional signals, however, may be suppressed by high perceptual competition where spatial attention filters out very early most of the distractors. (Lavie 2005) Finally, amygdala's influence can persist in conditions where cortical responses are reduced, contributing, thus, to the amplification of cortical processing when sensory inputs are insufficient. (Vuilleumier 2005)

Emotional effects act separately from attentional effects and provide an additional bias to the processes of sensory representations that lead to the selection of some among the items in the input, either adding to or competing with attention. The competition that emotional effects pose to attention is advantageous for an organism since unexpected events that have a particular emotional value can be detected, and influence behavioral responses, independently of the organism's current attentional loads.

Conclusion

Between 80 and 170 ms after stimulus onset an emotional effect is found in emotion sensitive areas like the OFC and the amygdala owing to bottom-up sensory signals. At 120 ms emotional influences start modulating perceptual processing in extrastriate cortex and at about 170 ms the processing of face selective neurons is affected by emotional signals. At 270 ms SSVEP signals are registered in early visual areas, driven by top-down emotional signals. In this latency, an EPN and perhaps a N2 effect due to affective modulation is found. Information concerning the emotional significance of visual stimuli reenters visual areas at about 120 ms the earliest, and continues for up to 1000 ms. Thus, the earliest affective influences reach visual areas at such latencies that fall outside the duration of early vision; they affect only late vision.

References

- Andersen, S., Muller, M., & Hillyard, S. (2012). Tracking the allocation of attention in visual scenes with SSEVP. In M. I. Posner (ed.), *Cognitive Neuroscience of Attention*. New York, N.Y: Guilford Press.
- Ashley, V., Vuilleumier, P., & Swick, D. (2003). Effects of orbitofrontal lesions on the recognition of emotional faces

- expressions. Paper presented at the Cognitive Neuroscience Society Meeting.
- Attar, C. H., Andersen, S., & Muller, M. M. (2010). Time course of affective bias in visual attention: convergent evidence from steady-state visual evoked potentials and behavioral data. *NeuroImage*, *53*, 1326-1333.
- Barr, M. (2009). The proactive brain: memory for predictions. *Philosophical Transactions of the Royal Society, Biology*, *364*, 1235-1243.
- Barrett, L. F., & Bar, M. (2009). See it with feeling: affective predictions during object perception. *Philosophical Transactions of the Royal Society*, *364*, 1325-1334.
- Bishop, S.J., Jenkins, R., Lawrence, A. D. (2007). Neural processing of fearful faces: effects of anxiety are gated by perceptual capacity limitations. *Cerebral Cortex*, *17*, 1595-1603.
- Brown, Ch., El-Deredy, W., & Blanhette, I. (2010). Attentional modulation of visual-evoked potentials by threat: investigating the effect of evolutionary relevance. *Brain and Cognition*, *74*, 281-287.
- Carretie, L., Mercedo, F., Hinojoja, J. A., Loeches, M., & Sotillo, M. (2004). Valence-related vigilance biases in anxiety studied through event-related potentials. *Journal of Affective Disorders*, *78*, 119-130.
- Conty, L., Dezechache, G., Hugueville, L., & Grezes, J. (2012). Early binding of gaze, gesture, and emotion: neural time course and correlates. *Neuroimage*, *28*, 4531-4539.
- Dehaene, S., Changeux, J-P., Naccache, L. Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Science*, *10*(5), 204-211.
- Holmes, A., Vuilleumier, P., & Eimer, M. (2003). The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. *Brain Research*, *16*, 174-184.
- Johnson, J. S. & Olshausen, B. A. (2005) The earliest EEG signatures of object recognition in a cued-target task are postsensory. *Journal of Vision*, *5*, 299-312.
- Kihara, K., & Takeda, Y. (2010). Time course of the integration of spatial frequency-based information in natural scenes. *Vision Research*, *50*, 2158-2162.
- Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, *7* (1), 12-18.
- Lavie, N. (2005). Distracted and confused? selective attention under load. *Trends in Cognitive Science*, *9*, 75-82.
- Muller, M. M., Andersen, S. K., & Keil, A. (2008). Time course of competition for visual processing resources between emotional pictures and foreground task. *Cerebral Cortex*, *18*, 1892-1899.
- Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: an integrative review of ERP findings. *Biological Psychology*, *77*, 247-265.
- Pessoa, L. & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. *Nature Reviews Neuroscience*, *11*, 773-783
- Peyrin, C., Michel, C. M., Schwartz, S., Thut, G., Seghier, M., Landis, Th., Marendaz, Ch., & Vuilleumier, P. (2010). The neural processes and timing of top-down processes during coarse-to-fine categorization of visual scenes: a combined fMRI and ERP study. *Journal of Cognitive Neuroscience*, *22*(12), 2678-2780.
- Phelps, E. A. (2006). Emotion and cognition. *Annual Review of Psychology*, *57*, 27-73.
- Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron* *48*, 175-187.
- Pylyshyn, Z. (1999). Is vision continuous with cognition? *Behavioral and Brain Sciences*, *22*, 341-423.
- Raftopoulos, A. (2009). *Cognition and Perception: How do Psychology and the Neural Sciences inform Philosophy*. Cambridge, MA: The MIT Press.
- Raftopoulos, A. (forthcoming). The cognitive impenetrability of perception and theory-ladenness. *Journal of General Philosophy of Science*.
- Santos, I. M., Iglesias, J., Olivares, E. I., Young, A. W. (2008). Differential effects of object-based attention on evoked potentials to fearful and disgusted faces. *Neurophysiology*, *46*, 1468-1479.
- Shupp, H. T., Junghoffer, M., Weike, A. J., & Hamm, A. O. (2004). Emotional facilitation of sensory processing in the visual cortex. *Psychophysiology*, *41*, 441-449.
- Siegel, S. (2006). Which properties are represented in perception? In T. S. Gendler & J. Hawthorne (eds.), *Perceptual Experience*. Oxford: Oxford University Press.
- Stokes, D. (2012). Perceiving and desiring: a new look at the cognitive penetrability of experience. *Philosophical Studies*, *158* (3), 479-92.
- Sugase, Y., Yamane, S., Ueno, S., & Kawano, K. Global and fine information coded by single neurons in the temporal visual cortex. *Nature*, *400*(6747), 869-873.
- Vuilleumier, P. (2005). How brains beware: neural mechanisms of emotional attention. *Trends in Cognitive Science*, *19*(12), 585-595.
- Vuilleumier, P., Richardson, M., Armony, J., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature Neuroscience*, *7*, 1271-1278.
- Vuilleumier, P. & Driver, J. (2007). Modulation of visual processing by attention and emotion: windows on causal interactions between human brain regions. *Philosophical Transactions of the Royal Society, Biology*, *362*, 837-855.
- Williams, M. A., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2005). Differential amygdala responses to happy and fearful facial expressions depend on selective attention. *Neuroimage*, *24*, 417-425.
- Pessoa, L. & Adolphs, R. (2010). Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating