Affective and motivational control of vision

Patrik Vuilleumier[a,b,c]

Purpose of review
It is increasingly recognized that affective values associated with visual stimuli can influence visual perception, attention, and eye movements. Recent research has begun to uncover the brain mechanisms mediating these phenomena. The present review summarizes the main paradigms and findings demonstrating emotional and motivational influences on visual processing.

Recent findings
Several pathways have been identified for enhancing neural responses of cortical visual areas to stimuli with intrinsic emotional value (e.g., facial expressions, social scenes, and others), including projections from the amygdala and ascending modulatory neurotransmitter systems from the brainstem. These pathways can guide attention and gaze to emotionally salient information with either negative (threatening) or positive (rewarding) associations. In addition, abundant research in recent years suggests that probabilistic reward learning can lead to powerful biases in visual attention and saccade control through subcortical pathways connecting visual areas with basal ganglia and superior colliculus. Time-resolved neuroimaging using electroencephalography or magnetoencephalography has begun to tackle the time course of these effects, and can now be complemented by neuroimaging and neurophysiology recordings in monkey.

Summary
These findings have implications for understanding and assessing affective biases in perception and attention in patients with psychiatric disorders, such as phobias, depression, and addiction, but also open new avenues for rehabilitation in neurological patients with attention disorders.

Keywords
attention, emotion, motivation, reward, vision

INTRODUCTION

In everyday life, love or happiness can make us see the world with rose-colored glasses, but we may see red because of anger. At other times, when feeling sad, the world appears dark and gloomy. Are these phrases just metaphors of common language, or can emotion truly change how we see?

Neuroscience research has begun to reveal the reality of such intimate links between affect and perception, particularly in vision, and uncover the underlying brain circuits. Although both scientists and philosophers have often distinguished aspects of the mind/brain related to 'high-level' processes, such as cognition and emotion, from 'low-level' operations mediating sensory processing, it is becoming increasingly evident that the former can be influenced by the latter in various ways [1]. This converges with the view that brain functions depend on highly interactive dynamics between distributed networks wherein top–down and predictive signals play a key role in guiding bottom–up information processing [2]. Thus, affective processes do not only contribute 'subjective' components to perception, by bringing 'colors' or 'flavors' to it, but may actually determine and shape the contents of perception itself through multiple effects on sensory pathways. These influences can operate using different channels, either directly via specific mechanisms interfacing affective and sensory processing, or indirectly via modulation of attentional systems that, in turn, also control

[a]Department of Neuroscience, Medical School, University of Geneva, [b]Department of Neurology, University Hospital of Geneva and [c]Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

Correspondence to Patrik Vuilleumier, LABNIC/NEUFO, University Medical Center, Rue Michel-Servet 1, Geneva 1205, Switzerland. Tel: +41 22 379 5381; fax: +41 22 379 5402; e-mail: patrik.vuilleumier@unige.ch

KEY POINTS

- Affective meaning of visual stimuli can enhance perceptual sensory analysis, facilitate orienting of attention, and capture eye movements.

- These effects may occur without voluntary control and without awareness.

- These effects are driven by either negative (threat) or positive (reward) affective signals.

- Affective modulation of visual perception operate through several routes, involving direct influences from amygdala, basal ganglia, and adrenergic projections on sensory cortical areas, frontoparietal areas, and superior colliculus.

- These effects may be amplified or attenuated in psychopathological conditions.

sensory processing, and in the case of vision, via possible influences on oculomotor processes that may drive the eyes to emotionally relevant cues.

Although much remains to be uncovered, research has begun to illuminate the neurobiological substrates of these phenomena with increasing precision, in both humans and animal models. The current review will focus on recent developments in this rapidly growing field.

EMOTIONAL ENHANCEMENT OF VISION

A large body of work has shown that visual perception is enhanced by affective information, both behaviorally and neurally [1,3]. For example, in visual search tasks, where a target must be detected amidst distractors, items with emotional meaning (e.g., fearful faces, snakes, violent scenes, and others) are found faster than neutral items, whereas emotionally significant distractors slow the detection of neutral targets [4]. Similarly, in attentional blink tasks where targets are frequently missed when following shortly after another target, emotional items are detected better than neutral items. A similar emotional advantage is found in many different visual tasks, indicating that these stimuli are processed more efficiently and capture attention more readily than neutral stimuli. Moreover, people tend to judge pictures with emotional content as visually more vivid and sharper than neutral pictures with similar contrast and luminance content [5]. Eye-tracking studies also found that emotionally meaningful information has greater impact on the number of fixations and more frequently attract the first saccade than visually salient details related to brightness and contrast [6,7]. Although these effects

are most often obtained with emotionally negative information, they also occur for positive and rewarding stimuli (see further below).

At the brain level, these perceptual enhancements are paralleled by increased activation of visual cortical areas, as measured with functional MRI (fMRI) and event-related potentials in electroencephalography (EEG). These increases involve stimulus-specific representations in visual cortex, such as fusiform or occipital extrastriate cortex for emotional face or bodily gestures, respectively, but also earlier processing stages down to V1 [1], which presumably account for the greater perceptual advantage of emotional stimuli. This has led to a general model of visual attention whereby different sources of modulatory control act simultaneously on visual pathways by regulating the gain of neuronal responses [3], including top–down endogenous and bottom–up exogenous processes as put forward by traditional models, but also object-based processes and motivational signals [8].

Recent EEG and magnetoencephalography studies have provided new insights into the rapid time course of these affective modulations [9]. Elegant work [10] combining event-related potentials (ERPs) and steady-state visual potentials showed enhanced cortical processing for task-irrelevant emotional stimuli starting around 190 ms (early negative potential, EPN), prolonged until 1000 ms (late positive potential, LPP), whereas ongoing oscillations produced by task-relevant flickering stimuli were reduced from 380 to 700 ms. These data indicate that emotional significance does not only boost visual responses at latencies corresponding to object recognition but also attenuates the representation of concomitant information in a temporal succession consistent with competitive interactions between inputs. These competition effects may change depending on task demands, as suggested by another study where steady-state visually evoked potentials to background scenes were enhanced (rather than suppressed) when a fearful face (vs. neutral) was presented at fixation during passive viewing [11], suggesting that the face increased the emotional salience of the background scene. Manipulating the task goals by requiring participants to rate emotion intensity or brightness of visual scenes did not change the EPN to emotional stimuli but produced additive or interaction effects on later components [12]. Similarly, higher task load for concurrent stimuli may reduce the LPP to irrelevant fearful face distractors but not an early signature of involuntary spatial orienting (N2Pc component) around 200 ms [13].

Although these results provide novel evidence that emotion processing may automatically operate

in some conditions, they also highlight that distinct features of automaticity must be distinguished, such as intention, resource competition, or explicit report [3▪], among others [14], each of which might concern distinct processing pathways or stages. Future research needs to more precisely tackle the temporal characteristics of emotion processing along these pathways as a function of these different factors.

ROLE OF AMYGDALA-CENTERED CIRCUITS

Several observations suggest that the emotional enhancement of visual perception and corresponding increases in visual cortex are at least partly dependent on modulatory signals from the amygdala [1,3▪,15], a brain structure central to emotion appraisal and learning. The amygdala has direct feedback projections to visual areas, including V1, which can modulate the gain of neuronal responses in parallel to other attention signals. Accordingly, amygdala damage in humans was shown to abolish the increased response of visual cortex to emotional faces in visual cortex with fMRI [16] and EEG [17]. Some authors reported that a detection advantage [18,19] and increased response of visual cortex [20] to complex emotional scenes may still exist in patients with amygdala resection for treatment of epilepsy. This discrepancy might result from compensatory mechanisms and plasticity subsequent to chronic epilepsy and/or other uncontrolled factors in stimulus content and task demands (e.g., visual saliency and voluntary attention). In monkeys, a recent study [21] convincingly showed that amygdala inactivation by focal neurotoxic injection suppressed emotion-related increases in extrastriate visual cortex, without disrupting face-selective activation, as previously shown in humans [16]. This study revealed an anatomical gradient with anterior and posterior amygdala lesions affecting more anterior and more posterior visual areas, respectively [21].

Single-cell recordings in monkeys also indicate that the amygdala combines information about both the value and spatial position of motivationally relevant stimuli. Peck *et al.* [22▪▪] showed that amygdala neurons respond stronger and faster to a visual cue predicting a rewarded stimulus in the contralateral hemifield, relative to the ipsilateral hemifield. These data suggest that amygdala code not only for the value of stimuli but also their location in visual space, supporting the notion that it may contribute to orient attention to relevant stimuli. Recent anatomical tracing data [23▪], however, show that bidirectional connections between amygdala and extrastriate visual cortex do not have a strict retinotopic organization, suggesting that spatial representations in amygdala might operate globally at the hemifield level. Thus, emotional feedback from amygdala may not only boost specific object representations in high-level visual areas (e.g., faces in fusiform cortex) but also more broadly increase sensitivity to inputs from other visual locations [24,25].

The amygdala can also influence visual processing indirectly via other cortical projections (such as orbitofrontal cortex, anterior cingulate cortex, and posterior parietal cortex) or via connections to subcortical nuclei mediating neuromodulatory functions (such as cholinergic, noradrenergic, and dopaminergic systems; see review [1]). The exact role of these pathways remains poorly known. A recent study points to a specific involvement of α2 receptors for noradrenergic effects on emotional attention, presumably mediated by the locus coeruleus [26▪]. However, these neuromodulatory systems may have a more general role on attention by increasing arousal and regulating executive control systems in prefrontal cortical areas [27], rather than directly modulating sensory processing [28].

In addition to modulating perception and attention, emotional feedback to the visual cortex may also modulate perceptual learning. Following fear conditioning to a specific face identity, people tend to show lower detection thresholds for this face in ambiguous images mixing two faces, an effect accompanied by increased sensitivity in both fusiform cortex and amygdala [29]. These data converge with data suggesting that emotional signals do not only amplify neuronal responses of sensory areas but also modulate their tuning to relevant stimulus properties [30]. Further research should explore whether these effects contribute to perceptual and memory biases observed in psychopathology disorders, including phobias and posttraumatic disorders.

MODULATION BY REWARD LEARNING

One of the most studied links between vision and motivational value in recent years concerns the effects of reward learning on selective visual attention. In these studies, participants first perform a stimulus discrimination task where one dimension of the stimulus (e.g., color or shape) is associated with high reward (when responses are correct), whereas another is associated with low or no reward. Subsequently, participants perform another visual task (e.g., visual search) where these dimensions are presented again in either the target or the distractor stimuli. Critically, in this phase, targets sharing the

previously rewarded feature show better and faster detection than targets without this feature, whereas distractors with this feature will impair performance more than distractors without [31,32,33■■,34,35]. This occurs even when the previously rewarded feature is irrelevant for the current task and when subjects are told to ignore it, showing that these effects are involuntary and presumably nonconscious [36]. Moreover, they may last for several weeks [37■] and transfer across tasks [38,39]. These attentional biases emerge only when a visual feature is uniquely predictive of the reward outcome, as opposed to other visual features, not when reward is given indiscriminately for all correct responses during the learning phase [40]. These findings support a causal role of associative reward learning mechanisms known to depend on dopamine signaling, which compute reward predictions and prediction errors, rather than more general motivational mechanisms. Contextual information is also important because these effects disappear when the visual screen background is changed between learning and testing phases [41]. Similarly, attention is oriented faster to visual objects previously paired with an appetitive odor (e.g., chocolate), but this effect is cancelled after satiation with the corresponding flavor [42], demonstrating that attentional biases generated by reward prediction depend on the current motivational value of the stimulus.

Recent work showed that reward-based biases are bound to not only object features (color or shape) but also spatial locations in the visual field [43■■,44], and that they operate independently and additively to biases learned from the probability of target appearance at a given location [45]. Furthermore, the reward value associated with a given visual feature may override the effect of low-level perceptual saliency or exogenous visual cues [45–47], and also suppress the 'gestalt' (object-based) advantage normally observed during shifts of attention within relative to between objects [48,49]. These data suggest that reward-induced biases arise at early stages of visual processing, in parallel to attentional selection processes operating on object and location representations.

Learned reward associations also influence eye movements. A visual feature (color) or location previously paired with higher reward may then elicit faster saccades toward them [50] or cause a deviation of voluntary saccades directed elsewhere [51,52]. This occurs despite opposite goals, for example, when such features are task irrelevant or must be avoided [36,52].

The neural underpinnings of these effects remain poorly known. Imaging and neurophysiology studies indicate that reward learning modulates neural responses in several brain areas associated with visual perception and attention, in addition to areas involved in memory and motivation. Both increases and decreases have been reported in contralateral V1 and extrastriate visual areas [48, 53,54,55■■], even when reward information is given without visual stimulation [55■■], presumably reflecting facilitation of sensory analysis. Reward expectation also modulates parietal (intraparietal sulcus) and frontal (frontal eye field) areas, which compute saliency maps of visual space and control top–down attention [48,56,57], as well as anterior and posterior cingulate areas [57,58,59■], which integrate reward signals with contextual task goals. Recent EEG and magnetoencephalography studies in humans also found modulations of early visual processing, including enhanced amplitudes of P1 or N2Pc components that reflect rapid attention orienting toward the location of targets [35,58, 60–62] or distractors [58,61] previously associated with reward. Interestingly, visual distractors modulate occipital activity around 180–200 ms when their color is shared with targets, but around 220–250 ms when their color is associated with higher reward probability [59■], indicating that influences from reward and goal relevance operate through distinct mechanisms.

The sources of these reward effects on visual processing and attention are still unclear but likely to involve the basal ganglia and dopaminergic projections from midbrain, known to play a key role in reward processing and learning [31,40,53,54,55■■]. Recent work in monkeys found that caudate neurons encode the reward value of visual objects in a task-irrelevant or task-dependent manner in posterior or anterior parts, respectively [63], and that their inactivation abolishes gaze biases toward reward-associated stimuli [64■]. The posterior caudate might provide a crucial pathway connecting visual cortices with superior colliculus and thus subserve a particular form of skill learning that allow efficient guidance of attention and eye movements to motivationally relevant visual cues [64■,65■■]. Accordingly, visually responsive cells in superior colliculus are modulated by reward learning [66,67] and constitute plausible substrates for reward-induced biases in saccadic behavior [50,51].

It remains unresolved whether the amygdala also plays a role in these effects, given its activation to both threat and reward-predicting cues [56] ,and its direct feedback influences on visual processing [3■,21], as described above. Future studies should more systematically compare visual enhancements produced by threat and reward, the relative contribution of amygdala and basal ganglia in specific conditions, and their differential impact on sensory,

attention, and oculomotor systems. It will also be important to determine whether similar effects arise when visual stimuli acquire motivational value by reward or negative outcomes instead, such as losses and punishment.

INDIVIDUAL DIFFERENCES AND PSYCHOPATHOLOGY

The influence of affective processes on vision and attention may vary depending on the emotional state and reactivity of individuals. It has long been known that people with anxiety and phobias show distinctive biases in attention, typically demonstrated by faster detection of and/or slower disengagement from visual threat stimuli [68,69]. Neuroscience research has attributed these effects to heightened amygdala responses causing perceptual enhancements as well as reduced control of voluntary attention by prefrontal executive systems [3■,70]. Both stimulus-specific and unspecific effects are observed but at different stages of visual processing, as indicated by recent EEG results. Spider phobics exhibit a larger N2pc component (at 160 ms) to spider targets or spider distracters presented contralaterally within a visual search array, reflecting involuntary orienting of spatial attention [71]; but they also show a more general amplification of early C1 (around 60 ms) to all contralateral (spider or nonspider) targets [72]. Transient anxiety states produced by social or physical stressors also modulate C1 responses to neutral, task-irrelevant stimuli (gratings) [73]. These data indicate that internal emotional states can affect early bottom–up visual processes, in addition to more delayed top–down feedback influences driven by stimulus meaning.

Less is known about how individual differences shape reward-induced biases in visual perception and attention [69]. Recent behavioral data show that these effects are amplified in individuals who have reward-seeking personality [74], greater sensitivity to gains than losses in economic choices [62], or cocaine addiction [75], even in simple visual search tasks as described above. Conversely, depressive traits correlate with weaker reward-induced biases [76]. At the neural level, positive mood induction may increase the C1 response to task-irrelevant visual stimuli, suggesting sensory gain effects independent of top–down attention control [77,78■], which go beyond the traditional notion that positive affect can broaden and boot attention capacity [79].

IMPLICATIONS FOR REHABILITATION OF VISUAL DISORDERS

Can affective processes be exploited to restore or improve visual impairments due to neurological diseases? A prime example is visuospatial neglect where conscious perception of visual stimuli in left hemifield is disrupted due to losses in top–down modulation from attentional networks following right parietal damage [80]. In neglect patients, pairing some visual stimuli with aversive reinforcement through classical conditioning can subsequently reduce neglect for these shapes when presented in the left visual field [81]. This improvement is accompanied by increased visual cortical response to these stimuli, presumably underlying their greater perceptual saliency and resulting from feedback from coactivated amygdala. These effects imply that affective meaning of contralesional visual information can be extracted prior to attention orienting, through initial cortical sweeps of inputs or subcortical pathways yet to be fully determined [1]. Visuospatial neglect can also be counteracted by reward learning processes associating left-sided locations in space with higher reward outcomes than right-sided locations [82■]. In the latter study, participants were asked to search for hidden rewarded targets within a bilateral array of stimuli. One group received larger rewards for left than right targets, whereas another received symmetrical rewards. In the asymmetric condition only, healthy participants as well as patients with left neglect showed a progressive shift of their search strategy toward the left side of the array, although they remained unaware of the asymmetrical reward distribution. These findings accord with results showing that reward history can enhance saliency maps of space [43■■]. The neural substrates of these effects are unknown but neglect patients whose lesion extended to basal ganglia showed weaker effects of reward on visual search biases [82■].

These preserved effects of emotion and motivation on visual attention should be further explored and usefully harnessed in future rehabilitation protocols of neglect and other attentional disorders.

CONCLUSION

Recent neuroscience research has revealed multiple ways by which affective processes can influence visual perception, both directly by modulating visual areas and indirectly via attention, oculomotor, and modulatory neurotransmitter systems. These effects may be driven by negative (threatening) or positive (rewarding) values assigned to visual objects, features, and even locations, which together act to bias perceptual representations and gaze behavior in favor of motivationally relevant information in the visual field. These findings highlight the notion that visual perception and awareness are governed not only by endogenous and exogenous

attention processes classically attributed to fronto-parietal networks operating on sensory cues but also by other subcortical pathways coding for the emotional and motivational value of these cues [83]. More research is needed to elucidate the respective role of the amygdala and basal ganglia circuits, the exact time course of neural events underlying these effects, and their modification in neuropsychiatric conditions.

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Conflicts of interest

There are no conflicts of interest.

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