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Multiple influences of reward on perception and attention

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Abstract

Visual processing is influenced by stimulus-driven and goal-driven factors. Recent interest has centered on understanding how reward might provide additional contributions to visual perception and unraveling the underlying neural mechanisms. In this review, I suggest that the impact of reward on vision is not unitary and depends on the type of experimental manipulation. With this in mind, I outline a possible classification of the main paradigms employed in the literature and discuss potential brain processes that operate during some of the experimental manipulations described.

Introduction

A frequent account of visual processing is one in which objects compete for limited perceptual processing capacity and control of behavior (Desimone & Duncan, 1995; Pashler, 1998). Because processing capacity for vision is limited (Tsotsos, 1990), selective attention to one part of the visual field comes at the expense of neglecting other parts. Thus, a popular notion is that there is *competition* for neural resources in visual cortex (Grossberg, 1980). Competition is influenced by multiple factors, which are usually divided into two major classes: *stimulus-driven* factors, such as stimulus contrast and motion energy, and *goal-driven* factors, such as based on task instructions (Figure 1A).

Another important class of influence on competition involves affective and motivational factors. Thus, negative images are detected faster than neutral ones and compete more effectively both in terms of space (Pourtois, Schettino, & Vuilleumier, 2012) and time (such as probed in the attentional blink; Anderson, 2005; Lim, Padmala, & Pessoa, 2009). Elsewhere, I have discussed how affective factors influence perception, and what mechanisms may be potentially involved (Pessoa, 2013). In this paper, I will discuss the role of motivation as manipulated via reward on visual processing and attention (Figure 1B–C). Early studies investigated how reward changes response criteria during visual tasks and whether subjects employ optimal decision criteria (for discussion, see Navalpakkam, Koch, & Perona, 2009). These “decisional” effects are qualitatively different from findings reported by more recent studies – for example, increased visual sensitivity (*d-prime*) in attention tasks and target/distractor effects (Engelmann, Damaraju, Padmala, & Pessoa, 2009; Engelmann & Pessoa, 2007). Indeed, recent findings fly in the face of traditional psychological models, which describe motivation as involving a “global activation” that varies independently of control demands and behavior direction (e.g. Duffy, 1962; Hull, 1943) – in other words, a rather blunt instrument. It is now clear that some of the effects of

reward, far from being global, reflect selective mechanisms that are manifested both behaviorally and neurally (Pessoa, 2013).

Empirical Studies

The ever expanding literature on reward and attention poses a considerable challenge to understanding the relationship between the two because of the many ways in which both reward and attention are manipulated across experiments. Consider the concluding sentence in a recent study by Lee and Shomstein (2013a): “Reward, we argue, is one of the contributing signals for attentional selection, similar to other units of attention.” While I second this conclusion, the statement must be considered in terms of the type of reward and attention manipulations considered in their study. What is more, the possible ways in which they are manipulated are sufficiently varied as to leave ample room for confusion. With this in mind, in this section, I outline a possible classification of the main paradigms employed in this literature (see also Camara, Manohar, & Husain, 2013; Della Libera, Perlato, & Chelazzi, 2011).

Proactive paradigm

In this type of paradigm, participants are informed that they will receive a reward (typically, real or play money) during certain trials, while no reward is involved in others. Importantly, on each trial, trial type is indicated via an initial cue stimulus that precedes the target stimulus on which participants perform the task. In analogy to the attentional control literature (Braver, 2012), I refer to this paradigm as *proactive*. In this paradigm, reward is often administered in a *performance-contingent* fashion, namely, reward is attained in a trial if the answer is correct, and at times also “fast enough”.

An example of this paradigm is a study that investigated the effects of reward during a response-conflict task (where the critical stimulus primes two competing motor responses) (Padmala & Pessoa, 2011) (Figure 2A). We expected that potential reward would improve behavioral performance, possibly via mechanisms amplifying task-*relevant* information or by mechanisms improving filtering of task-*irrelevant* information. As anticipated, we observed behavioral response interference: performance was slower on incongruent trials than on neutral (without conflict) ones. But, importantly, response interference was *reduced* with reward. Given that reward also decreased response facilitation (i.e., the beneficial effect of a congruent task-irrelevant item), the results supported the inference that reward enhanced *attentional filtering*, thereby reducing the influence of the task-irrelevant word item.

In another study with a similar design, we asked whether participants would be able to ignore potent distractors if sufficiently motivated (Padmala & Pessoa, 2014). We chose negative images of mutilation as distractor stimuli that were presented centrally on the screen. Participants were asked to determine if two peripherally presented bars were like oriented or not (Erthal et al., 2005). As in the experiment described in Figure 2A, an initial cue stimulus informed participants about the possibility of reward. As anticipated, in the no-reward condition, negative images slowed performance relative to neutral ones. However, this slowing down was completely eliminated when a potential reward was at stake. Thus, although the impact of aversive pictures is often described as fairly automatic, our results

demonstrated that, when sufficiently motivated, participants were able to reduce/eliminate their deleterious impact.

Reactive, no extensive learning paradigm

In another important class of paradigm, the possibility of reward is not cued in advance, and instead a specific stimulus feature is linked with reward. This means that participants cannot proactively engage in strategies that might enhance performance; instead, they can only react to stimulus features that are linked (or not) with reward. I illustrate in this section paradigms without extensive learning; the next section will address cases when extensive learning is involved.

In one experiment, Kristjansson et al. (2010) investigated “priming of pop-out”, a situation where participants perform better when a target feature is repeated during a task in which features “pop out” (and presumably would *not* benefit from priming). Subjects performed a visual search for a color-singleton target (say, a red item among green distractors), whose shape was then interrogated (“Is the small notch on the target at its top or bottom?”). They were told that they would be rewarded for fast and accurate performance, but without the relative values of specific target colors being explained. For one half of the subjects, a correct response for a red target earned 10 points on 75 percent of such trials and 1 point on the other 25 percent, and vice versa for a green target; for the other half, this was reversed (incorrect responses earned 0 points). The authors found that the benefit of target repetitions (i.e., the priming of pop-out effect) was larger for the more highly rewarded target color, showing that priming of pop-out is enhanced for targets tied to reward.

Several other important experimental properties are varied across studies. In some experiments, at the beginning, participants are *instructed* about the stimulus feature that is associated with reward. For example, in one study, we told participants that all trials showing a picture of, say, a skyscraper would be rewarded (100% of the time) if the answer was correct and fast, but those involving houses would not (0% of the time; Hu, Padmala, & Pessoa, 2013). Although the possibility of reward was not signaled in advance at the beginning of each trial, we found that reward-associated stimuli were *not* slowed down by the presentation of a simultaneous negative “CS+ background” (a color patch that had been previously paired with mild electrical stimulation). This was unlike stimuli not associated with reward, which as anticipated suffered interference by the CS+ background.

Another key experimental design property is whether the manipulation of reward is task *relevant*. For example, in the study by Kristjansson et al. (2010) described above, reward was tied to a stimulus feature that defined the task *target* (item color). Likewise, in our study (Hu, et al., 2013), participants were asked to determine if the foreground stimulus was a skyscraper or a house and one of the two categories was linked to reward; thus reward was task relevant. Below, cases where reward is task *irrelevant* will be described.

Another class of reactive paradigm has investigated *reward priming* effects. For example, Hickey et al. (2010) investigated how low or high reward on current trial n influenced performance on trial $n + 1$. In their study, reward magnitude was randomized, such that it was actually independent of performance. The subject’s task was to detect a uniquely shaped

item (say, circle) within a circular array of same-shape items (say, diamonds). All items had the same color (say, red), except for a salient distractor shown in another color (say, green). Thus, in this example, the target was a red circle and the distractors were red diamonds, with the one exception being a salient green diamond distractor. Their design insured that target color was task *irrelevant*. They found that participants favored stimulus features associated with reward. Hence, if on trial n a participant received a high reward, detection was faster on trial $n + 1$ if the target was shown in the same task-irrelevant color, but was slower on trial $n + 1$ if the target was shown in the other color (in this case the distractor on trial $n + 1$ was shown in the color of the target on trial n , what the authors termed the “swap” condition). Note, however, that a recent study suggests that the conditions in which reward priming is observed may be limited (Asgeirsson & Kristjansson, 2014).

Reactive with learning paradigm

Reward can also be manipulated via an extensive training phase that follows the tradition of reinforcement learning. This type of paradigm takes the general form employed by Kristjansson et al. (2010) described above, but is applied for hundreds or trials, possibly more. The training phase is followed by a subsequent task phase during which the effect of learning is evaluated. Moreover, the task is often performed under “extinction”, in other words, without any pairing between reward and the previously-paired feature and reward. For example, in one study, during an initial training phase, participants searched for a red or green target among differently colored non-targets (Anderson, Laurent, & Yantis, 2011). At the end of each trial, they received reward-related feedback. One target color (red or green, counterbalanced) was associated with a high probability (0.8) of a high reward (5 cents) and a low probability (0.2) of a low reward (1 cent); for the other target color, this mapping was reversed. Participants were not explicitly informed of this reward contingency, but had to learn it over the course of approximately 1,000 trials. Importantly, the participant’s response did not depend on color; rather, they discriminated bar orientation. Thus reward was associated with color, and not with a particular behavioral response. In this manner, training linked one color with high value and the other color with lower value. During a subsequent test phase during which no rewards were offered, Anderson et al. (2011) found that a nonsalient (i.e., one that did not produce pop out), task-*irrelevant* distractor previously associated with reward slowed visual search. Notably, the magnitude of slowing was spatially specific, such that when a target appeared in a location occupied by a high-value distractor on the previous trial, slowing was especially prolonged.

We recently also investigated the impact of training on task-irrelevant information (Yokoyama, Padmala, & Pessoa, submitted). During training, participants performed a color discrimination task on green/yellow fixation squares that were superimposed on task-irrelevant images. One image category (e.g., houses) was associated with a high probability (0.8) of winning 25 cents (0.2 chance of earning zero), and another category (e.g., skyscrapers) was associated with a low probability (0.2) of winning 25 cents (0.8 chance of earning zero). Participants were neither informed about the background category that was associated with high/low reward probability nor the actual reward probabilities; they were just asked to respond fast and accurately to the fixation square color so as to maximize their earnings on each trial. During a subsequent test phase, participants were asked whether a

house of skyscraper was presented within a rapid visual stream. Negative distractor images presented before targets interfered with target detection more so than neutral images (an effect known as emotion-induced blindness; Most, Chun, Widders, & Zald, 2005). However, the size of this interference effect was smaller for high- than low-value targets – even though no rewards were administered during this test phase. Thus, like in the situation in which reward was task relevant (Hu, et al., 2013), reward-associated items countered the deleterious impact of negative stimuli.

Multiple time scales

Reward effects involving training occur over multiple time scales. For instance, in the attentional capture study discussed above, Anderson and colleagues (2011) employed approximately 1,000 training trials. Raymond and O'Brien (2009) employed 600 training trials in their attentional blink experiment. Overall, this type of training can be accomplished in an hour or less, and typically does not require multiple sessions (in some cases, a few sessions are employed; see Della Libera & Chelazzi, 2009).

An example of a shorter time scale was a follow-up experiment of priming of pop-out in the investigation by Kristjansson et al. (2010) discussed above. They found that the extent of priming of pop-out dynamically tracked reward levels when rewards changed unpredictably; for instance, the high-reward color on trial n became associated with low reward on trial $n + 1$ and the low-reward color on trial n became associated with high reward on trial $n + 1$. Notably, behavioral changes were observed in as few as 5–10 trials after the reversal, and the effect was stable within approximately fifteen trials of reversing color-reward contingencies.

Summary

The classification outlined above is but one way to cluster the many paradigms that are employed in studying reward and attention. Here, it is instructive to briefly comment on a related scheme proposed by Chelazzi and colleagues (2013). They suggested that *proactive* paradigms rely on a form of “incentive motivation”, which mobilizes cognitive resources for the achievement of the reward at stake, including the deployment of attention toward task-relevant items. *Reactive* paradigms without extensive training correspond closely to their suggestion of “effects of reward on the immediate deployment of attention”. Finally, *reactive* paradigms with more extensive training are similar to their proposal of “reward-dependent attentional learning”.

An important distinction raised by Chelazzi and colleagues (2013) concerns potential learning mechanisms. They state that, if rewards are thought to depend on performance by task participants, learning modulates not just a generic stimulus representation, but specifically the attentional “prioritization process” acting on this representation. Their distinction is important because it attempts to explain not only why reward-associated *targets* are selected more efficiently, but also why reward-associated *distractors* are *ignored* more effectively (see Della Libera & Chelazzi, 2009). The latter finding poses problems for less nuanced schemes that posit a single, simple form of “value learning”, for instance. This is because simple value learning would enhance the salience of distractors (in addition to

targets), which would thus be more *difficult* to inhibit. To account for better distractor inhibition, learning must affect a more abstract “prioritization process”.

The goal of this section on empirical studies was not to provide a comprehensive review of the literature. Indeed, this literature has been growing rapidly in the past few years. Some of the recent exciting studies not cited here include, for example, Bucker and Theeuwes (2014), Chelazzi et al. (2014), Hickey et al. (2014), Lee and Shomstein (2013b), and Stankevich and Geng (2014).

Brain mechanisms

Given the range of experimental manipulations of reward, several classes of brain mechanisms are going to be necessarily involved. Here, I focus the discussion on a few of the mechanisms that are believed to be particularly important in *proactive* manipulations of reward. As it will become clear, current knowledge is cursory and much remains to be unraveled.

Interactions between fronto-parietal control regions and valuation regions

The advance cue indicating the possibility of reward in a *proactive* paradigm gives participants the chance to strategically prepare for the upcoming task. In other words, the cue allows them to engage proactive control mechanisms that are beneficial to behavioral performance (Monsell & Driver, 2000). It is in this sense that several authors have argued that this type of reward manipulation is “just attention” (or that it cannot be separated from attention; see Maunsell, 2004). I have argued elsewhere against the strict separation of attention and motivation, and suggested that we should seek to understand how motivational signals are *embedded* into perception and cognition through multiple mechanisms – in this view, the “inextricably confounded” relationship between attention and reward discussed by Maunsell (2004), for one, ceases to be a problem and can be seen as a *property* of brain organization. Granted, this view is far from universal and requires a view of brain architecture that is strongly *non*-modular (for further discussion, see Pessoa, 2008; Pessoa, 2013).

Among others, attentional control relies upon fronto-parietal regions (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002) – mostly in dorsal aspects of these lobes. Interactions between reward and cognition rely on the communication between “task networks” (such as dorsal fronto-parietal regions engaged by attentional control) and “valuation networks,” which involve both subcortical regions, such as those in the striatum, and cortical ones, such as orbitofrontal cortex. Like all brain regions, the striatum and the orbitofrontal cortex are involved in many functions. Nevertheless, they play an important role in stimulus valuation, helping determine if a stimulus should be approached or avoided (Haber & Knutson, 2010; Zald & Rauch, 2007).

Interactions between reward and attentional control are suggested to take place via multiple modes of communication. The first mode involves direct anatomical pathways between task and valuation networks, such as the pathway between orbitofrontal cortex and lateral prefrontal cortex (Barbas & Pandya, 1989). In this case, a brain region that is particularly

sensitive to stimulus value (such as orbitofrontal cortex) can directly influence brain regions that are important for implementing attentional control. Another example involves pathways between the lateral surface of the prefrontal frontal cortex and cingulate cortex (Morecraft & Tanji, 2009); this latter cortex has many regions that are sensitive to stimulus/task value (Amiez, Joseph, & Procyk, 2006; Rushworth & Behrens, 2008; Shidara & Richmond, 2002; Shima & Tanji, 1998).

A second mode of communication relies on “*hub*” regions at the intersection of task and valuation networks. Hubs are highly connected and central regions that play a key role in information communication between different parts of a network (ref). Dorsal-medial prefrontal cortex plays a prominent role as a hub region, or *common node*, because of its participation in integrating inputs from diverse sources, notably cognitive and motivational ones (e.g., Devinsky, Morrell, & Vogt, 1995; figure 7.6). This region is involved in multiple executive functions, such as conflict detection, error likelihood processing, and error monitoring (Alexander & Brown, 2011; Botvinick, Braver, Barch, Carter, & Cohen, 2001). It is also important for attentional processing more generally, including spatial attention (Pessoa & Ungerleider, 2004). In addition, it is important for motivation in general, and reward in particular (see refs in previous paragraph).

Interactions involving direct anatomical pathways, hub regions, as well as indirect anatomical pathways, lead to changes in responses in brain regions, and changes in signaling between regions, that culminate in distributed effects over large-scale brain networks. In this context, whole-brain functional MRI provides valuable data to attempt to characterize such distributed effects. So-called network analysis provides useful tools to quantitatively characterize relationships within and between brain networks (Newman, 2010). This is the approach we took in a recent study in which we reanalyzed data of a previous investigation (Padmala & Pessoa, 2011) and compared network properties and relationships in attentional and valuation networks during trials with or without reward (Kinnison, Padmala, Choi, & Pessoa, 2012). We found that on control trials (without reward), attentional and valuation networks were relatively segregated and locally “efficient”. In other words, they exhibited high *within*-network functional connectivity, where *functional* connectivity refers to the degree to which responses of two regions covary, regardless of the status of their *anatomical* connectivity (which can be direct or indirect). But on reward trials, *between*-network connectivity increased, *decreasing* the segregation of the two networks (Figure 3). This finding suggests that a consequence of potential reward is to increase the coupling and integration between motivational and attentional brain networks (because functional connectivity is considered an indication of “integration of information.”).

While network analysis provides a characterization of the overall pattern of co-activation across brain regions, it is also instructive to discuss other aspects of brain responses that speak to the interactions between reward and attention – again, in the context of our response-conflict study (Padmala & Pessoa, 2011). We anticipated that reward cues would enhance engagement of fronto-parietal attentional regions and, consequently, that these regions would be better positioned to exert goal-directed control affecting visual processing. Indeed, during the cue phase when subjects were told whether a reward was possible, responses in fronto-parietal regions were stronger with reward—consistent with increased

attention. During the target phase when subjects performed the actual task, we were interested in probing responses in dorsal-medial prefrontal cortex, a region that, as mentioned, is sensitive to response conflict (Botvinick, et al., 2001). In the context of our task, we assumed that responses in this region to incongruent trials (relative to neutral trials that did not produce conflict) would index the amount of response-selection demand (or “interference”). As in our behavioral data, we observed a reward by cognition interaction: interference-related responses (in dorsal-medial prefrontal cortex) *decreased* during reward trials, suggesting that selection demands were reduced during those trials.

Importantly, larger *cue*-related responses were associated with larger *decreases* in interference-related responses in dorsal-medial PFC during the subsequent *target* phase. This pattern of cue and target responses was thus compatible with the idea that upregulation of control during the cue phase led to decreased interference during the target phase (Figure 4). How were cue and target responses related to the selection of visual information during the task? The relationship between cue and target responses was consistent with a *mediation* role for responses in visual cortex sensitive to word-related processing (in the left parahippocampal gyrus, a region responsive to word stimuli). As indicated in Figure 2B, during the target phase, visual responses linked to distractor processing *decreased* in the reward condition. Collectively, our findings suggest that subjects were able to employ motivationally salient cues to upregulate attentional control mechanisms that influenced the selection of visual information in a way that *reduced* both behavioral conflict and related brain responses (Figure 4).

We also observed responses to the reward cue in several subcortical sites that are engaged during reward-related processing, including the caudate and putamen in the dorsal striatum, the nucleus accumbens in the ventral striatum, and the midbrain. Interestingly, some of these regions also exhibited increased functional connectivity with fronto-parietal regions engaged robustly by the cue. For instance, during reward trials, we detected increased correlation of trial-by-trial responses between the intraparietal sulcus in parietal cortex and striatal regions (putamen, caudate, and nucleus accumbens). Notably, the strength of the correlation was linearly related to individual differences in reward sensitivity (as assessed through standardized questionnaires; see Carver & White, 1994), revealing that the functional interaction between these regions was stronger for subjects who scored higher in this dimension (Figure 4, scatter plot).

Related findings were obtained by Harsay and colleagues (2011), who studied the role of reward during the antisaccade task, where subjects must exercise deliberate/endogenous control in order to execute a saccade to the opposite side of a target stimulus (a briefly flashed asterisk in their case). Subjects performed faster and more accurate antisaccades when potential reward was involved. Harsay and colleagues also observed increased functional connectivity during the reward condition. The caudate exhibited increased correlation with several cortical regions linked to the execution of eye movements, including the frontal eye field (frontal cortex) and the intraparietal sulcus (parietal cortex). Notably, increased functional connectivity was tied to higher benefits of reward on reaction time.

Several other examples of increased functional connectivity during reward conditions have been reported in the literature. For example, enhanced coupling between regions in the striatum and fronto-parietal cortex was detected by Schmidt and colleagues (2012) in a rewarded response-interference task. In a long-term memory study, Adcock and colleagues (2006) observed increased correlated activity between the hippocampus and midbrain during high reward, and the correlation strength predicted memory formation.

Thus, I suggest that functional interactions between task- and valuation-related brain regions play an integral role in coordinating and integrating signals when reward influences proactive control (Figure 5). Thus far, I have emphasized functional interactions between valuation-related regions and attentional control regions. Yet, an equally important type of functional interaction involves valuation regions and sensory cortex. These interactions may resemble those observed by Winkowski and colleagues (2013), who found that pairing orbitofrontal cortex stimulation with sounds caused selective changes in sensory responses in primary auditory cortex. The orbitofrontal-induced influences on auditory responses resembled those observed during behavior, indicating that orbitofrontal activity could underlie the coordination of rapid changes in auditory cortex to dynamic sensory environments.

Neurotransmitter systems: the role of dopamine

A third mode of communication between valuation and task-based networks relies on more diffuse signals tied to particular neurotransmitter systems, notably the dopaminergic “system” (Aarts, van Holstein, & Cools, 2011; Robbins, 2000). For example, Noudoost and Moore (2011; see also Soltani, Noudoost, & Moore, 2013) found that dopamine-mediated activity in the frontal eye field (which is important for attention and eye movements) during a visual task not only caused the monkey to select specific visual targets more frequently, but also led to enhanced and more selective responses of neurons in visual area V4. Notably, the effects in visual cortex were comparable in magnitude to the effects of goal-directed attention. Together, their findings suggest that dopamine contributes to the frontal eye field’s modulation of visual cortex via a mechanism analogous to attention, namely, by modulating long-range connections between frontal cortex and visual cortex. However, because Noudoost and Moore altered dopamine-related activity via a local pharmacological manipulation, their findings do not elucidate the operations that normally occur during unaltered motivated behavior. Nevertheless, given the extensive dopaminergic innervation of the frontal cortex, related processes might be at play during normal situations (Figure 6).

Widespread neuromodulatory connections reach cortical and subcortical regions across the brain. What is their function? Goldman-Rakic and colleagues (1989) suggested that dopamine helps control cortical excitability, thereby increasing the fidelity of signals within local networks. Indeed, the effects of dopamine appear to enhance the neuronal signal-to-noise ratio (Sawaguchi & Matsumura, 1985), consistent with computational modeling results of the contribution of dopamine in working memory function (Gruber, Dayan, Gutkin, & Solla, 2006; see also Murphy & Sillito, 1991 and Sato, Hata, Masui, & Tsumoto, 1987 for a related role of acetylcholine in enhancing signal-to-noise). It is thus possible that dopaminergic (and cholinergic) neuromodulation provides a key mechanism by which

reward “sharpens” executive control (and hence behavioral performance), for instance, by improving the signal-to-noise ratio of relevant neurons. In this fashion, reward may enhance processing efficiency in target cortical and subcortical regions.

In the context of considering multiple time frames of reward effects, one of the most intriguing instances is perhaps the case of *next-trial* effects. In this case, reward improves performance during a trial that follows correct performance and reward *delivery*. It is important to note that in these experiments, reward is contingent on performance; thus next-trial effects are *unlike* situations involving “reward priming” discussed previously in which reward is delivered *randomly*, as in the work by Hickey and colleagues (Hickey, et al., 2010). In fact, in the experiments discussed next, reward was signaled via advance cues, thus these paradigms are *proactive* in the terminology adopted here.

Using functional MRI, Pleger and colleagues (2008) tested whether reward could influence somatosensory judgments and modulate activity in somatosensory cortex. Participants discriminated electrical somatosensory stimuli delivered to the index finger, with correct performance rewarded at the end of the trial at one of four levels. Higher rewards improved tactile performance and led to increased responses on rewarded trials. Importantly, the level of reward received on a particular trial influenced somatosensory performance and brain activity on the *subsequent* trial, with better discrimination and enhanced responses in primary somatosensory cortex for trials that followed higher rewards.

The results by Pleger and colleagues (2008) are all the more important because, remarkably, primary somatosensory cortex was “reactivated” at the point of reward *delivery* – that is, despite the absence of concurrent somatosensory input at that point in time. Moreover, this reactivation of primary somatosensory cortex increased monotonically with level of reward. Analogous results were obtained in a study of visual discrimination (see Weil et al., 2010).

As dopamine is centrally involved in reward-related processes, in a follow up study, Pleger and colleagues (2009) employed pharmacological manipulations to evaluate its role in next-trial effects. With the same somatosensory discrimination paradigm, they found that both the behavioral and brain-response impact of reward delivery was enhanced by a dopamine agonist and attenuated by a dopamine antagonist.

More broadly, although next-trial effects are fast when one considers a trial as the unit of time, they still require processes that operate over several seconds, thus allowing reward delivery to affect subsequent behavior. Intriguingly, some dopaminergic mechanisms have a time course that can in fact extend for several seconds (Izhikevich, 2007; Otmakhova & Lisman, 1996). At least in the case of the primate visual system, however, because dopaminergic innervation of visual cortex is quite sparse, it is unlikely that direct connections are involved (Berger, Trottier, Verney, Gaspar, & Alvarez, 1988; Oades & Halliday, 1987). Next-trial effects on visual responses may thus depend on *source* regions in frontal and parietal cortex that exert top-down control on sensory processing. In other words, dopaminergic innervation of, say, frontal cortex would lead in turn to effects on visual cortex (see Figure 6), much like the mechanisms involving the frontal eye field and visual cortex reported by Noudoost and Moore (2011) and previously discussed.

Conclusions

Information with motivational content can influence perception and attention in powerful ways. The impact can be discerned at both the perceptual competition and executive competition levels – in what was called the *dual competition* framework (Pessoa, 2009; 2013). In broad terms, the framework sees perception and executive functions as capacity-limited processes engaged in evaluating the behavioral relevance of stimuli and tasks in question. At the perceptual level, reward-associated items act at times as if they had increased *salience*, which improves performance if they are task relevant but impairs it if they are task irrelevant. At the executive level, some effects of motivation on performance can be thought of in terms of competition for resources, a notion that is reinforced by the existence of performance trade-offs when incentives are at stake (in some cases, reward can be detrimental to performance; see (Padmala & Pessoa, 2011)).

The architecture portrayed in Figure 5 implies that signals with motivational significance are not confined to specific brain regions but are broadcast extensively across the brain. One example of such “broadcast” was a study by Vickery and colleagues (2011), who observed reward-related signals distributed quite broadly in the brain even when reward was not paired with a specific visual stimulus or motor response. As they state, “such distributed representations would have adaptive value for optimizing many types of cognitive processes and behavior in the natural world.” (Vickery, et al., 2011, p. 175). It is clear that the years to come will rapidly expand our knowledge of the many ways in which reward impacts both brain and behavior.

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Figure 1.

Visual competition. (A) Traditional scheme with influences of stimulus-driven and goal-driven factors. (B) Does reward act as a “top-down” or “bottom-up” factor? (C) Reward effects take place at multiple levels, some of which can be understood as closer to stimulus-driven or goal-driven processes.

Figure 2.

Response-conflict paradigm. (A) In the reward condition shown here, a cue stimulus (“\$20”) signaled that subjects would be rewarded for fast and correct performance; in the control condition (not shown here), a cue stimulus (“\$00”) signaled that there would be no reward. During the target phase, a stimulus picture of a house or building was presented together with a task-irrelevant word (an incongruent condition is illustrated here). After the target stimulus, subjects were informed about the reward and about the total number of points accrued. (B) Decreased activation in the left parahippocampal gyrus (circled area) in the reward condition was interpreted in terms of reduced word-related processing in visual cortex due to improved distractor filtering. Panel A reproduced with permission from Padmala and Pessoa (2011). Panel B reproduced with permission from Pessoa (2013).

Figure 3. Changes in functional connectivity with reward. For abbreviations, see Kinnison et al. (2012). The inset shows the changes from the perspective of a single region, illustrating the fact that changes in functional connectivity with reward were observed broadly across many pairs of regions.

Figure 4.

Network interactions. Distractor processing in visual cortex mediated the relationship between attentional control implemented in fronto-parietal cortex during the cue phase and conflict-related activity in medial prefrontal cortex during the subsequent target phase. The shaded area shows interactions during cue processing between fronto-parietal cortex and subcortical regions involved in reward processing. The inset with the scatter plot shows (for a sample participant) how the correlation of trial-by-trial responses between the ventral striatum and intraparietal (IPS) cortex increased with reward. For illustration, trial-by-trial responses are shown only for the reward condition. Every point represents a trial (x coordinate: response amplitude in ventral striatum; y coordinate: response amplitude in intraparietal cortex). The best-fit line is shown in blue, and the difference in slope between the two lines indicates the effect of reward. Finally, the difference in slope correlated with individual differences in reward sensitivity (BAS scores). mPFC, medial prefrontal cortex.

Figure 5.

Modes of interaction between attentional control and motivation/reward. (1) Specific brain regions link the two networks, either directly or indirectly (for instance, via the thalamus). (2) Interactions rely on *hub* regions, such as those in dorsal-medial prefrontal cortex, which are part of both attentional and motivational networks (hub region in the slice and gray node in the cortical valuation network). (3) Finally, motivational signals are further embedded within attentional mechanisms through the action of diffuse neuromodulatory systems. ant., anterior; NAcc, nucleus accumbens; OFC, orbitofrontal cortex; PCC, posterior cingulate cortex; PFC, prefrontal cortex; SN, substantia nigra; VTA, ventral tegmental area. Reproduced with permission from Pessoa and Engelmann (2010).

Figure 6.

Interactions between reward, attention, and vision. Visual processing is influenced by signals in attentional control areas, such as the frontal eye field (FEF). Similar interactions involve the intraparietal sulcus (IPS). Attentional areas, by their turn, are influenced by signals in valuation regions, including the ventral striatum. The red, dotted lines indicate signals related to dopamine function from the midbrain and/or ventral striatum.