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Implicit guidance of attention: The priority state space framework

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ABSTRACT

Visual selective attention is the process by which we tune ourselves to the world so that, of the millions of bits per second transmitted by the retina, the information that is most important to us reaches awareness and directs action. Recently, new areas of attention research have opened up as classic models dividing attention into *top-down* and *bottom-up* systems have been challenged. In this paper, we propose a theoretical framework, the priority state space (PSS) framework, integrating sources of salience that guide visual attention according to a nested hierarchy of goals. Using the PSS framework as a scaffold, we review evidence of selected sources of implicit attentional guidance, including recent research on statistical learning, semantic associations, and motivational and affective salience. We next summarize current understanding of the underlying neural circuitry facilitating guidance of attention by specific sources of salience, including key neuro-modulator systems, with an emphasis on affective salience and the noradrenergic system. Finally, we discuss evidence for common mechanisms of prioritization, including integration of sources of salience via priority maps, and introduce the concept of the PSS as a model for mapping a complex dynamic attentional landscape.

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For a time, it seemed, everyone knew what attention was. We had a pretty good grip on the underlying neural systems as well. Selective attention is the process by which we tune ourselves to the world so that the information that is most important to us reaches awareness and guides action. In this case it was thought to be characterized by the tension between two clearly delineated control systems: *Top-down* or *endogenous* processes involving volitional, executive attention to task-relevant stimuli, mediated by a dorsal attention network (DAN), and *bottom-up*, or *exogenous* processes involving attentional capture by low-level features of a stimulus (e.g., colour, contrast, or motion) mediated by a ventral

attention network (VAN) (Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). A large body of research in humans and non-human animals has provided support for the function of both attentional systems [e.g., (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001; Reynolds & Chelazzi, 2004)]. Yet in the past few years that simple dual process model has been challenged. Research delineating influences on attentional prioritization that defy straightforward characterization as either top-down or bottom up has proliferated, inspiring an influential paper to declare the simple model to be “a failed attentional dichotomy” (Awh, Belopolsky, & Theeuwes, 2012).

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As a result, there has been a push towards expanding and refining models of attentional guidance, which were originally developed in highly constrained laboratory contexts, to accommodate other sources of attentional modulation of perceptual systems. Emerging conversations between researchers coming out of previously silo-ized lines of research have further delineated a wide range of implicit sources of prioritization—including priming, semantic associations, statistical learning, working memory, long-term memory processes, emotional salience and reward. They are also beginning to elucidate the neural processes that subserve these processes [for review see (Anderson, 2016a; Awh et al., 2012; Bourgeois, Chelazzi, & Vuilleumier, 2016; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Hutchinson & Turk-Browne, 2012; Jiang, Swallow, & Rosenbaum, 2013; Kristjansson & Campana, 2010; Markovic, Anderson, & Todd, 2014; Pourtois, Schettino, & Vuilleumier, 2013; Shomstein & Gottlieb, 2016; Soto, Hodson, Rotshtein, & Humphreys, 2008; Vuilleumier, 2015)]. From these conversations, more comprehensive theoretical frameworks of attentional guidance have been emerging [e.g., (Awh et al., 2012; Jiang, Swallow, & Rosenbaum, 2013; Shomstein & Gottlieb, 2016)]. These frameworks share the goal of incorporating multiple sources of salience that dynamically tune the attentional landscape.

The goal of this paper is to review recent research on implicit guidance of attention arising out of often-isolated sub-disciplines of neuroscience and psychology, with a focus on visual attention. Based on this body of research, we will propose the priority state space (PSS) framework of attentional guidance. Briefly, the PSS framework proposes distinct sources of salience that modulate an attentional landscape that is both spatially and temporally dynamic. These sources are contextually prioritized according to a nested hierarchy of long and short-term goals. Processes of attentional guidance can unfold at time scales ranging from milliseconds to years. They can include deployment of explicit task-related attentional sets mediated by fronto-parietal modulation of visual cortex. They also include implicit tuning processes involving modulation of the visual system by both cortical and subcortical systems. At longer time-scales such tuning can involve long-term memory consolidation processes and/or repeated experience. We propose that such sources of salience may be reconciled at the level of *priority maps*. Priority maps are neural representations of the relative salience of locations in the visual field that determine spatial allocation of attentional resources (Awh et al., 2012; Bisley & Goldberg, 2010; Chelazzi et al., 2014; Itti & Koch, 2001; Ptak, 2012).

The PSS framework is informed by the dynamic nature of priority maps as they have been conceptualized (Bisley & Goldberg, 2010). This framework proposes that, at any given moment, sources of salience are prioritized based on past experience of a given context, or category of situation, such as sitting in a classroom or dining with close friends. Our conception of *state* is borrowed from the reinforcement learning literature. It refers to a schema representing a state of the world in which aspects of the environment are prioritized based on our experience of what was most beneficial to our goals in similar situations in the past (Redish, Jensen, Johnson, & Kurth-Nelson, 2007). The concept of the *state space* comes from dynamical systems theory and refers to the set of all

possible states of the system. Within the PSS model a state space constrains the landscape of priorities that may be activated within that context. We propose that a change of context—leaving a classroom to drive home in the snow on a slippery road, or leaving a dinner party to walk down a poorly lit urban street—precipitates a bifurcation in the state space that gives rise to a new landscape of possibilities. A PSS is a conceptual map illustrating the landscape of possible priorities within that context.

Sources of salience. Building on previous models [e.g., (Awh et al., 2012).], we propose three broad categories of attentional guidance. We suggest that attention is prioritized by 1) **featural salience** of stimuli, or canonical *bottom up* influences, 2) short-term **executive attention** to explicit, task related goals, or canonical *top-down* influences, and 3) **history**, a broad category that includes multiple, mostly-implicit, sources of prioritization possessing qualities of both *top-down* and *bottom-up* control. These sources include shorter-term influences, which can develop over the course of a task, such as selection history, statistical learning, and rapid associative learning processes. They also include longer-term influences such as long-term memory processes, semantic associations, and repeated processes of associative learning that can unfold over the course of years. In this paper, we focus on evidence for the role of *history* in attentional guidance and discuss the goals that attending to and learning from specific sources of salience in this category may serve. We focus particularly on affective-motivational sources of salience in relation to long and short-term goals of approaching pleasure and avoiding pain. Because neuro-modulator systems, in particular dopamine (DA) and norepinephrine (NE), play a central role in modulating attention to affective and motivational salience, the PSS framework stresses the role of these systems in tuning the visual cortex to what is significant over time.

In the present paper, we will use the PSS framework as a theoretical scaffold to review evidence for (I) selected sources of implicit attentional guidance, including recent research on statistical learning, semantic associations, and motivational and affective salience. We will next (II) summarize current understanding of the underlying neural circuitry facilitating guidance of attention by specific sources of salience, including key neuromodulator systems. As the role of affective salience in guiding attention has been somewhat neglected in the attention literature, we will place particular emphasis on affective salience and the noradrenergic system. We will also review evidence for specific neuronal processes underlying visual cortex plasticity with tuning to affective-motivational salience. We then (III) discuss evidence for common mechanisms of prioritization, including integration of sources of salience in parietal priority maps and rhythmic processes underlying attentional sampling. Finally, in the light of this evidence we will (IV) discuss the concept of the PSS as a model for mapping a complex dynamic attentional landscape.

1. Sources of salience

We learn to navigate the world by attending to the predictability and frequency of objects and events, their meanings in

relation to each other, and their associations with reward and punishment. These are aspects of cognition that are highly evolutionarily conserved. Such fundamental learning processes influence what aspects of the environment stand out to guide attention and action in service of the ultimate goal of survival. They can be observed to an extent in octopuses, fruit flies and even in plants (Anderson, Mather, Monette, & Zimzen, 2010; Gagliano, Vyazovskiy, Borbely, Grimonprez, & Depczynski, 2016; Siwicki & Ladewski, 2003). These processes may be directed towards goals achieved by our capacity for statistical learning, mapping semantic meaning, and learning from reward and punishment, some of which we discuss below. Here we briefly review recent literature suggesting key sources of salience related to these capacities and, within the PSS framework, propose the type of goal that each source of salience may serve.

1.1. Statistical learning

One recent line of research has concerned the influence of incidental statistical learning on attentional guidance. A series of studies by Jiang, Swallow, and Rosenbaum (2013) pitted the influence of statistical learning against that of explicit attentional goals within a visual search task. The authors varied the probability that a target would appear in a given location and also manipulated an endogenous cue to compare effects of statistical learning with those of executive attention. Results showed that incidental learning (learning not dictated by the demands of the task) of the spatial distribution of the targets influenced attention. Moreover, effects of statistical learning were distinct from those of ‘top-down’ executive attention, suggesting that statistical learning provides a unique source of guidance. Subsequent eye tracking experiments demonstrated that gaze patterns favoured regions of space where targets were more frequently presented (Jiang, Won, & Swallow, 2014). Other studies have demonstrated that statistical learning can drive feature-based as well as spatial attention (Zhao, Al-Aidroos, & Turk-Browne, 2013). Jiang and colleagues further propose that probability cueing is a form of procedural attention, and thus a form of premotor attention that guides future action (Jiang, Swallow, Rosenbaum, & Herzog, 2013). Within the PSS framework, statistical learning serves the goal of predicting frequently occurring events required for action.

1.2. Semantic associations

The semantic meaning of a stimulus has also been implicated in the implicit guidance of attention [for review see (Shomstein & Gottlieb, 2016)], and engages regions of parietal cortex implicated in priority mapping (Shomstein & Behrmann, 2006). At the most basic level, we suggest that semantic information subserves a fundamental and universal goal of carving up the world into objects that can be remembered and identified, despite changes to the specifics of their appearance. Yet semantic associations *between* objects also guide attention. The semantic relatedness of two objects (e.g., the relatedness of a hammer to a nail) can capture attention even when task-irrelevant (Malcolm, Rattinger, & Shomstein, 2016; Moores, Laiti, & Chelazzi, 2003). Semantic relatedness has also been

found to modulate electrophysiological signatures of selective attention (Telling, Kumar, Meyer, & Humphreys, 2010), and modulate attention independently of featural salience (de Groot, Huettig, & Olivers, 2016). Such guidance of attention by semantic associations may result from long-term statistical learning of the frequent co-occurrence of semantically associated objects in real environments. As a result, it has been suggested that executive attention to task-relevant targets may spread to related distractors (Moores et al., 2003). Looking at such findings through the lens of the PSS framework, we propose that tuning to the co-occurrence of related objects may serve the ongoing pursuit of a task-related goal. For example, selective attention to both the slice of bread and the butter may be beneficial for performing the task of spreading the butter on the slice of bread.

1.3. Reward

A growing body of research has focused on the influence of reward on attentional prioritization [for review see (Chelazzi et al., 2013)]. In humans these studies have typically involved training phases in which participants learn to associate certain stimulus features, such as colour (Anderson, Laurent, & Yantis, 2011), or regions of space (Chelazzi et al., 2014) with higher or lower probability of financial reward. Attentional prioritization is subsequently tested by examining reaction time or accuracy in visual search tasks where the rewarded feature or location is irrelevant to the search goals. It has also been examined by testing accuracy in reporting reward-related versus neutral stimuli that are difficult to perceive due to competition with other stimuli presented in close temporal proximity (Raymond & O'Brien, 2009). These studies have shown that attention is guided by both stimulus features and spatial locations that have been associated with reward (Anderson et al., 2011; Chelazzi et al., 2014), and reward-associated stimuli are prioritized under conditions where attentional resources are constrained in time as well as space (Raymond & O'Brien, 2009). Importantly, learning to associate locations in the visual field with reward has been found to shape priority maps in a fashion that endures over time. In a 4-day experiment by Chelazzi et al. (2014), on days one and four, participants had to identify either one or two targets in a circular array both before and after training. On days two and three, participants learned to identify a target in the same spatial configuration, but correct performance was more likely to be highly rewarded at some target locations than others. Changes in the *gain* in priority of different regions of space after learning (Fig. 1) indicated that priority maps had been reshaped to favour locations with a history of being more highly rewarded. Moreover, recent research suggests that reward-biased attention is context specific, such that attentional capture depends on whether a stimulus feature has been previously rewarded within the current situation (Anderson, 2015). These findings provide evidence that reward not only influences attentional tuning to currently rewarded aspects of the environment, but that such tuning to the environment is shaped by a longer term history of association with reward in a context-dependent fashion. We suggest that the goal served by such guidance of attention by reward is that of acquiring and holding on to sources of pleasure.

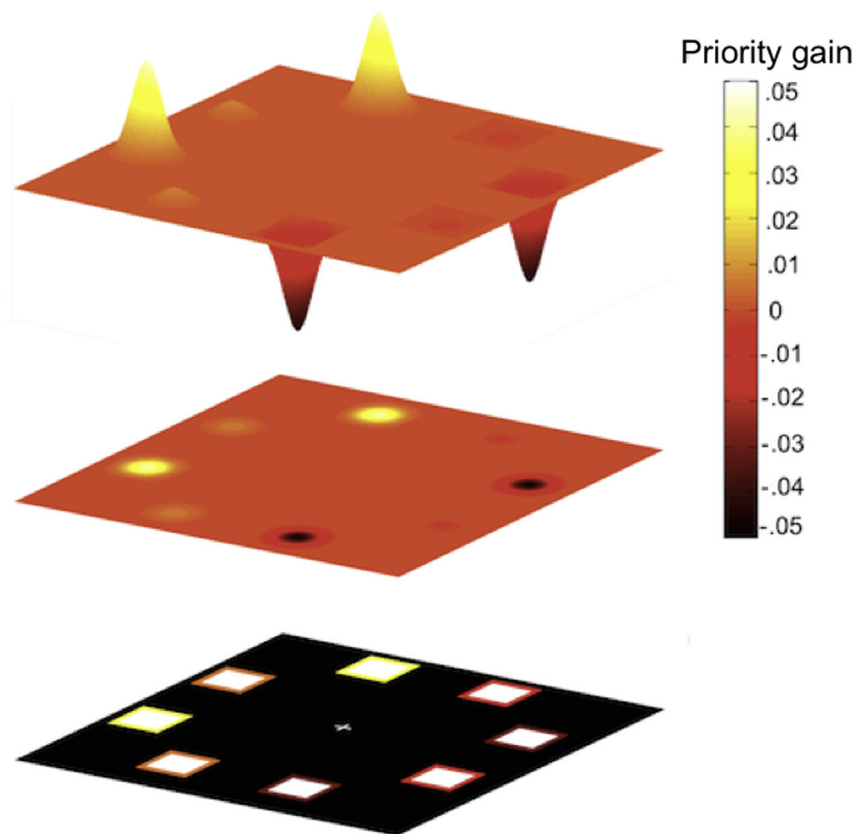


Fig. 1 – From a study examining the influence of reward-based learning on spatial priority maps by Chelazzi et al., 2014. Average priority gain illustrates the plasticity of priority maps, indicating that with training participants prioritized regions of space associated with higher probability of high reward (indexed by higher accuracy for high reward locations in the array). Priority gain was computed for each reward-associated spatial location, both in a 2D plane (middle) and in a 3D representation (top). For a given reward level, the average priority gain was calculated by averaging the change in the probability following training for accurately reporting targets at the spatial location associated with that reward level. The bottom panel depicts regions of the visual search array associated with different reward contingencies in this example. Figure adapted with permission from Chelazzi et al., *Journal of Neuroscience*, 2014. Copyright 2014 by the Society for Neuroscience.

1.4. Affective salience

Separate from—but highly overlapping with—research on reward-biased attention is research on *affect-biased attention*, or attentional guidance by associations with emotional arousal. In this line of research, it has been the degree to which a stimulus evokes psychological or physiological arousal, rather than its association with the probability of reward, that is viewed as the index of stimulus salience. Much of this research has focused on the attentional influence of stimuli that are commonly threatening or appetitive to humans, such as snakes, erotica, and facial expressions. Recently, studies looking for more experimental control of arousal levels have employed appetitive and aversive conditioning of neutral stimuli to rapidly build associations with arousal in the lab. By this point, almost two decades of research have revealed that association with emotional arousal, both positive and negative, prioritizes attention when spatial and temporal resources are limited [for review see (Markovic et al., 2014; Mather & Sutherland, 2011; Todd, Cunningham, Anderson, & Thompson, 2012; Vuilleumier, 2015)].

Whereas much laboratory research focuses on processes occurring over minutes, hours or days, tuning of attention by affective salience can also result from experience over a developmental time scale occurring over months or years. Our own research has shown prioritization of combat-related stimuli for combat veterans returned from duty in Afghanistan (Todd, MacDonald et al., 2015). This effect was heightened in the presence of post-traumatic stress disorder, where reduced activation in cingulate regions associated with fear circuitry regulation was accompanied by increased activation in visual cortex for combat related stimuli. Similarly, passengers who were on a flight that nearly avoided crashing in the middle of the Atlantic showed attentional tuning to stimuli associated with the crash years after the event (Lee, Todd, Gardhouse, Levine, & Anderson, 2013). Other research investigating changes in the relative salience of positive versus negative stimuli across the lifespan has indicated that the prioritized stimulus category shifts with developmental context (Mather & Carstensen, 2003; Mather et al., 2004; Picardo, Baron, Anderson, & Todd, 2016; Todd, Evans, Morris, Lewis, & Taylor, 2011).

We propose that the long-term and mostly implicit goals served by affect-biased attention, like those subserved by reward-biased attention, include the goal of approaching pleasure. Complementing this, however, they also include the goal of actively avoiding pain. The differently operationalized constructs of motivational and affective salience seem to be highly overlapping; however, one distinction may be that affective salience is characterized by the goal of avoiding pain (physical and/or emotional), whereas motivational salience is characterized by avoiding the loss of pleasure. It could also be argued that affective and motivational salience reflect a common source of salience, and that any distinctions between them come from the different operationalizations stemming from relatively isolated research traditions.

In much laboratory-based attention research, goals associated with top-down attention have been short-term goals defined by the demands of an experimental task (e.g., identify the unique item in a visual search task). Such explicit goals have been pitted against low-level visual salience such as colour, motion, or brightness in the competition for attentional resources. We suggest that each of the additional sources of salience described above also serve to further goals that guide attentional priorities, although such goals may remain outside of explicit awareness. Predicting regularities to guide expectations, carving the world into meaningful categories, gaining and maintaining reward, approaching pleasure, and avoiding pain all constitute long-term goals that facilitate survival. These goals may be more or less in the foreground in any given situation. In addition to serving distinct goals, such implicit sources of guidance may also serve to enhance executive attention to the explicit goals of an immediate task. We next focus on a) neural systems underlying attentional guidance by affective and b) motivational salience in the service of such goals below.

2. Neural processes subserving affective and motivational guidance of attention

The PSS framework highlights distinct sets of circuitry underlying modulation of attention by affective and motivational salience as well as common systems for integration of all sources of salience. In this section we focus on the former, reviewing seminal research mapping basic neural circuitry underlying the influence of arousal and reward on the visual system, as well as more recent research focussing the role of DA and NE. The PSS also emphasizes dynamic temporal updating of priorities. We therefore further review recent research mapping fine-grained delineation of underlying neural processes across short-term temporal scales as well as modulation of circuitry over longer timespans.

2.1. Large-scale brain systems

Research within cognitive neuroscience has focused on delineating distinct and overlapping patterns of neural circuitry underlying influences of affective and motivational salience on visual cortex plasticity. These studies, which we review in the section below, have operationalized salience by using (relatively) universally salient stimuli as well as

employing associative learning to examine effects of reward and punishment on visual tuning. To delineate neural processes at different temporal and spatial scales, researchers have employed electrophysiology in non-human primates, as well as a range of techniques in humans. These include measuring effects of cortical stimulation on behaviour, examining electroencephalogram (EEG) oscillations and event-related potentials (ERPs), using positron emission tomography (PET) and genotyping to probe neuromodulator function, and using classifiers with functional magnetic resonance imaging (fMRI) to predict effects of attention on neural representations of distinct categories. We next review key findings outlining (i) the role of midbrain systems in reward-biased attention, (ii) DA-mediated modulation of reward-biased attention, (iii) the role of the amygdala in biasing attention to reward and punishment, and (iv) recent research outlining the role of NE in affectively biased attention. As the PSS framework emphasizes a hierarchy of prioritization functioning at different time scales, we subsequently review evidence suggesting distinct mechanisms of attentional tuning by affective-motivational salience at different time scales.

2.1.1. Midbrain systems and reward

As mentioned above, the influence of reward circuitry on attentional guidance has been generating a great deal of interest in recent years. An elegant recent fMRI study examined the relationship between activity in reward circuitry and representations of reward-related stimuli in the visual cortex (Hickey & Peelen, 2015). The authors employed multivoxel pattern analysis (MVPA) to examine the degree to which the blood-oxygen-level dependent (BOLD) representation of a stimulus category that had been associated with reward (e.g., a tree) influences the BOLD representation of a naturalistic scene containing an example of that category (tree). Here they examined patterns of activation in object-sensitive visual cortex (OSC) for scenes containing both task relevant and task irrelevant objects. They then compared representations of reward-associated objects to those of reward-neutral targets and distractors. They also examined whether activity in dopaminergic midbrain structures was associated with OSC representation of reward-related targets and distractors. Crucially, results showed *reduced* encoding of reward-related distractors, which was interpreted as suppression of representations of more salient information when it is task-irrelevant. Importantly, the degree to which information about a reward-related distractor was suppressed in OSC was predicted by the degree to which the rewarding distractor elicited midbrain activity. It was also predicted by activity in other regions with high connectivity with the midbrain, including the orbitofrontal cortex (OFC), anterior cingulate cortex (ACC), and dorsolateral prefrontal cortex (DLPFC). In summary, these findings indicated that association with reward influenced the salience of entire object categories. Moreover, this plasticity of response was associated with the sensitivity of mid-brain and prefrontal regions to the presence of reward, indicating a relation between activity in nodes of reward circuitry and visual cortex modulation by reward. A more comprehensive review of circuitry by which subcortical regions contribute to visual cortex activity in reward-biased attention can be found in (Anderson, 2016a).

2.1.2. The role of DA in reward-biased attention

Non-human animal research has stressed the role of midbrain DA in predicting reward [e.g., (Schultz, Dayan, & Montague, 1997)]. Moreover, as we have seen, human imaging has outlined the importance of the striatum in reward-associated prioritization of attention [e.g., (Hickey & Peelen, 2015; Krebs, Boehler, Roberts, Song, & Woldorff, 2012)]. A study by Anderson et al. (2016) employed PET in humans to directly examine associations between individual differences in striatal DA availability and susceptibility to reward-biased attention. They used [^{11}C] raclopride as a tracer to examine individual differences in changes in tracer binding (interpreted as greater DA availability) while participants performed a visual search task in two separate scans, one with and one without reward-related distractors. Results showed that changes in the level of DA availability were associated with the magnitude of attentional capture by previously rewarded distractors in regions of the caudate nucleus and putamen. This finding suggested links between individual differences in DA response to reward and susceptibility to attentional biases that characterize addiction-related cravings. Importantly, the authors do not suggest that DA modulates visual cortex activity directly. Rather, they suggest its influence is via other brain regions, such as the ACC and DLPFC, which are dense in DA receptors. Interestingly, measures of learning rate during training were not related to DA availability, suggesting that it is attention rather than learning rate that was associated with DA activity. In contrast, at least in rodents, there is evidence that NE activity modulates visual cortex activity directly as well as via the thalamus (Jones & Moore, 1977). Thus, it is possible that noradrenergic systems play a more important role than DA systems in the process of associative learning itself.

2.1.3. The role of the amygdala in biasing attention to reward and punishment

Whereas a great deal of human and non-human research has focused on the role of DA midbrain systems in guidance of attention by reward, electrophysiological studies in non-human primates also indicate an important role for the amygdala. In a recent study (Peck, Lau, & Salzman, 2013), monkeys performed a task in which cues that were associated with high versus low reward appeared in different spatial locations. Individual neurons in the amygdala responded to both the spatial location and the motivational significance (reward value) of stimuli, and their activity predicted behavioural measures of attentional allocation in each trial. The authors concluded that, beyond mediating global arousal, the amygdala plays a key role in guiding spatial attention to locations of motivationally relevant stimuli. These findings were subsequently extended to aversive stimuli, suggesting the amygdala modulates visual attention for salience in general rather than associations with reward or punishment specifically (Peck & Salzman, 2014). To help determine the extent to which this holds true, future research should investigate direct influences of the amygdala on neural representations of spatial attention in the ventral visual cortex. It is also notable that the amygdala is dense in NE receptors and projects directly to all regions of the ventral visual stream

(Amaral, Behnia, & Kelly, 2003; Catani, Jones, Donato, & Ffytche, 2003). This indicates a pathway by which the locus coeruleus-norepinephrine (LC-NE) system can modulate visual cortex activity in guiding attention to both rewarding and punishing aspects of the environment. Whereas a body of research has probed the role of DA systems that habitually bias attention to reward cues that characterize addiction (Anderson, 2016b), the role of NE systems in development and maintenance of such biases is underexplored and will be an important area for future research.

A number of human lesion and imaging studies have implicated the amygdala in prioritization of affectively salient stimuli as well. Based on seminal research conducted over the past two decades on the influence of emotional arousal on attention, theoretical models have emphasized amygdala modulation of visual cortex activity [for review see (Markovic et al., 2014; Pourtois et al., 2013)]. Studies of patients with amygdala lesions have found that deficits in facial emotion recognition occur because patients fail to deploy spatial attention to eye regions (Adolphs et al., 2005). Such findings indicate that the amygdala plays a causal role in human spatial attention to salient information. Another influential line of research has examined the role of the amygdala in prioritizing awareness of affectively salient stimuli when there is temporal competition for resources. This line of research employed a variant of a rapid serial visual presentation (RSVP) task known as an *attentional-blink* (AB) task (Raymond, Shapiro, & Arnell, 1992) to examine prioritization of emotionally salient stimuli under conditions of high attentional demand (Anderson, 2005; Keil, Ihssen, & Heim, 2006). In this version of the AB task, participants must identify two targets: T1, which is a neutral stimulus such as a repeated number (e.g., 5555), and T2, which is an emotionally arousing or neutral word (e.g., *rape* vs *rope*) in a stream of distractor words (Fig. 3a). In general, the AB occurs when observers are unable to identify T2 when it is presented in close temporal proximity to T1 (within 500 msec). That is, it is as if the mind blinks. There are many interpretations of the AB phenomenon, most emphasizing limitations of attentional resources; however, one influential interpretation emphasizes a failure to switch attentional sets from tuning to the category of T1 to that of T2 (Di Lollo, Kawahara, Shahab Ghorashi, & Enns, 2005). In the emotional variant of the AB task, when T2 is emotionally significant, an *emotional sparing*, or reduced blink for T2, is observed (Anderson, 2005). The PSS framework suggests that this sparing, or prioritized awareness of emotionally arousing stimuli, reflects the persistence of an implicit attentional set for emotionally salient information (Todd et al., 2013). Early evidence of a key role for the amygdala in such affectively biased attention came from a study of SP, a patient with extensive amygdala damage. Compared to healthy controls, SP showed a deficit in the ability to report emotionally arousing relative to neutral T2 words (Anderson & Phelps, 2001). These results indicated that the amygdala directly and selectively influences perceptual awareness. The authors concluded that it does so by enhancing sensitivity in perceptual cortices to favour the emotionally significant over the mundane (Anderson & Phelps, 2001).

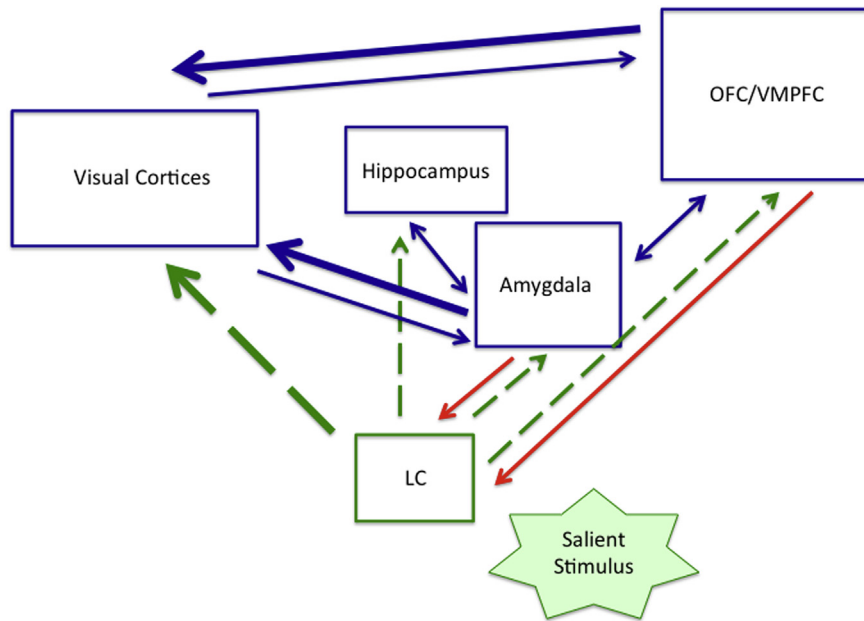


Fig. 2 – Key pathways emphasized by the biased attention by norepinephrine (BANE) model: Green dashed lines indicate norepinephrine (NE) pathways. Red lines indicate projections to the locus coeruleus (LC). Thicker lines indicate direct modulation of visual cortex activity in affect-biased attention. NE activity is implicated in both stimulus encoding and selective attention (Sara, 2009). A salient stimulus activates locus coeruleus (LC) neurons, which project widely to cortical and subcortical regions. Adapted with permission from “Neural and genetic processes underlying affective enhancement of visual perception and memory” by J. Markovic, A. K. Anderson and R.M. Todd, 2014, *Behavioural and Brain Research*, 259, p. 229–241. Copyright 2014 by Elsevier.

The studies described above employed stimuli that are normed for being high in arousal, and are thus typically salient to human adults. Yet such stimuli, however well controlled, are subject not only to low level featural confounds but also to individual differences in stimulus salience due to differences in life experience. A subsequent fMRI study built on these seminal lesion findings by employing a version of the emotional AB task with Pavlovian conditioning. The use of conditioning eliminated confounds due to low level features of complex images while creating equivalent aversive associations in all participants (Lim, Padmala, & Pessoa, 2009). Here Lim and colleagues endowed images of houses with salience by pairing them with shock (CS+). They then examined the BOLD response during an attentional blink task using the CS+ and matched images of houses that were unpaired with shock (CS−) as T2 stimuli. They found that, relative to CS− stimuli, CS+ stimuli elicited co-activation between the amygdala and place-sensitive visual cortex (parahippocampal place area), suggesting that emotional learning via the amygdala partly underlies prioritized attention to stimuli associated with emotional arousal. Based on these findings—as well as others associating emotional arousal with amygdala and visual cortex co-activation (Pessoa, Kastner, & Ungerleider, 2002)—our own biased attention by norepinephrine (BANE) model (Markovic et al., 2014) and the Multiple Attention Gain Control (MAGiC) model (Pourtois et al., 2013; Vuilleumier & Driver, 2007) have emphasized amygdala projections to the visual cortex in affectively-biased attention.

Although they cannot speak to the influence of the amygdala, studies using ERPs have provided further evidence that

affective/motivational modulation of visual cortex can occur rapidly and early in the visual stream. The C1 component, which is observed between 50 and 90 msec after stimulus onset and is thought to reflect activity of striate cortex, has been found to reflect prioritization of negatively conditioned stimuli (Stolarova, Keil, & Moratti, 2006), threatening stimuli (Rossi & Pourtois, 2014), and stimuli associated with the loss of reward (Rossi et al., 2017). Just as the visual cortex is modulated by fronto-parietal networks, V1 activation has been found to reflect patterns associated with biased competition for fearful relative to neutral facial expressions (West, Anderson, Ferber, & Pratt, 2011). Such preferential activation for facial emotion potentially reflects salience learned over the course of development. With regard to the role of the amygdala, slightly later ERP activation, between 100 and 150 msec following stimulus onset, is diminished for fearful relative to neutral faces in patients with amygdala lesions (Rotshtein et al., 2010). This again suggests that amygdala modulation of visual activity may be necessary for certain relatively rapid aspects of affective prioritization. Such patterns of prioritization may reflect implicit attentional sets tuned to features typical of affectively and motivationally salient stimuli, with the amygdala and locus coeruleus (LC) potentially playing important roles in tuning the system (Todd, Cunningham, et al., 2012).

2.1.4. The role of NE in affectively-biased attention

The PSS framework emphasizes the role of neuromodulator systems in biasing attention as it is shaped historically via emotional learning. Building on the foundational studies reviewed above, our more recent research has moved to

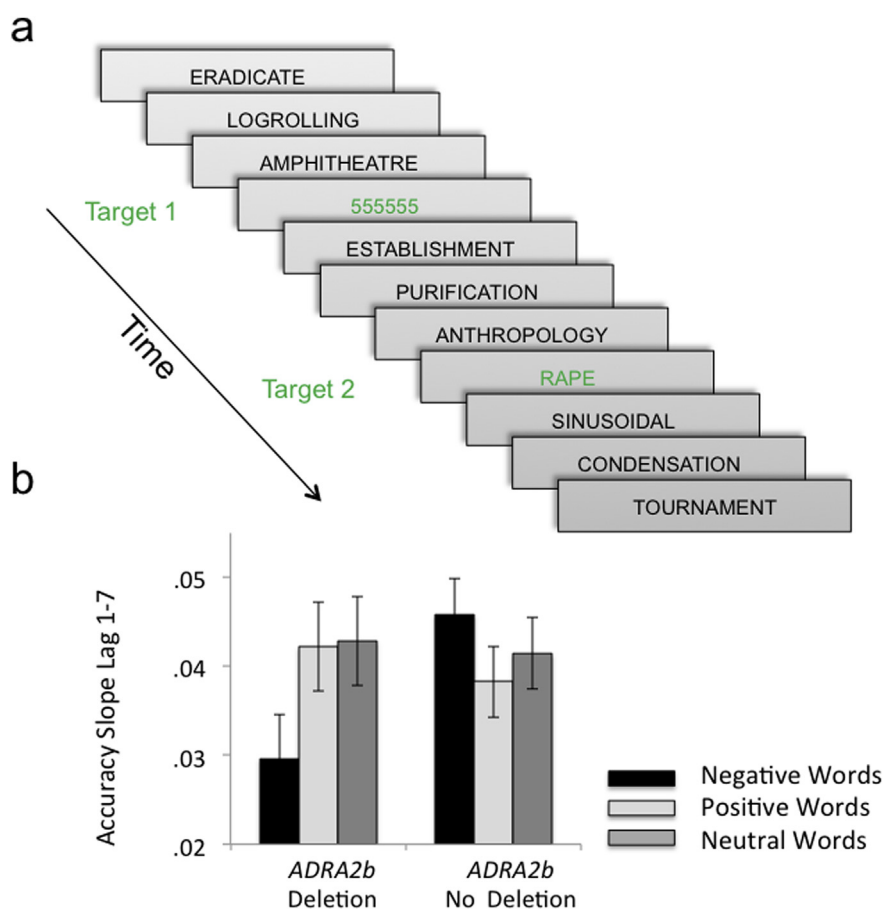


Fig. 3 – a. Sample trial in attentional-blink (AB) task. Two targets were presented among several distractors: Target 2 was a positive, negative or neutral word. It was presented after Target 1 after zero (Lag 1), one (Lag 2), three (Lag 4) or six (Lag 7) distractors. At the end of each trial, participants had to report both targets. **b.** Proportion of correct responses for ADRA2b deletion carriers and non-carriers as a function of the lag between the two targets and emotion category. Adapted from “Genes for emotion-enhanced remembering are linked to enhanced perceiving” by R. M. Todd, D. J. Muller, D. H. Lee, A. Robertson, T. Eaton, N. Freeman, ... A. K. Anderson, 2013, *Psychological Science*, 24, p. 2244–2253. Copyright 2013 by Sage Publications.

examine the role of the LC-NE system in amygdala modulation of visual cortex activity associated with affectively biased attention (Markovic et al., 2014). The LC is a brainstem nucleus composed primarily of NE-producing neurons (Aston-Jones & Bloom, 1981; Grant, Aston-Jones, & Redmond, 1988; Herve-Minvielle & Sara, 1995; Rasmussen & Jacobs, 1986). Importantly LC-NE activity plays a role in the establishment of biases for particular categories of stimulus via associative learning: LC neurons that initially fire in response to direct reward and punishment can very quickly shift to responding to stimuli associated with the salient event (Sara, 2009). According to the BANE model (Markovic et al., 2014) (Fig. 2), activity in the LC-NE system contributes to attentional prioritization of salient stimuli by modulating visual cortex both directly and indirectly via the amygdala and ventromedial prefrontal cortex (VMPFC). In turn, input from these regions allows NE-releasing LC cells to modulate responses to salience based on contextual relevance. Because it is positioned to be sensitive to contextual information, we suggest that beyond simply mediating affective-motivational prioritization, the LC-NE system may play a role in contextualizing

the sources of salience that are prioritized in any given state space.

Our own research has employed genotyping to probe effects of NE on affective modulation of attention and its underlying large-scale circuitry in humans. A common deletion variant of the ADRA2b gene that codes for alpha2b adrenoceptors is thought to be associated with increased intercellular NE availability. Using a version of the emotional attentional blink paradigm described above (Anderson, 2005), we found that while both carriers and non-carriers of the ADRA2b deletion variant showed attentional prioritization of both positive and negative stimuli, measured as emotional sparing of the AB, deletion carriers showed an even greater prioritization of negative stimuli (Fig. 3). This suggests a role for NE in affectively-biased attentional prioritization (Todd et al., 2013). Furthermore, in an fMRI study, we found that ADRA2b deletion carriers subjectively perceived emotionally salient stimuli—both positively and negatively valenced—as more perceptually vivid relative to neutral stimuli than non-carriers (Todd, Ehlers et al., 2015) (Fig. 4a and b). This effect of emotionally enhanced vividness (EEV) had been previously

associated with amygdala modulation of visual cortex (Todd, Talmi, Schmitz, Susskind, & Anderson, 2012). Consistent with the nodes of brain networks emphasized by the BANE model, this effect of putatively greater NE availability on EEV was associated with enhanced activity in hubs of the BANE network, particularly VMPFC (Fig. 4c–e). These studies provide evidence that the LC-NE system plays an important role in circuitry important for affective-motivational guidance of attention, as well as potentially for guidance from other sources of salience. Because the PSS framework emphasizes a history of learning, it will be important for future research to examine how life experience interacts with naturally occurring differences in NE availability to tune biases to specific categories of stimuli in different contexts.

Future research can also further probe NE influences on specific neuronal response patterns underlying affective-motivational biasing of attention. To date, the bulk of

attention has focused on biased competition. Prominent models focus on evidence that NE release can facilitate biased competition processes underlying selective attention. That is, NE reduces the threshold of sensory neurons to cues that are relevant either due to explicit task-related demands or due to motivational/affective salience acquired through life experience. At the same time, it raises the threshold for neurons processing irrelevant ones (Aston-Jones & Cohen, 2005; Eldar, Cohen, & Niv, 2013). The influential glutamate amplifies noradrenergic effects [GANE] model emphasizes role of glutamate in local ‘hotspots’ of NE release that serve to bias responses to relevant representations at the expense of lower priority ones (Mather, Clewett, Sakaki, & Harley, 2015). Yet, LC-NE activity is also implicated in recruitment of previously unresponsive neurons without suppression of surrounding neurons (Sara, 2009; Waterhouse et al., 1988). Consistent with the latter observation, human studies have suggested

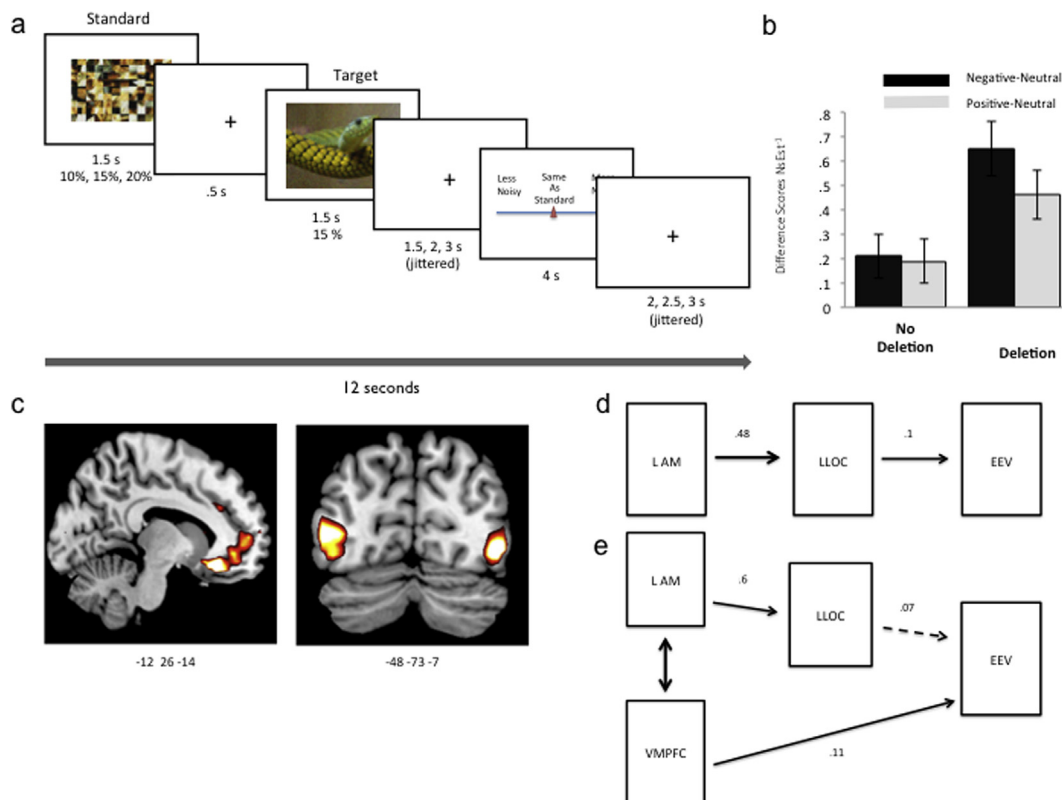


Fig. 4 – a. Noise estimation task to determine emotionally enhanced vividness (EEV). A standard (scrambled image) was overlaid with varying levels of noise. The standard was followed by the target overlaid with 15% noise. Participants were asked to indicate whether the target had more or less noise relative to the standard. b. Difference scores for ratings of inverse noise estimation (NsEst⁻¹), a measure of perceptual vividness for negative and positive > neutral stimuli in non-carriers and carriers of the ADRA2b deletion variant. Deletion carriers show greater EEV than non-carriers. c. Statistical maps showing parametric modulation by EEV in the ventromedial prefrontal cortex for ADRA2b carriers > non-carriers, and in the lateral occipital complex showing modulation by EEV across both groups. d. Simple model predicting behavioural effects of emotionally enhanced vividness (EEV) in non-carriers (n = 18) of the ADRA2b polymorphism by left lateral occipital complex (LLOC) activity mediated by the left amygdala (L AM). e. Complex model predicting EEV in ADRA2b deletion carriers (n = 21) of the ADRA2b polymorphism. The dual-route model demonstrates that the left amygdala mediates the effect of left LOC on EEV and simultaneously ventromedial prefrontal cortex (VMPFC) contributes to EEV. Adapted with permission from “Neurogenetic variations in norepinephrine availability enhance perceptual vividness” by R. M. Todd, M. R. Ehlers, D. J. Muller, A. Robertson, D. J. Palombo, N. Freeman, B. Levine, A. K. Anderson, 2015, *Journal of Neuroscience*, 35, p. 6506–6516. Copyright 2015 by the Society for Neuroscience.

patterns of “bias without competition” in visual cortices for affectively salient stimuli (Wieser, McTeague, & Keil, 2011). Our own preliminary research indicates that the presence of negatively-valenced distractors increases perceptual acuity and visual cortex resources for a spatially overlaid target stimulus without reducing cortical resources devoted to the distractor. We have further found that carrying the ADRA2b deletion variant enhances this overall pattern (Ehlers et al., 2016). This finding is consistent with a recruitment model of *biased facilitation* and suggests that facilitation may be modulated by NE availability, such that putatively higher levels increase the effect.

2.2. Neuronal processes implicated in visual cortex modulation by motivational-affective experience

As the PSS framework emphasizes, mechanisms of attentional tuning by affective-motivational salience may vary at different time scales. The data reviewed below support this proposal, indicating that distinct processes underlie very rapid visual cortex plasticity relative to modulation over longer time periods.

2.2.1. Direct modulation of visual cortex

Research in non-human animals indicates that acquisition of affective salience directly tunes activity in early sensory cortices to stimuli in several ways. Associating stimuli with aversive conditioning elicits sparse coding, by which fewer sensory neurons respond selectively to conditioned stimuli, as well as stronger (higher amplitude) responses within that population of neurons (Gdalyahu et al., 2012). Primary auditory cortex conditioning has been observed to induce increased metabolic activity as well as shifts in tuning of individual neurons to or towards the conditioned auditory frequency, and to modulate tonotopic maps (Weinberger, 2004). Such plasticity can be observed very rapidly and altered patterns of response can increase in both strength and specificity with longer-term consolidation (Weinberger, 2004). In humans, research suggests that rapid visual cortex sensitivity to affective-motivational salience occurs via increased gain for neurons preferentially tuned to relevant features (van Koningsbruggen, Ficarella, Battelli, & Hickey, 2016). Increased visual sensitivity to salience may also be facilitated by increased specificity of representations occurring via lateral inhibition processes that suppress activation to non-conditioned stimuli with similar features (McTeague, Gruss, & Keil, 2015). Patterns of generalization, potentially involving recruitment of previously “agnostic” neurons to salient stimuli (Waterhouse et al., 1988), have also been observed following aversive conditioning (McTeague et al., 2015; Sterpenich et al., 2014).

2.2.2. Rewarding experience increases visual cortex sensitivity

In humans, a study by van Koningsbruggen et al. (2016) used transcranial random noise stimulation (tRNS) to test hypotheses that motivationally biased attention involves changes in representations in the visual cortex itself. Since modulation by reward is thought to reflect sensitivity in the visual cortex, the authors hypothesized that stimulating occipital cortex

with tRNS should enhance attentional capture by reward-related stimuli. Indeed, the results demonstrated that occipital tRNS stimulation (but not frontal regions) led to increased reward-associated distraction – precisely the behavioural effect previously linked to individual differences in DA availability (Anderson et al., 2016). The authors surmised that the effect of tRNS may be to strengthen communication between visual cortex neurons, and thus increase perceptual sensitivity to motivationally salient distractors—an effect that was not reflected in patterns of frontal activity.

2.2.3. Aversive experience increases specificity and rapid generalization of visual cortex responses

Similar patterns of rapid visual cortex plasticity have also been observed as a result of aversive conditioning in studies of affect-biased attention (Miskovic & Keil, 2012, 2013). Such lines of affective research have begun to investigate population-level neuronal processes underlying rapid visual cortex plasticity, as well as modulation of visual cortex by nodes of larger-scale circuitry mediating affective-motivational salience. Keil and colleagues have effectively used steady-state visual evoked potentials (ssVEPs, or EEG activity elicited by measuring power evoked by flickering stimuli at a steady frequency) as an index of selective visual attention. For example, Miskovic and Keil (2013) demonstrated that selective amplification of visual cortex activity occurred for conditioned stimuli only when the reinforcer followed the threat-predicting stimulus in close temporal proximity. The authors interpreted their results as reflecting the importance of Hebbian associations between cell assemblies within the visual cortex rather than by prefrontally mediated executive processes. In a subsequent study directly examining neural functions associated with short-term plasticity associated with attentional modulation, ssVEPs were employed to examine effects of conditioning on orientation tuning in populations of visual cortex neurons (McTeague et al., 2015). Interestingly, rapidly appearing patterns of ssVEP activity reflecting *lateral inhibition* were observed over early visual cortex. That is, enhancement of activity for the conditioned orientation was accompanied by the greatest suppression of activity for orientations that were most similar to the conditioned one (Fig. 5a and c top). This pattern was reflected in patterns of trial-by-trial functional synchrony between occipital and fronto-temporal electrodes. During extinction trials an inverse pattern showing suppression of activity for conditioned orientations and enhancement of activity for nearby cells was observed (Fig. 5a and c top). In contrast, over parietal regions the pattern of ssVEP activity reflected *generalization* (i.e., enhanced activation for the most similar stimuli), a pattern that also reversed during extinction trials (Fig. 5b). Of note, this second pattern was reflected in explicit verbal reports of unpleasantness as well as physiological measures of both emotional arousal and startle reflex magnitude. It is also consistent with other human studies indicating greater generalization/poorer discrimination with aversive conditioning (Resnik, Sobel, & Paz, 2011). Observation of two distinct patterns of tuning (Fig. 5c) may reflect the role of different neural processes potentially operating in parallel and/or at different time scales. Specifically, they suggest that lateral inhibition within the visual cortex functions as one

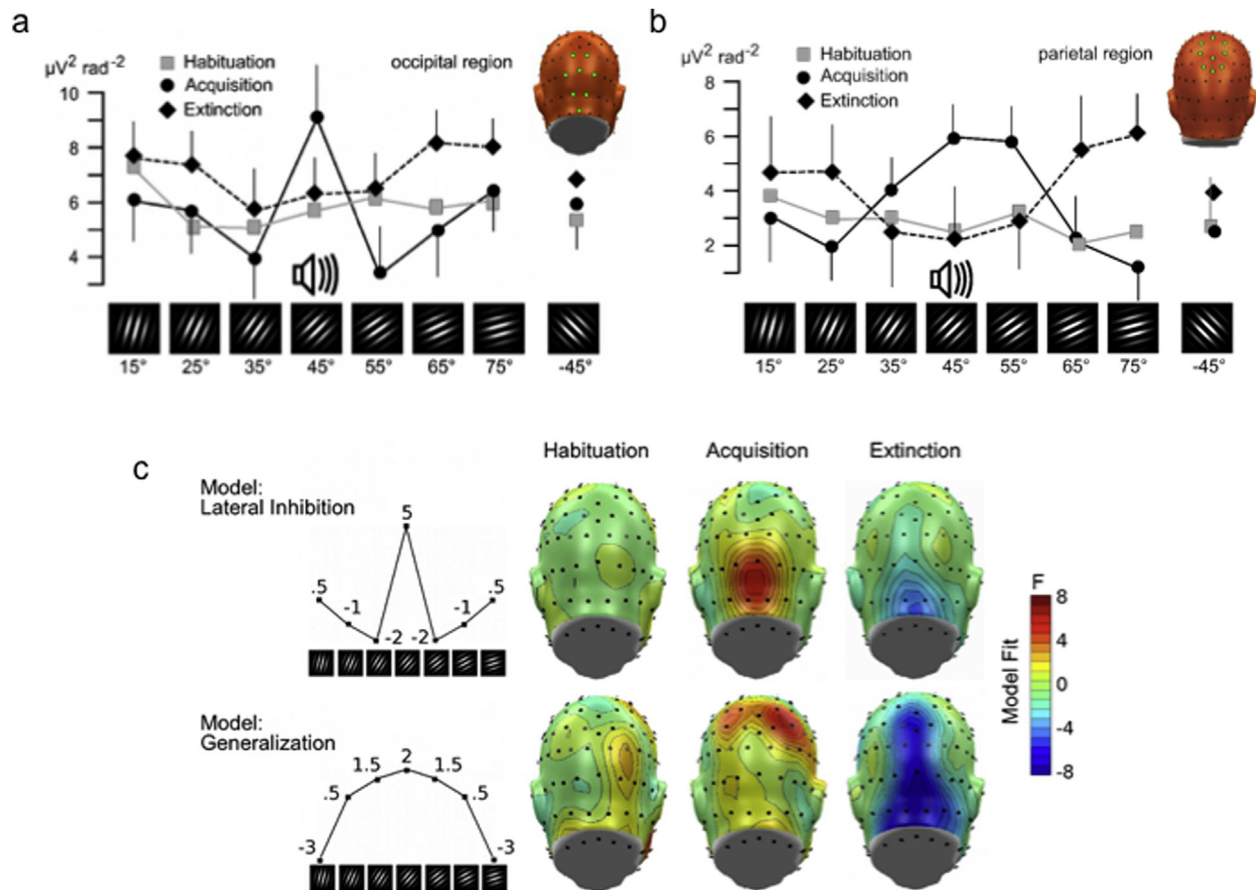


Fig. 5 – Researchers at University of Florida (McTeague et al., 2015) examined plasticity in orientation tuning in response to conditioning by examining electrophysiological activity in response to angled gratings (gabor patches). Grating orientations were parametrically varied in their degree of similarity to a target orientation, which came to be associated with an aversive sound (CS+). Electrophysiological responses were measured during three phases of conditioning: habituation, acquisition, and extinction. Patterns of orientation tuning were then modelled with a function indicating a pattern of lateral inhibition, such that activity for the stimuli with the orientations most similar to the conditioned stimulus was suppressed, and a function modelling a generalization gradient indicating gradual decrease in activity with distance from the conditioned orientation. a. Patterns of electrophysiological activity reflecting lateral inhibition were observed over early visual cortex. b. Over parietal regions the pattern of ssVEP activity reflected generalization, a pattern that also reversed during extinction trials. c. topographic maps depicting the fit of the lateral inhibition and generalization models to EEG scalp activity. Open access material reproduced under creative commons licence from “Aversive learning shapes neuronal orientation tuning in human visual cortex”, by L. M. McTeague, L. F. Guss, & A. Keil, 2015, *Nature Communications*, 6, doi:10.1038/ncomms8823, https://www.nature.com/articles/ncomms8823?WT.ec_id=NCOMMS-20150729&spMailingID=49200939&spUserID=ODkwMTM2NjQyNgS2&spJobID=723804686&spReportId=NzIzODA0Njg2S0.

short-term process involving implicit modulation of visual cortex activity. In contrast, as the association with verbal reports and psychophysiological measures suggests, parietal patterns of generalization may reflect explicit processes as well as sustained emotional responses.

2.2.4. Modulation by affective-motivational salience at longer time-scales

Beyond affective associations acquired over milliseconds, minutes, and days, the PSS framework emphasizes implicit modulation of attention by affective associations acquired or

maintained over years. In some cases, a single traumatic event can serve to enduringly tune attention to stimuli associated with the trauma. Using an attentional blink paradigm, we examined passengers of a transatlantic flight that nearly crashed into the Atlantic (Lee et al., 2013). We found that, for passengers, words that were uniquely associated with the crash (e.g., “Azores”) were prioritized a decade after the event. Control participants showed no such patterns of prioritization. In other cases, broader patterns of preferential tuning to valenced stimulus categories can be associated with a particular stage of life, such as childhood or old age, and can

shift over the lifespan. In developmental studies, we found that children (ages 4–9 years) showed more correlated activity between the amygdala and fusiform face area for positive versus negative facial expressions. In contrast, young adults showed no such evidence of bias (Todd et al., 2011). Moreover, young children, but not young adults, experienced positive facial emotion as more intense and more arousing than negative emotion (Picardo et al., 2016). The strength of this positivity bias was predicted by parental beliefs about the malleability of human nature. These beliefs in turn have been linked to parenting style (Dweck, 1999). While we did not directly measure attention, these findings parallel patterns of biased attention favouring positive stimuli in older adults (Mather & Carstensen, 2003, 2005). Together this line of evidence suggests that aspects of the environment that are typical of a developmental stage shape amygdala-visual cortex circuitry based on implicit goals that may be specific to that phase of life. Rather than reflecting a few incidents of high arousal, such as are used in laboratory conditioning experiments, we suggest such tuning may arise from many repeated experiences of lower arousal pain and pleasure (Lebrecht, Bar, Barrett, & Tarr, 2012). Future research can outline the specific neuronal processes by which such long-term low-intensity contextual modulation may occur.

2.3. Summary

On the one hand, the PSS framework emphasizes the importance of distinct sets of circuitry for modulation of attention by reward and emotional salience. This circuitry is tuned as associations are learned both rapidly and slowly. We have reviewed evidence that larger-scale systems involve the influence of the midbrain and amygdala on visual cortex plasticity. They can also include prefrontal regions as well as DA and NE systems. Such large-scale circuitry may be tuned by an intense, high arousal, “single-blow” traumatic event or by repeated experiences of lower-arousal pain and pleasure over years. At the level of neuronal activity, activation of the visual cortex associated with attentional guidance by motivational and affective salience results in relatively rapid plasticity in the visual cortex. Direct modulation of plasticity in visual cortex has been observed to occur rapidly with learning; however, whether rapid visual cortex plasticity necessarily results from modulation by other cortical or subcortical regions is still an open question. Certainly visual plasticity entails slower consolidation processes as well. Potential mechanisms of visual cortex plasticity include both sharpening of representations by lateral inhibition and broadening of representations via generalization. Together, these data suggest a multiplicity of neural pathways through which the influence of affective-motivational salience can facilitate attentional prioritization. Some of these, such as systems involving amygdala and mid-brain centred circuitry, may be specific to the influence of affective and motivational salience. Other distinct networks are likely recruited to modulate prioritization by other sources of salience. Yet beyond distinct sources of salience, the PSS framework also suggests that distinct sources of salience are integrated and reconciled with other sources at the level of the priority map. They may also be integrated via common rhythmic processes among populations of neurons.

3. Common neural substrates of attentional guidance

3.1. Priority maps

Spatial priority maps are topographically organized neural representations of behaviourally relevant aspects of the environment. For example, these representations are instantiated in activity in the lateral intraparietal area (LIP) in non-human primates and posterior parietal lobe (PPL) in humans (Bisley & Goldberg, 2010; Shomstein & Behrmann, 2006; Shomstein & Gottlieb, 2016). Rather than representing the entire visual field, priority maps represent only the most salient features of the environment. Patterns of activity within these regions can thus predict where spatial attention will be directed from instant to instant – or at least from saccade to saccade. Previous research has established evidence for their modulation by both low-level featural salience and executive attention (Bisley & Goldberg, 2010). Additional studies have provided compelling evidence for the influence of both reward and semantic meaning on behavioural indices of priority mapping (Chelazzi et al., 2014) as well as parietal brain regions supporting priority maps (Lee & Shomstein, 2013; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009). These findings have informed a view of priority maps as sites for the integration of distinct sources of attentional guidance via a common population of cells (Shomstein & Gottlieb, 2016). Evidence that, with training, priority maps can be reshaped to prioritize spatial locations associated with reward (Chelazzi et al., 2014) further indicates that these sources are integrated in a dynamic fashion (Lee & Shomstein, 2013; Shomstein & Gottlieb, 2016). We have further suggested that LIP connections with the pulvinar nucleus of the thalamus, and indirectly with the amygdala, can allow for modulation of priority maps by affective salience as well (Niu, Todd, & Anderson, 2012). Thus, the PSS framework hypothesizes that putative priority maps in parietal cortex—as well as other brain regions—may constitute a common substrate integrating diverse sources of salience, including affective and motivational salience, statistical learning and long-term memory processes [e.g., (Hutchinson & Turk-Browne, 2012; Jiang, Swallow, & Rosenbaum, 2013; Niu, Todd, & Anderson, 2012; Niu, Todd, Kyan, & Anderson, 2012)].

3.2. Temporal sampling

In addition to its emphasis on the longer time scales over which attentional tuning is shaped, the PSS framework also emphasizes the importance of sampling processes subserving the allocation of attention over milliseconds. Whereas priority maps may serve to integrate and prioritize guidance of attention in space, temporal sampling may provide a domain general mechanism organizing attentional allocation over time across networks. It has been recently proposed that that attention is an oscillatory process occurring at an 8 hz sampling rate (Landau & Fries, 2012). Landau and Fries (2012) took inspiration from research on neural dynamics that implicates rhythmic oscillations in the coordination of brain systems subserving attention. Here they investigated

the hypothesis that rhythmic attentional sampling provides a neurocognitive process that allows coordination of underlying neural systems (Landau & Fries, 2012). Their findings indicated that attentional sampling fluctuated at a rate of ~8 Hz, indicating a potentially common rhythmic sampling pattern for spatial attention. Other findings suggest that both executive attention and affective salience influence time perception in a manner thought to be linked to temporal sampling [e.g., (Angrilli, Cherubini, Pavese, & Mantredini, 1997; Dirnberger et al., 2012)]. Future research can investigate the role of attentional sampling in prioritization of attention by distinct sources of salience, and the potential modulation of sampling rate by affective-motivational attention.

4. Integrating sources of salience in the PSS framework

In summary, the PSS framework outlines guidance of attention by three categories of attentional process: Explicit task-related goals, featural salience, and the agent's short and long-term history (Fig. 6a). In this paper, we have discussed the role of processes related to aspects of one's history that may implicitly guide attentional prioritization. In particular, we have focused on motivational and affective factors and the underlying neural pathways that modulate attention in the ultimate service of acquiring pleasure and avoiding pain.

At the level of neural implementation we have reviewed evidence that attentional prioritization involves modulation of the visual system by affective and motivational salience, and discussed some roles for neuromodulator systems. Overall, evidence suggests there are multiple processes by which the visual system is tuned to what is salient based on affective and motivational experience, some of which operate rapidly—and potentially directly—on early visual cortex and some of which involve longer-term consolidation processes and subcortical modulation of higher order visual regions. Studies pitting affective or motivational salience against task relevance suggest that, at any given time, activity in networks that modulate visual attention (e.g., reward and dorsal attention) may be either mutually competitive or mutually enhancing. We propose that in any given context competitive interactions may be resolved at the level of priority maps. Moreover, some neuromodulator systems such as LC-NE, which is sensitive to multiple sources of salience (Sara, 2009), may shape the attentional landscape by prioritizing attention to those aspects of attention best suited to one's present goals. We suggest that they may act on populations of neurons via mechanisms of biased facilitation/gating as well as biased competition.

Building on existing models of priority mapping [e.g., (Awh et al., 2012; Bisley & Goldberg, 2010; Shomstein & Gottlieb, 2016)], the PSS framework proposes that resolution of distinct sources of salience may be implemented in common prioritization processes and instantiated in priority maps. The constraints on the priorities that can predominate in any given context are determined by the PSS. That is, the influence of competing or mutually reinforcing sources of

salience are collapsed into a state space, informed by what has been relevant in similar past situations, that contains a range of possible priority mapping configurations. At any given time, a state space is characterized by such landscape features as attractors and repellers representing categories of stimulus or locations that will push and pull attention in that context. For example, in the experiments reviewed above, regions of space previously associated with a high probability of high reward, for which attention is prioritized, would constitute attractors, and regions of space associated with a high probability of low reward would constitute repellers (Chelazzi et al., 2014) (Figs. 1 and 6). Likewise, distractor categories previously associated with reward, for which attention is suppressed, would constitute repellers (Hickey & Peelen, 2015) – at least as long as one is in a laboratory setting in which shapes and colours presented on computer screens lead to meaningful outcomes. Processes such as inhibition of return, in which attention is deflected from recently visited regions of space (Klein, 2000), illustrate the plasticity of the landscape, as a previous attractor becomes a repeller immediately after it has been sampled. Thus even within a given state space, priority maps are continuously moulded by our own actions within them, reflecting recent as well as more distant history. It is important to clarify that, whereas a priority map may be concretely implemented in patterns of neuronal firing in regions such as LIP, a PSS is a conceptual landscape of context-specific priority map possibilities. We further propose that rhythmic sampling processes guide attentional foraging over time within the contours of the state space.

Given that what is most salient in one situation is not necessarily what is salient in another, each new context should precipitate a bifurcation into a new state space with a new set of possible priorities. This in turn is characterized by a reconfiguration of the priority map, where a different arrangement of goals prioritizes new classes of feature. That is, once we have left the lab and are getting ready to drive across town, colours and shapes on a computer screen are no longer nearly as salient as the configuration of shiny features that identify our car keys and the digits on our cell phone indicating the time.

Thus, for any type of situation, if it is possible to quantify the relative weight of specific sources of salience—for example to quantify the intensity of affective or motivational salience relative to the weighting of other aspects of history, featural salience, and task-related goals—it should be theoretically possible to formally model the parameters of each potential priority map configuration within a state space. These could be used to predict eye gaze movement, much as has been done for low-level featural salience (Itti & Koch, 2000; Wang, Borji, Jay Kuo, & Itti, 2016), as it unfolds dynamically in a more complex environment. Such predictions would be based on the kind of complex hierarchies of goals that shape real world attentional demands.

4.1. Relation to other frameworks of attentional priority

The PSS framework is a synthetic framework that overlaps in content with several existing models of attentional

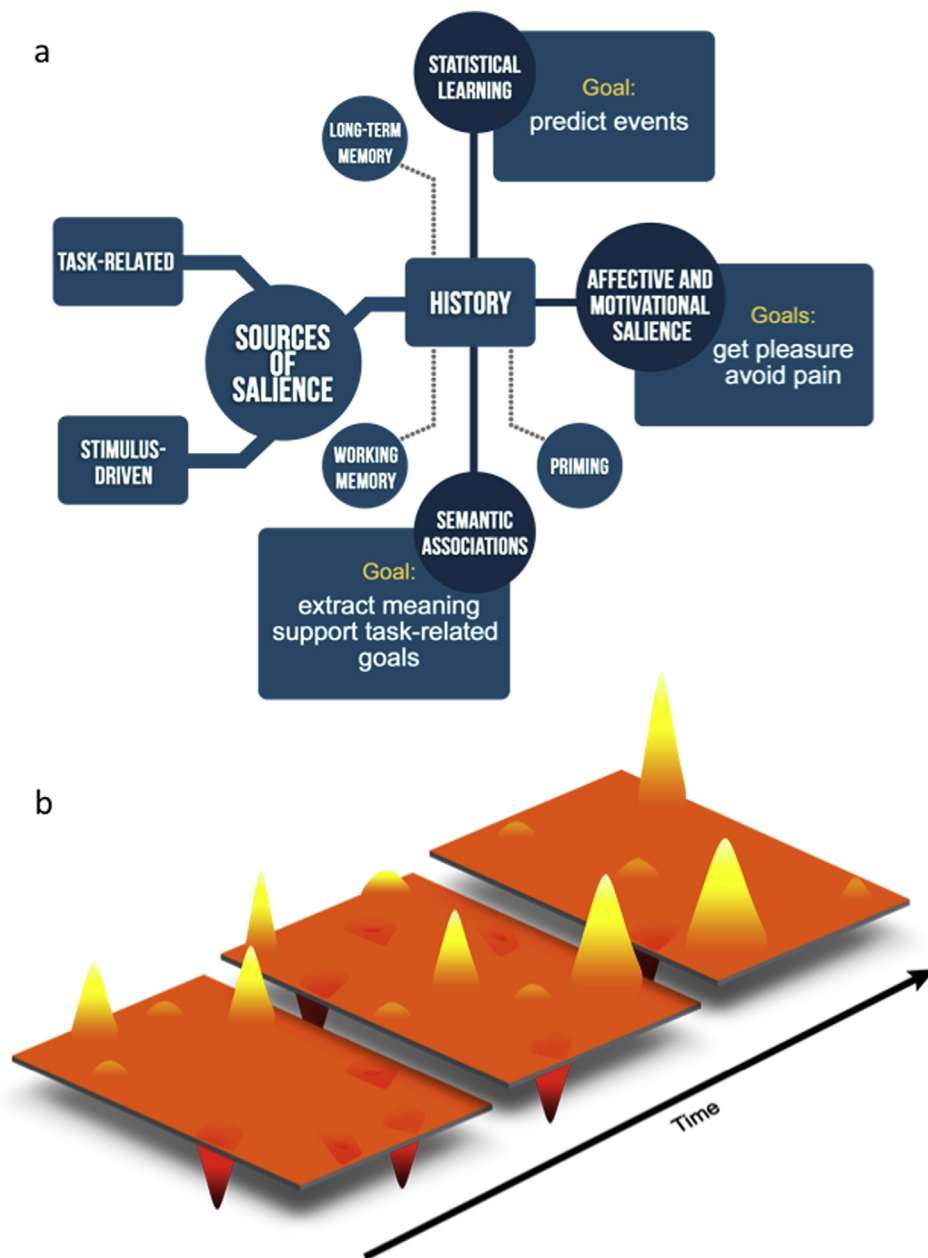


Fig. 6 – a. Sources of salience proposed by the priority state space (PSS model) with an emphasis on those sources related to an agent's history and the goals served by statistical learning, semantic associations, and motivational/affective history reviewed in this paper. b. Hypothetical modulations of a priority landscape within a state space over time. Within the range of possible sources of salience, the regions of the landscape that attract and repel attention can shift over time.

prioritization, including the Integrative Priority Map (IPM) framework of Awh et al. (2012) and the MAGiC model of Pourtois et al. (2013); however, it focuses on processes that are not emphasized in other frameworks and has areas of divergence from each.

4.1.1. IPM framework

As the title of the PSS framework suggests, the PSS framework is strongly influenced by the IPM framework (Awh et al., 2012); however, it expands on the IPM in several key ways, and in particular in the focus on temporal processes in

several forms, including (a) an expanded concept of history that emphasizes developmental processes, (b) the notion of the state space, and (c) specification of rhythmic processes underlying selective attention. It also (d) categorizes emotional salience under the rubric of history rather than physical salience. We describe each of these in more detail below.

4.1.2. History

We are indebted to the IPM framework for adding a third source of history-based attentional guidance to the classical

dual-process constructs of task and feature-based guidance, as well as the integration of sources at the level of the priority map; however, while it does not preclude developmental processes per se, the IPM category of *selection history* focuses on effects of recent history of short-term selection and reward (Awh et al., 2012). Also the term *selection history* appears to preclude passive learning processes such as Pavlovian learning which we argue are important to the acquisition of emotional salience. In contrast, the PSS model expands the category of *selection history* into the broader category of *history* to encompass a broader range of time scales – including a developmental time scale that unfolds over years and even decades. Thus, in the PSS model the category of *history* emphasizes a collection of learnt sources of attentional priority acquired through very different processes, widely diversified both in space and in time, but showing coherence in their impact on attention. We stress that it is precisely the contextually modulated sensitivity to history that makes selective attention fully adaptive in a complex and ever-changing world.

4.1.3. The dynamic state space

The PSS framework also builds on the notion of integration at the level of the priority map. While the IPM model acknowledges the plasticity of the system, we further extend the metaphor of a map, which represents unchanging features of a landscape, to the notion of a state space, or all of the possible states of the system in a single context. We also go beyond the IPM model to hypothesize that non-linear processes, as formalized by dynamical systems theory, underlie transitions from one state space to another. We propose that such bifurcations in the state space result in shifts in the landscape of priorities based on the ongoing interactions of the individual with the environment. Moreover, by integrating rhythmic temporal mechanisms of attentional sampling, PSS emphasizes temporal as well as spatial dimensions of attentional control.

4.1.4. Emotional salience

The PSS framework also differs from the IPM framework in its characterization of emotional salience. Awh et al. (2012) discuss emotional salience as a type of salience that falls within the grey areas of the category of *physical salience* rather than *selection history*. They describe it as a fundamental characteristic of the stimulus itself (based on its evolutionary relevance). As such, it is qualitatively different from reward history, reflecting the historical categorization of emotional salience as “hard-wired” and thus “bottom-up.” In contrast, based on research reviewed here, we propose that affective salience, like motivational salience, is based on learned associations that fall under the expanded category of *history*. Alongside models of reward-biased attention [e.g., (Anderson, 2016a)], we emphasize the role of associative learning and the plasticity of what is emotionally salient in a given context.

4.1.5. MAGiC model

As a comprehensive account of effects of emotional salience on attention, the MAGiC model stresses the capacity of emotional circuitry to modulate attention independently of

executive attention, and emphasizes the role of the amygdala in tuning visual cortex activity in affectively-biased attention, as reviewed in this paper (Pourtois et al., 2013). We additionally emphasize the role of the LC/NE system and suggest that this circuitry may respond to salience defined more broadly than emotional arousal. Finally, along with much of the research on effects of emotion on visual attention, the MAGiC model emphasizes the evolutionarily conserved nature of responses to universally salient stimuli. In contrast, the PSS framework emphasizes history, plasticity and learning, as well as multiple sources of salience dynamically integrated at the level of the PSS.

5. Conclusions

In the present paper, we have synthesized findings from several distinct lines of research to support the PSS framework proposed here. We focused on forms of attentional guidance shaped by multiple aspects of an organism’s history and the goals served by such sources of prioritization. Specifically we briefly reviewed evidence of implicit guidance of attention by statistical learning, semantic associations, and motivational and emotional salience (a list that is not by any means exhaustive). In subsequent sections, we focused on neural circuitry and mechanisms underlying affective and motivational influences on attentional selection. Finally, we discussed the integration of multiple sources of attentional guidance within the PSS and discussed the framework in more detail in relation to other theoretical frameworks. Future research can directly test the proposition—which is not unique to this framework—that multiple sources of attentional priority are supported by prioritization of neural representations in regions supporting priority maps (e.g., IPS). Related specifically to the PSS framework, future research can further attempt to model the dynamics of such representations within and between state spaces as they shift with time and context, both in the short term and over the human lifespan.

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