Title

Reward rapidly enhances visual perception

Word count

4401

Authors:

Phillip (Xin) Cheng^{1,2}

Anina N. Rich^{2,3}

Mike E. Le Pelley¹

Affiliations:

¹ School of Psychology, UNSW Sydney, Australia

² Perception in Action Research Centre (PARC) & Department of Cognitive Science, Macquarie University, Sydney, Australia

³ Centre for Elite Performance, Expertise and Training (CEPET), Macquarie University, Sydney, NSW, Australia

Corresponding author:

Phillip (Xin) Cheng, School of Psychology, UNSW Sydney, Australia.

Email: phillip.cheng@unsw.edu.au

Abstract

Rewards exert a deep influence on our cognition and behaviour. Here, we used a paradigm in which reward information was provided at either encoding or retrieval of a brief, masked stimulus to show that reward can also rapidly modulate early neural processing of visual information, prior to consciousness. Experiment 1 showed enhanced response accuracy when a to-be-encoded grating signalled high reward relative to low reward, but only when the grating was presented very briefly and participants were not consciously aware of it. Experiment 2 showed no difference in response accuracy when reward information was instead provided at the stage of retrieval, ruling out an explanation of the reward-modulation effect in terms of differences in motivated retrieval. Taken together, our findings provide the first behavioural evidence for a rapid reward-modulation of visual perception, which does not seem to require consciousness.

1 The effect of reward on human behaviour has often been studied in terms of its ability to motivate
2 overt responses: we might choose this job over that job because it has a higher salary, choose to
3 order cake rather than salad because it tastes better, or choose to swipe right on a dating app for an
4 attractive individual. A body of recent research demonstrates that reward also exerts an influence
5 prior to overt choice, by modulating cognitive processing (Pessoa & Engelmann, 2010). In
6 particular, reward influences the likelihood that stimuli will command attentional resources: reward
7 cues are prioritised for further processing and action (Della Libera & Chelazzi, 2009; Le Pelley,
8 Mitchell., Beesley., George., & Wills., 2016; Le Pelley, Pearson, Griffiths, & Beesley, 2015). Here,
9 we investigate whether the effect of reward can be observed even earlier in the stream of neural
10 information processing, through modulating early perceptual processes. Beyond its theoretical
11 significance in terms of understanding the varied roles of reward in the information-processing
12 cascade, this study has potential clinical significance because reward-related processing biases are
13 implicated in a range of addictive and obsessive-compulsive behaviours (Albertella, Le Pelley, et
14 al., 2019; Field, Munafò, & Franken, 2009; Robbins, Gillan, Smith, de Wit, & Ersche, 2012).

15
16 Reward often aligns with our task goals, such that people prioritise cognitive processing of reward
17 information in a goal-directed way (Engelmann, Damaraju, Padmala, & Pessoa, 2009; Hickey,
18 Chelazzi, & Theeuwes, 2010; Maunsell, 2004; Stankevich & Geng, 2015). For example, if
19 responding to events in location X provides more reward than in location Y, people will typically
20 choose to allocate more attention to location X (Engelmann et al., 2009). Beyond this effect of
21 reward on strategic attention, recent studies have demonstrated that reward also influences the
22 extent to which stimuli automatically capture attention, even when they are task-irrelevant so that
23 attending to these stimuli is contrary to task goals (Le Pelley et al., 2016). Overall, this attention-
24 based research has shown an involuntary enhancement in cognitive processing at the location in
25 space and time at which reward-signalling stimuli appear (or impaired processing at other
26 locations). However, reward could play an even earlier role in neural information processing, by
27 modulating our perceptual encoding of stimuli. The possibility that reward exerts a fundamental
28 influence on visual perception is suggested by neurobiological studies in rats and primates showing
29 that reward modulates neural gain in early sensory areas (e.g., primary visual cortex) that encode
30 low-level visual features (Serences, 2008; Shuler & Bear, 2006; Stănişor, van der Togt, Pennartz, &
31 Roelfsema, 2013), and human studies showing perceptual learning for low-level features paired
32 with intrinsic reward (e.g., Seitz, Kim, & Watanabe, 2009). This raises the intriguing possibility that
33 neural encoding of visual stimuli might be modulated by their reward status: establishing a neutral

stimulus as a signal of high reward might enhance the speed and accuracy of encoding that stimulus relative to when it signals low reward. If participants become ‘better at seeing’ high-reward signals than low-reward signals when their perceptual features are otherwise equivalent, it would be a remarkable finding. It would suggest that fundamental aspects of our phenomenological experience of the world are shaped by our previous experience of reward. In the current study, we investigate this idea of sharpened perception of high-reward stimuli.

Consistent with the idea that reward-related stimuli can be perceived rapidly, previous research has shown that subliminally presented reward cues (i.e., reward cues that are presented briefly and masked, so participants report no conscious awareness of them) can influence ongoing cognitive processing (Pessiglione, Schmidt, Palminteri, & Frith, 2011; Zedelius et al., 2014). For example, subliminal presentation of an image of a high-value coin, relative to a low-value coin, can enhance both cognitive performance (Bijleveld, Custers, & Aarts, 2009; Bourgeois, Chelazzi, & Vuilleumier, 2016; Capa, Bouquet, Dreher, & Dufour, 2013) and physical effort (Pessiglione et al., 2007; Ziauddeen et al., 2012) for a subsequent task, demonstrating that even subjectively invisible reward signals can elevate motivation and affect subsequent behaviour. However, while this research suggests that subliminal reward cues can be encoded and influence ongoing behaviour, it does not establish whether the perceptual processing of the cues themselves is influenced by their reward-signalling status. That is, we cannot tell whether reward modulates perception of the stimuli (a high-reward coin is more likely to be encoded than a low-reward coin), or whether observed effects instead reflected ‘downstream’ influences of reward on later cognitive processing (high- and low-reward coins are encoded equally, but a high-reward coin provides greater motivation for subsequent behaviour). In the current study, we investigated whether reward enhances perception, such that high-reward signals are perceived faster or more precisely than low-reward signals.

To investigate the influence of reward on the speed and fidelity of perceptual encoding, we developed a novel adaptation of a task used by Soto et al. (2011) to include a manipulation of reward. On each trial of this task, participants were presented with a cue stimulus — a Gabor patch of a particular orientation (see Figure 1). This cue appeared for either 17ms (short-cue) or 200ms (long-cue), and was immediately followed by a 100ms pattern mask. This masking procedure rendered the cue subjectively invisible to participants on short-cue trials, but left it clearly visible on long-cue trials. After a delay interval of 2000ms, participants were then shown a test stimulus, which was a second Gabor patch with an orientation that differed by 30° from that of the cue.

Participants' task was to respond according to whether the cue stimulus would have to be rotated clockwise or counterclockwise to match the test stimulus. After making this orientation response, participants reported their subjective perception of the cue on a 4-point scale (0: did not see anything; 1: maybe saw the cue; 2: saw the cue but not its orientation; 3: saw the cue and its orientation). This self-report approach has been shown to reliably track the amount of relevant information that can be decoded from cortical activity (Dehaene & Changeux, 2011; King, Pescetelli., & Dehaene., 2016).

The critical aspect of the current task was the manipulation of reward. In Experiment 1 ($n = 30$), participants were informed that the spatial frequency of the cue signalled whether a correct response would earn high reward (500 points) or low reward (1 point; points were later converted into money; see Figure 1a). Importantly, the cue's *reward-related* information (spatial frequency) was unrelated to its *response-related* information (orientation), so that the reward-signalling feature was not predictive of the correct response. Our primary question was whether this manipulation of reward-signalling information influenced rapid perceptual encoding of the cue. If that were the case, then we should observe greater response accuracy for high-reward cues than low-reward cues in the short-cue condition, when rapid encoding of the cue is required. Furthermore, by looking at the effect of reward on accuracy as a function of participants' self-report of their subjective experience of the cue, we could investigate whether reward-related influences on performance require conscious awareness of the cue. By contrast, rapid encoding is not required in the long-cue condition. When the cue is presented for 200ms, there is plenty of time for encoding, and hence here we would expect high accuracy regardless of the reward-signalling nature of the cue.

In Experiment 2 ($n = 29$), all cue stimuli had the same (medium) spatial frequency, and instead it was the spatial frequency of the *test stimulus* that signalled whether high or low reward was available (Figure 1b). This allowed us to establish whether reward influenced the retrieval of information that had previously been encoded: since encoding of the cue would be similar across all trials — as cues were equivalent on all trials — any enhancement of performance on trials with a high-reward-signalling test stimulus must reflect participants' greater motivation to retrieve the cue on these trials, since more was at stake for a correct response.

a. Experiment 1

b. Experiment 2

Figure 1. In this task, a cue stimulus was presented for 17ms or 200ms, and then masked. After a 2000ms delay, a test stimulus appeared: participants' task was to indicate (via button press) whether the orientation of the test stimulus represented a clockwise or anti-clockwise tilt. They then rated their awareness of the cue (0: did not see anything; 1: maybe saw the cue; 2: saw the cue but not its orientation; 3: saw the cue and its orientation). Feedback then showed perceptual response accuracy and reward. **(a)** In Experiment 1, the spatial frequency of the cue (0.02 or 0.05 cycles/pixel [c/p]) signalled if a correct response would earn high or low reward (500 points or 1 point). **(b)** In Experiment 2, spatial frequency of the test stimulus signalled reward. The relationship between spatial frequency and reward was counterbalanced across participants. Note that the contrast of the cue and test stimuli are increased here for visualisation.

Results

Experiment 1

Figure 2a shows accuracy of orientation responses in Experiment 1 as a function of the duration of the cue (short: 17ms; or long: 200ms) and the magnitude of reward signalled by the cue. As anticipated, participants found the task relatively straightforward in the long-cue condition: mean accuracy was high (>85% correct), and it did not differ significantly as a function of reward ($t(29) = 0.17$, $p = .869$, $d_z = 0.03$, Bayes Factor (BF_{10}) = 0.20). In this study, we used $BF_{10} < 1/3$ as substantial evidence in favour of the null hypothesis (Jeffreys, 1961). Performance was generally poorer in the short-cue condition than the long-cue condition, but one-tailed t-tests confirmed that short-cue accuracy remained significantly above chance (50% correct) for both the high-reward condition ($t(29) = 5.40$, $p < .001$, $d_z = 0.99$) and low-reward condition ($t(29) = 3.71$, $p < .001$, $d_z = 0.68$), indicating that the masked 17ms cue was encoded on at least a subset of trials. Critically, performance in the short-cue condition differed as a function of reward: accuracy was significantly greater for high-reward cues than low-reward cues ($t(29) = 2.38$, $p = .012$, $d_z = 0.43$), consistent with the idea of perceptual enhancement for high-reward cues.

Figure 2. Data from Experiment 1 ($n = 30$). **(a)** Bars show mean accuracy for trials with a long cue duration (200ms) and a short cue duration (17ms), as a function of whether the cue signalled availability of high reward (blue bars) or low reward (white bars). **(b)** Accuracy for short-cue trials in which participants reported having no awareness or some awareness of the cue, as a function of reward. Error bars represent within-subject 95% confidence intervals. Grey markers linked by lines show performance of individual participants as a function of reward. Dashed grey lines represent chance-level performance (50% correct). * indicates $p < .05$. ns indicates $p > .05$. **(c)** Number of ratings at each awareness level by each participant for short-cue trials in which the cue signalled high reward. **(d)** Number of ratings at each awareness level by each participant for short-cue trials in which the cue signalled low reward.

Next we considered participants' self-reported awareness of the cue. Figures 2c and 2d show the distribution of participants' awareness ratings (0-3) across trials with high-reward and low-reward cues. If participants were aware of any reward-related enhancement in perceptual encoding, we would observe a difference in the pattern of awareness ratings between reward conditions (with more evidence of awareness for high-reward cues). However, analysis using a multinomial mixed-effect model with participants as the random intercept revealed that the pattern of awareness ratings did not differ significantly between reward conditions ($F(3, 232) = 1.76, p = .157, R^2_{Adjusted} = .01$). We then compared the proportion of high-reward and low-reward trials on which participants gave a zero rating, indicating no awareness of the cue. There was no significant difference in 'no awareness' reporting as a function of reward ($t(29) = 1.19, p = .242, d_z = 0.22, BF_{10} = 0.37$). The Bayes Factor suggests that the reward-signalling status of the cue did not alter participants' subjective experience of that cue (though we note that the evidence is only moderately in favour of the null hypothesis).

Finally, we examined whether the reward-related enhancement observed in orientation responses differed as a function of the awareness of the cue (Figure 2b). For this analysis, we divided trials into two types: those in which participants indicated no awareness of the cue (awareness rating of 0), and those in which participants indicated some awareness of the cue (combined data from trials with awareness rating of 1, 2, or 3; in Supplementary Materials we present results of a finer-grained analysis examining accuracy at each awareness level separately). We excluded participants who had fewer than 10 trials for a given awareness level, to ensure reliable estimates of performance. This left a final sample of 18 and 29 participants for analysis of no-awareness trials (ratings of 0) and some-awareness trials (ratings of 1 to 3, pooled), respectively.

For no-awareness trials, response accuracy was significantly greater than chance for high-reward cues ($t(17) = 4.08, p < .001, d_z = 0.96$), but not for low-reward cues ($t(17) = 0.46, p = .327, d_z = 0.11, BF_{10} = 0.14$), with the Bayes Factor in the latter case suggesting substantial evidence in favour of the null hypothesis. Notably, accuracy was significantly greater for high-reward than low-reward cues for these trials in which participants reported no conscious awareness of the cue ($t(17) = 2.76, p = .007, d_z = 0.65$), demonstrating a reward-related performance enhancement in the absence of awareness.

For some-awareness trials, performance was significantly above chance for both high-reward ($t(28) = 4.64, p < .001, d_z = 0.86$) and low-reward cues ($t(28) = 4.79, p < .001, d_z = 0.89$), with no significant difference between reward conditions ($t(28) = 0.19, p = .427, d_z = 0.03, BF_{10} = 0.10$). This suggests that when participants had at least partial awareness of the cue, the reward-signalling status of that cue had no effect on response accuracy.

In summary, Experiment 1 found a reward-related performance benefit under the most challenging condition: when cue presentation was very brief, and participants reported having no awareness of the cue. This could reflect enhanced neural encoding of high-reward cues relative to low-reward cues. An alternative possibility is that encoding was similar for both cue types, but that participants were more motivated to retrieve information about the high-reward cue when presented with the test stimulus, since they could earn a larger reward for a correct response on high-reward trials. Experiment 2 probed this idea, by testing for an influence of reward on motivated retrieval of cue information.

Experiment 2

In Experiment 2, the cue stimulus had the same (medium) spatial frequency on every trial, and hence provided no reward information. Instead, the spatial frequency of the test stimulus signalled whether high or low reward was available for a correct response. This test stimulus was presented until response, so the reward information was clearly visible to participants on every trial. If the reward-related performance enhancement observed in Experiment 1 reflected greater motivation to retrieve the cue when high reward was at stake, then we should observe a similar effect in Experiment 2 (or if anything a larger effect, because reward information was more visible). In contrast, if the findings of Experiment 1 reflected an influence of reward on neural *encoding* of the cue stimulus, then there should be no corresponding effect in Experiment 2 since here encoding of the cue stimulus occurred before any reward information was provided.

Figure 3a shows accuracy of orientation responses in Experiment 2 as a function of the duration of the cue, and the magnitude of reward signalled by the test stimulus. As in Experiment 1, accuracy on long-cue trials was generally high (>85% correct), but somewhat counterintuitively, accuracy was significantly lower for high-reward trials than low-reward trials ($t(28) = 2.60, p = .015, d_z = 0.48$). We return to this surprising finding in Discussion. In the short-cue condition, accuracy was

significantly above chance for both high-reward trials ($t(28) = 3.70, p < .001, d_z = 0.69$) and low-reward trials ($t(28) = 3.84, p < .001, d_z = 0.71$). Critically, and unlike Experiment 1, there was no enhancement of performance on high-reward relative to low-reward trials ($t(28) = 0.73, p = .765, d_z = 0.14, BF_{10} = 0.13$), with the Bayes Factor suggesting substantial evidence for the null. This latter finding suggests that performance on short-cue trials is unaffected by differences in reward-motivated retrieval.

Figure 3. Data from Experiment 2 ($n = 29$). **(a)** Bars show mean accuracy for trials with a long cue duration (200ms) and a short cue duration (17ms), as a function of whether the test stimulus signalled availability of high reward (blue bars) or low reward (white bars). **(b)** Accuracy for short-cue trials in which participants reported having no awareness or some awareness of the cue, as a function of reward. Error bars represent within-subject 95% confidence intervals. Grey markers linked by lines show performance of individual participants as a function of reward. Dashed grey lines represent chance-level performance (50% correct). * indicates $p < .05$. ns indicates $p > .05$. **(c)** Number of ratings at each awareness level by each participant for short-cue trials in which the test signalled high reward. **(d)** Number of ratings at each awareness level by each participant for short-cue trials in which the test signalled low reward.

Figures 3c and 3d show the distribution of awareness ratings for short-cue trials in Experiment 2. As in Experiment 1, a multinomial mixed-effect model revealed that the pattern of awareness ratings did not differ significantly between high- and low-reward conditions ($F(3, 224) = 2.03, p = .111, R^2_{Adjusted} = .28$). In addition, there was no significant difference in reporting of no subjective awareness of the cue (zero ratings) as a function of reward ($t(28) = 1.30, p = .205, d_z = 0.24, BF_{10} = 0.42$). Thus, reward did not appear to change subjective awareness of the cue, though as in Experiment 1 the Bayes Factor here suggests that the evidence is only moderately in favour of the null hypothesis.

Figure 3b shows response accuracy for short-cue trials in Experiment 2 in which participants reported no awareness of the cue (ratings of 0) or some awareness (ratings of 1-3). As for Experiment 1, we removed participants with fewer than 10 trials for a given awareness level, leaving 24 and 26 participants for no-awareness and some-awareness trials, respectively. For no-awareness trials, accuracy was not greater than chance for high-reward trials ($t(23) = 0.49, p = .684, d_z = 0.10, BF_{10} = 0.13$) or low-reward trials ($t(23) = 0.11, p = .456, d_z = 0.02, BF_{10} = 0.11$). Notably, and unlike Experiment 1, there was no evidence of higher accuracy for high-reward than low-reward trials ($t(23) = 0.57, p = .714, d_z = 0.12, BF_{10} = 0.13$). For some-awareness trials, accuracy was above chance for both high-reward trials ($t(25) = 3.73, p < .001, d_z = 0.73$) and low-reward trials ($t(25) = 3.50, p < .001, d_z = 0.69$), and did not differ between reward conditions ($t(25) < 0.01, p = .500, d_z < 0.01, BF_{10} = 0.11$). Consistent with the analysis collapsing over all short-cue trials of Experiment 2, these findings suggest that reward did not influence performance as a consequence of differences in motivated retrieval.

Discussion

The present study investigated the influence of reward on very rapid visual perception. In Experiment 1, the cue contained both reward-related information (spatial frequency signalled whether a high or low reward was available) and response-related information (orientation defined the correct response in a subsequent test). We found a reward-related increase in accuracy when the cue was presented briefly (for 17ms) and immediately masked. In contrast, in Experiment 2 it was the test stimulus that signalled reward magnitude: the cue stimulus provided no reward information and hence reward could not influence perceptual encoding of this cue. Under these conditions, there was no evidence of greater accuracy on high-reward versus low-reward short-cue trials. This

suggests that the reward-related advantage observed in Experiment 1 did not reflect a difference in motivated retrieval of cue information, because if this were the case we should have seen a similar (or larger) effect in Experiment 2. Instead, these findings imply that the reward advantage observed in Experiment 1 stems from the presence of reward information at the time of perceptual encoding of the cue, despite it being masked from consciousness.

One interpretation of these findings is that reward induces changes in perceptual encoding. In effect, the visual system becomes more sharply ‘tuned’ to high-reward information than low-reward information such that high-reward stimuli undergo rapid neural encoding with higher fidelity. This possibility is consistent with neuroimaging findings showing that reward modulates neural gain in early visual areas that are responsible for encoding low-level features (Serences, 2008; Serences & Saproo, 2010; Stănişor et al., 2013). In line with this account, Experiment 1 found evidence of a reward advantage only when the cue was presented very briefly (17ms), and not when it was presented for longer (200ms). In the long-cue condition, there was plenty of time to encode the cue and so reward modulation of encoding would have no detectable effect. In the short-cue conditions, however, very little time was available, and so differences in encoding speed for high- versus low-reward cues would have a more noticeable effect on performance.

Deeper analysis of short-cue trials of Experiment 1 showed that the influence of reward on accuracy was significant for the subset of trials in which participants reported no conscious awareness of the cue, but not for trials in which they reported at least partial awareness of the cue. The no-awareness trials are those on which neural encoding of the cue was presumably most limited, and this limitation may have rendered these trials most likely to reveal an effect of reward-modulated encoding on performance. The finding of reward modulation on no-awareness trials also suggests that the reward information that gives rise to this effect is extracted at a very early stage of neural information processing, prior to conscious awareness, raising the possibility that the underlying neural mechanisms might involve subcortical reward-processing regions that are distinct from the consciousness-generating network (Gottfried, O’Doherty, & Dolan, 2003; McFadyen, Dolan, & Garrido, 2020). Our findings also indicate that the extensive cortical processing triggered by conscious awareness swamps the reward effect, consistent with previous evidence that conscious information results in greater and more widespread neural activity than unconscious information (Dehaene & Changeux, 2011; Dehaene, Lau, & Kouider, 2017; Yi, Woodman, Widders, Marois, & Chun, 2004). This latter idea is consistent with the unexpected finding of Experiment 2 that

accuracy in the long-cue was impaired when the test stimulus (presented until a response) was high reward. Under this account, the high-reward test stimulus triggers such strong cortical processing that it interferes with the memory of the cue (which is relatively weak since the cue presented for only 200ms). Returning to the discussion of awareness, while reward influenced the accuracy of orientation responses, it did not significantly alter the proportion of short-cue trials on which participants reported no versus some awareness of the cue. Thus, enhanced perception of the cue in the high-reward condition did not seem to increase its subjective visibility, consistent with the idea that reward modulation operates outside awareness — though we should be cautious in drawing this conclusion, since the results of Bayesian analyses here indicated only moderate support for the null.

In the discussion above we interpreted the effect of reward as changing the nature of the neural encoding process itself, so that high-reward stimuli could be encoded more rapidly and with sufficient precision to allow an accurate orientation response. However, an alternative interpretation is that high- and low-reward cues might initially be encoded equivalently, but this neural representation may be propagated more successfully over the 2s delay between the cue and test for the high-reward stimulus. This latter account sees reward as influencing the maintenance of a stimulus representation. Our finding of reward modulation for no-awareness trials is notable here, in that it seems contrary to traditional views of working memory, which hold that active maintenance requires consciousness (Baddeley, 1992, 2000). However, recent research using an approach similar to that employed here (though not in the context of reward) indicates that briefly presented visual information can be maintained even if it is subjectively invisible (King et al., 2016; Soto & Silvanto, 2014; Soto. et al., 2011). Thus, reward here might also have facilitated the sustained processing of weak visual signals until the test, when they could influence performance.

In summary, our findings indicate that reward information present at the time of encoding exerts a rapid influence on visual perception. Within this idea, it is possible that reward operates at the encoding stage itself, enhancing the ability to form mental representations of high-reward stimuli, or by modulating the maintenance of the neural representation, or both. The current data do not allow us to decide between these alternatives. Future studies could further investigate the processing stage at which reward operates by using neuroimaging with high temporal resolution (EEG or MEG) to track changes in neural information over time (King et al., 2016; M. G. Stokes, Wolff, & Spaak, 2015).

As noted earlier, our procedure for assessing perception and awareness of masked stimuli was adapted from a previous study (Soto. et al., 2011). Soto et al. did not manipulate reward, but showed above-chance accuracy of the orientation response across trials in which participants reported no awareness of the cue. This finding is somewhat at odds with our data: in Experiment 2 when no reward information was present at encoding, accuracy was at chance on no-awareness trials. Indeed, we found above-chance accuracy on no-awareness trials only when the cue signalled high reward in Experiment 1. The reason for this discrepancy between studies is unclear, but there were some procedural differences that may have played a role. First, the cue and test stimuli in Soto et al.'s study were identical in spatial frequency, whereas in our procedure they differed. Since performance relied on comparing cue and test stimuli, the variation in spatial frequency may have made our task harder. Second, the masks differed. Soto et al.'s mask was a black circle, but pilot testing for the present study suggested that this rarely masked the 17ms cue. Consequently, we used a plaid mask instead, which was more effective. Although Soto et al. did not detail the proportion of no-awareness ratings their participants gave, another study replicating Soto et al.'s results with a similar paradigm reported this as ~7% (King et al., 2016), whereas in the current study the corresponding proportion was ~19%. Thus, participants may have had less cue-related perceptual information in our study. Finally, whereas our study included both short- and long-cue trials, Soto et al. had only short-cue trials, and this may have increased use of rapid perceptual processes.

The current results demonstrate that early perceptual processes are malleable, and can be shaped by our knowledge and experience related to reward. In effect, the perceptual system modulates to enhance rapid processing of high-reward information. This influence of reward on perception may be implicated in previous demonstrations of reward modulation of cognitive functions. For example, previous research shows that high-reward-signalling stimuli are more likely than low-reward stimuli to capture visual attention in a rapid and automatic way (Anderson, Laurent, & Yantis, 2011; Le Pelley et al., 2016; Le Pelley et al., 2015; Le Pelley, Seabrooke, Kennedy, Pearson, & Most, 2017), indicating that reward influences salience on an attentional priority map (Belopolsky, 2015; Failing & Theeuwes, 2018; Pearson et al., 2016). The effect of reward on perception shown in the current study may contribute to this reward-modulated attention: if high-reward stimuli are encoded more rapidly, then they can exert an earlier influence on activity on the priority map, which may drive more rapid capture of attention. Thus, in situations involving multiple stimuli competing for cognitive resources, reward-modulation of perception may have long-lasting effects.

In addition to its theoretical significance, the idea of perceptual enhancement for reward-related information may have clinical implications. For example, drugs of abuse produce potential neural reward signals (Berridge, Robinson, & Aldridge, 2009; Hyman, 2005; Robinson & Berridge, 2001), and recent work suggests that addictive behaviours (and impulsive behaviours more generally) may be associated with individual differences in reward-related attentional biases (Albertella, Le Pelley, et al., 2019; Albertella, Watson, Yücel, & Le Pelley, 2019; Anderson, Faulkner, Rilee, Yantis, & Marvel, 2013; Colaizzi et al., 2020). The current findings suggest that reward can exert even earlier influences on information processing, and raise the possibility of reward-related perceptual differences that are associated with addictive behaviours. Future studies could test this hypothesis by comparing the degree of reward-modulation of perception between drug users and control groups.

In conclusion, the present study provides the first behavioural evidence for a rapid, reward-related modulation of visual perception. Our findings show that reward is fundamentally implicated in neural information processing, exerting an influence that can occur early and without conscious awareness. More generally, these findings provide clear evidence for the *cognitive penetrability* of perception (Marchi & Newen, 2015; D. Stokes, 2013) by demonstrating that the ‘high-level’ beliefs and desires implicated in reward knowledge can influence early, rapid, and unconscious aspects of perception, and raise the intriguing possibility that dysfunction in this relationship may play a role in addictive and impulsive behaviour.

Author Contributions

All authors contributed to the conceptualisation and design of the study. P.X.C programmed the experiment, performed data collection and data analyses, and drafted the manuscript. A.N.R provided critical comments to the final draft. M.L.P provided critical revisions to all drafts and supervised the research.

1 **Acknowledgements**

2 We thank Peter Humburg for helpful advice regarding statistical analyses. This research was
3 supported by Australian Research Council grants DP200101314 to M.L.P and DP170101780 to
4 A.N.R.

5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

Methods

Participants

A total of 68 participants (23 males, age $M = 20.72$, $SEM = 0.37$) participated in exchange for course credit or AU\$20. All participants reported normal or corrected-to-normal vision. We removed 9 participants due to their low accuracy ($<60\%$) in the long-cue condition. The final sample comprised 59 participants (Experiment 1: $n = 30$; Experiment 2: $n = 29$). For both experiments, we used pilot data to determine the sample size sufficient to reach $>80\%$ power. All participants received an additional monetary reward based on their performance ($M = AU\$4.92$, $SEM = AU\$0.15$). This study was approved by the UNSW Sydney Human Research Ethics Advisory Panel (Psychology). Experiment scripts and raw data relating to this study are publicly available via the Open Science Framework: <https://osf.io/9vuj6/>.

Apparatus

Participants were seated ~ 60 cm from a 23-inch monitor (resolution: 1980×1080 ; refresh rate: 120Hz). Stimuli were presented using MATLAB with Psychtoolbox-3 extensions (Kleiner, Brainard, & Pelli, 2007), and participants made responses via the keyboard.

Stimuli

The cue and test stimuli (Figure 1a) were Gabor gratings with spatial frequency of 0.02, 0.05, or 0.08 cycles/pixel (c/p), centrally presented on a mid-grey background (RGB value: [128, 128, 128]). The mask was a plaid comprising two overlaid gratings (spatial frequency 0.05 c/p) oriented at 45° and 135° from vertical. Michelson contrast was 0.1 for both the cue and the test grating, and 0.8 for the mask. The cue and test stimuli had diameter subtending 4.9° of visual angle, and the mask had diameter subtending 6.9° of visual angle. The orientation of the cue stimulus ranged from 10° to 160° relative to vertical in steps of 30° . The orientation of the test stimulus was always 30° different from the cue, in either a clockwise or anti-clockwise direction.

Design

Each trial began with a central fixation cross displayed for 500ms, followed immediately by presentation of the cue stimulus for either 17ms (short-cue condition) or 200ms (long-cue). In Experiment 1, the spatial frequency of the cue was either 0.02 or 0.08 c/p. In Experiment 2, the cue had the spatial frequency of 0.05 c/p on all trials. The mask appeared immediately after the cue

stimulus for 100ms. This was followed by a blank delay of 2000ms, after which the test stimulus appeared. The spatial frequency of this test grating was 0.05 c/p in Experiment 1, and could be either 0.02 or 0.08 c/p in Experiment 2. Participants' task was to indicate whether the cue stimulus would have to be rotated clockwise or anti-clockwise to match the orientation of the test stimulus, by pressing the 's' or 'a' key, respectively, using the left hand. The test stimulus remained visible until participants made their orientation response, or until the trial timeout after 10s. Participants were then prompted to rate their subjective awareness of the cue on a 0-3 scale (0: did not see anything; 1: maybe saw the cue; 2: saw the cue but not its orientation; 3: saw the cue and its orientation) by pressing the appropriate key on the numeric keypad, using the right hand. Finally, participants received on-screen feedback for their orientation response. If the response was correct, feedback stated 'Correct' (in green text) and the number of points earned (500 points in high-reward trials, and 1 point in low-reward trials). If the response was incorrect (or the trial timeout with no response), feedback stated 'Wrong' (in red text) with no points earned. Feedback was presented for 500ms. The next trial then began after a blank intertrial interval of 500ms.

For half of participants in each experiment, a cue stimulus (Experiment 1) or test stimulus (Experiment 2) with a spatial frequency of 0.02 c/p signalled that a high reward (500 points) was available for a correct response, and a stimulus with a spatial frequency of 0.08 c/p signalled that a low reward (1 point) was available. For the other half of participants, this assignment was reversed.

There were 240 trials in the main phase of the experiment. This comprised 5 repetitions of each combination of reward magnitude (high vs low), cue duration (short vs long), cue orientation (10°, 40°, 70°, 100°, 130° or 160°), and test stimulus tilt (clockwise vs anti-clockwise). Trials were presented in random order.

Procedure

The experimenter took the participants through initial instructions describing the task. Participants were told that sometimes the cue would be very brief, but they should try to hold this cue in mind even if they could not consciously perceive it. They were also informed that the number of lines in the cue stimulus (Experiment 1) or test stimulus (Experiment 2) indicated the amount of reward available (e.g., 'If there are more lines in the cue, you'll earn 1 point for a correct judgment. If there are fewer lines in the cue, you'll earn 500 points for a correct judgment' - the 'number of lines' in the stimulus corresponds to its spatial frequency). Finally, participants were told that the points they

earned during the task would be converted into cash at the end of the experiment, but were not told the exchange rate.

Each participant performed 24 practice trials before completing 240 trials in the main phase of the experiment. Participants took a self-paced break after every 60 trials. During each break the screen displayed the current total of accumulated points.

Data analysis

We analysed trials from the main phase of the experiment, excluding trials in which no orientation response was made before the test stimulus disappeared after 10s (0.21% of all trials). Within the bound of this 10s timeout limit, this was not a speeded task: participants could take as long as they wanted to make their orientation response. Consequently our analyses focused on response accuracy.

The long-cue condition (200ms cue presentation) should have been relatively straightforward for participants: this condition was included in the task for two reasons: (1) to ensure that participants received regular, clear exposure to the contingencies between spatial frequency and reward; and (2) so that some trials were not very difficult, to maintain motivation. We also used the long-cue condition to define an exclusion criterion: participants scoring below 60% accuracy in this easy condition were removed from analyses (four participants in Experiment 1, five in Experiment 2). The accuracy was high for the long-cue condition in both experiments (Experiment 1: high-reward: $M = 87.43\%$, $SD = 11.44\%$; low-reward: $M = 87.65\%$, $SD = 9.35\%$; Experiment 2: high-reward: $M = 87.12\%$, $SD = 12.23\%$; low-reward: $M = 89.85\%$, $SD = 10.34\%$). Subsequently, our analyses focused on the short-cue (17ms presentation) condition, because in this condition, rapid perceptual processing (the focus of the current research) is critical for accurate response (Dehaene & Changeux, 2011). As expected, performance was generally poorer in the short-cue condition (Experiment 1: high-reward: $M = 63.98\%$, $SD = 14.18\%$; low-reward: $M = 58.80\%$, $SD = 12.98\%$; Experiment 2: high-reward: $M = 57.62\%$, $SD = 11.10\%$; low-reward: $M = 58.74\%$, $SD = 12.25\%$) relative to the long-cue condition. In both experiments, we used t-tests to compare overall accuracy in the short-cue condition between high-reward and low-reward trials, and also compared each of these values to chance performance (50% correct). We then analysed accuracy in high- and low-reward trials as a function of participants' self-reported awareness of the cue on each trial. For this analysis, we divided trials into two types: those in which participants indicated no awareness of the

cue (awareness rating of 0), and those in which participants indicated some awareness of the cue (combined data from trials with awareness rating of 1, 2 or 3). We excluded participants from this analysis who had fewer than 10 trials for a given awareness level to ensure reliable estimate of performance. In both experiments, performance was generally poorer for no-awareness trials (Experiment 1: high-reward: $M = 60.77\%$, $SD = 11.20\%$; low-reward: $M = 51.20\%$, $SD = 11.16\%$; Experiment 2: high-reward: $M = 48.80\%$, $SD = 12.08\%$; low-reward: $M = 50.34\%$, $SD = 15.00\%$) relative to some-awareness trials (Experiment 1: high-reward: $M = 64.63\%$, $SD = 16.99\%$; low-reward: $M = 64.18\%$, $SD = 15.95\%$; Experiment 2: high-reward: $M = 61.74\%$, $SD = 16.05\%$; low-reward: $M = 61.74\%$, $SD = 17.12\%$). In Supplementary Materials we present results of a finer-grained analysis examining accuracy at each awareness level separately.

Unless otherwise stated, analyses were two-tailed. Bayes Factors (BF_{10}) were calculated for nonsignificant results ($p > 0.05$) of t-tests to distinguish between insufficient sensitivity and true evidence for the null (Dienes, 2014; Wagenmakers, 2007). As recommended in the literature (Jeffreys, 1961), we set the scale for the Cauchy prior as 0.707, and interpretation of Bayes Factors followed Jeffreys (Rouder, Speckman, Sun, Morey, & Iverson, 2009).

References

- Albertella, L., Le Pelley, M. E., Chamberlain, S. R., Westbrook, F., Fontenelle, L. F., Segrave, R., . . . Yücel, M. (2019). Reward-related attentional capture is associated with severity of addictive and obsessive-compulsive behaviors. *Psychology of Addictive Behaviors*, 33, 495-502. doi:http://dx.doi.org/10.1037/adb0000484
- Albertella, L., Watson, P., Yücel, M., & Le Pelley, M. E. (2019). Persistence of value-modulated attentional capture is associated with risky alcohol use. *Addictive Behaviors Reports*, 10.
- Anderson, B. A., Faulkner, M. L., Rilee, J. J., Yantis, S., & Marvel, C. L. (2013). Attentional bias for nondrug reward is magnified in addiction. *Experimental and Clinical Psychopharmacology*, 21, 499–506. doi:http://dx.doi.org/10.1037/a0034575c
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011). Value-driven attentional capture. *Proceedings of the National Academy of Sciences*, 108, 10367-10371. doi:10.1073/pnas.1104047108
- Baddeley, A. (1992). Working memory. *Science*, 255, 556-559.
- Baddeley, A. (2000). The episodic buffer: a new component of working memory? *Trends in Cognitive Sciences*, 4, 417-423. doi:10.1016/s1364-6613(00)01538-2
- Belopolsky, A. V. (2015). Common Priority Map for Selection History, Reward and Emotion in the Oculomotor System. *Perception*, 44, 920-933. doi:10.1177/0301006615596866
- Berridge, K. C., Robinson, T. E., & Aldridge, J. W. (2009). Dissecting components of reward: 'liking', 'wanting', and learning. *Curr Opin Pharmacol*, 9, 65-73. doi:10.1016/j.coph.2008.12.014
- Bijleveld, E., Custers, R., & Aarts, H. (2009). The unconscious eye opener: Pupil dilation reveals strategic recruitment of resources upon presentation of subliminal reward cues. *Psychological Science*, 20(11), 1313-1315.
- Bourgeois, A., Chelazzi, L., & Vuilleumier, P. (2016). How motivation and reward learning modulate selective attention. In *Progress in brain research* (Vol. 229, pp. 325-342): Elsevier.
- Capa, R. L., Bouquet, C. A., Dreher, J.-C., & Dufour, A. (2013). Long-lasting effects of performance-contingent unconscious and conscious reward incentives during cued task-switching. *Cortex*, 49(7), 1943-1954.
- Colaizzi, J. M., Flagel, S. B., Joyner, M. A., Gearhardt, A. N., Stewart, J. L., & Paulus, M. P. (2020). Mapping sign-tracking and goal-tracking onto human behaviors. *Neuroscience & Biobehavioral Reviews*, 111, 84-94. doi:10.1016/j.neubiorev.2020.01.018
- Dehaene, S., & Changeux, J.-P. (2011). Experimental and theoretical approaches to conscious processing. *Neuron*, 70(2), 200-227.

Dehaene, S., Lau, H., & Kouider, S. (2017). What is consciousness, and could machines have it? *Science*, 358(6362), 486-492.

Della Libera, C., & Chelazzi, L. (2009). Learning to attend and to ignore is a matter of gains and losses. *Psychological Science*, 20(6), 778-784.

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontier in Psychology*, 5, 1-17.

Engelmann, J. B., Damaraju, E., Padmala, S., & Pessoa, L. (2009). Combined effects of attention and motivation on visual task performance: transient and sustained motivational effects. *Frontiers in Human Neuroscience*, 3, 4.

Failing, M., & Theeuwes, J. (2018). Selection history: How reward modulates selectivity of visual attention. *Psychonomic Bulletin & Review*, 25, 514-538. doi:<https://doi.org/10.3758/s13423-017-1380-y>

Field, M., Munafò, M. R., & Franken, I. H. (2009). A meta-analytic investigation of the relationship between attentional bias and subjective craving in substance abuse. *Psychological Bulletin*, 135, 589 – 607. doi:<http://dx.doi.org/10.1037/a0015843>

Gottfried, J. A., O'Doherty, J., & Dolan, R. J. (2003). Encoding predictive reward value in human amygdala and orbitofrontal cortex. *Science*, 301, 1104-1107.

Hickey, C., Chelazzi, L., & Theeuwes, J. (2010). Reward changes salience in human vision via the anterior cingulate. *Journal of Neuroscience*, 30, 11096-11103. doi:10.1523/JNEUROSCI.1026-10.2010

Hyman, S. E. (2005). Addiction: a disease of learning and memory. *Am J Psychiatry*, 162, 1414-1422. doi:10.1176/appi.ajp.162.8.1414

Jeffreys, H. (1961). *The Theory of Probability*. Oxford, England: Oxford University Press.

King, J.-R., Pescetelli, N., & Dehaene, S. (2016). Brain Mechanisms Underlying the Brief Maintenance of Seen and Unseen Sensory Information. *Neuron*, 92, 1122-1134. doi:<http://dx.doi.org/10.1016/j.neuron.2016.10.051>

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception*, 36, 14-14.

Le Pelley, M. E., Mitchell, C. J., Beesley, T., George, D. N., & Wills, A. J. (2016). Attention and Associative Learning in Humans: An Integrative Review. *Psychological Bulletin*, 142, 1111-1140. doi:<http://dx.doi.org/10.1037/bul0000064>

Le Pelley, M. E., Pearson, D., Griffiths, O., & Beesley, T. (2015). When goals conflict with values: Counterproductive attentional and oculomotor capture by reward-related stimuli. *Journal of Experimental Psychology: General*, 144, 158–171.

- 1 Le Pelley, M. E., Seabrooke, T., Kennedy, B. L., Pearson, D., & Most, S. B. (2017). Miss it and
2 miss out: Counterproductive nonspatial attentional capture by task-irrelevant, value-related stimuli.
3 *Attention Perception & Psychophysics*, 79, 1628-1642. doi:10.3758/s13414-017-1346-1
- 4 Marchi, F., & Newen, A. (2015). Cognitive penetrability and emotion recognition in human facial
5 expressions. *Frontiers in Psychology*, 6, 828. doi:10.3389/fpsyg.2015.00828
- 6 Maunsell, J. H. (2004). Neuronal representations of cognitive state: reward or attention? *Trends in*
7 *Cognitive Sciences*, 8, 261-265. doi:10.1016/j.tics.2004.04.003
- 8 McFadyen, J., Dolan, R. J., & Garrido, M. I. (2020). The influence of subcortical shortcuts on
9 disordered sensory and cognitive processing. *Nature Reviews Neuroscience*, 21, 264-276.
10 doi:10.1038/s41583-020-0287-1
- 11 Pearson, D., Osborn, R., Whitford, T. J., Failing, M., Theeuwes, J., & Le Pelley, M. E. (2016).
12 Value-modulated oculomotor capture by task-irrelevant stimuli is a consequence of early
13 competition on the saccade map. *Attention, Perception, & Psychophysics*, 78, 2226-2240.
- 14 Pessiglione, M., Schmidt, L., Draganski, B., Kalisch, R., Lau, H., Dolan, R. J., & Frith, C. D.
15 (2007). How the brain translates money into force: a neuroimaging study of subliminal motivation.
16 *Science*, 316(5826), 904-906.
- 17 Pessiglione, M., Schmidt, L., Palminteri, S., & Frith, C. D. (2011). Reward processing and
18 conscious awareness. *Decision making, affect, and learning*, 329-348.
- 19 Pessoa, L., & Engelmann, J. B. (2010). Embedding reward signals into perception and cognition.
20 *Frontiers in Neuroscience*, 4, 1-8. doi:10.3389/fnins.2010.00017
- 21 Robbins, T. W., Gillan, C. M., Smith, D. G., de Wit, S., & Ersche, K. D. (2012). Neurocognitive
22 endophenotypes of impulsivity and compulsivity: towards dimensional psychiatry. *Trends in*
23 *Cognitive Sciences*, 16. doi:10.1016/j.tics.2011.11.009
- 24 Robinson, T. E., & Berridge, K. C. (2001). Incentive-sensitization and addiction. *Addiction*, 96,
25 103-114. doi:10.1046/j.1360-0443.2001.9611038.x
- 26 Rouder, J. N., Speckman, P. L., Sun, D. C., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for
27 accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review*, 16, 225-237.
28 doi:10.3758/Pbr.16.2.225
- 29 Seitz, A. R., Kim, D., & Watanabe, T. (2009). Rewards evoke learning of unconsciously processed
30 visual stimuli in adult humans. *Neuron*, 61(5), 700-707. doi:10.1016/j.neuron.2009.01.016
- 31 Serences, J. T. (2008). Value-based modulations in human visual cortex. *Neuron*, 60, 1169-1181.
32 doi:10.1016/j.neuron.2008.10.051
- 33

Serences, J. T., & Saproo, S. (2010). Population response profiles in early visual cortex are biased in favor of more valuable stimuli. *Journal of Neurophysiology*, 104, 76-87. doi:10.1152/jn.01090.2009

Shuler, M. G., & Bear, M. F. (2006). Reward timing in the primary visual cortex. *Science*, 311(5767), 1606-1609.

Soto, D., & Silvanto, J. (2014). Reappraising the relationship between working memory and conscious awareness. *Trends in Cognitive Sciences*, 18, 520-525.

Soto., D., Mäntylä., T., & Silvanto., J. (2011). Working memory without consciousness. *Current Biology*, 21, R912-R913.

Stănişor, L., van der Togt, C., Pennartz, C. M., & Roelfsema, P. R. (2013). A unified selection signal for attention and reward in primary visual cortex. *Proceedings of the National Academy of Sciences*, 110(22), 9136-9141.

Stankevich, B. A., & Geng, J. J. (2015). The modulation of reward priority by top-down knowledge. *Visual Cognition*, 23, 206-228.

Stokes, D. (2013). Cognitive penetrability of perception. *Philosophy Compass*, 8, 646-663. doi:doi:10.1111/phc3.12043

Stokes, M. G., Wolff, M. J., & Spaak, E. (2015). Decoding Rich Spatial Information with High Temporal Resolution. *Trends in Cognitive Sciences*, 19, 636-638. doi:10.1016/j.tics.2015.08.016

Wagenmakers, E. J. (2007). A practical solution to the pervasive problems of p values. *Psychonomic Bulletin & Review*, 14, 779-804. Retrieved from <https://www.ncbi.nlm.nih.gov/pubmed/18087943>

Yi, D. J., Woodman, G. F., Widders, D., Marois, R., & Chun, M. M. (2004). Neural fate of ignored stimuli: dissociable effects of perceptual and working memory load. *Nature Neuroscience*, 7, 992-996. doi:10.1038/nn1294

Zedelius, C. M., Veling, H., Custers, R., Bijleveld, E., Chiew, K. S., & Aarts, H. (2014). A new perspective on human reward research: How consciously and unconsciously perceived reward information influences performance. *Cognitive, Affective, & Behavioral Neuroscience*, 14(2), 493-508.

Ziauddeen, H., Subramaniam, N., Gaillard, R., Burke, L., Farooqi, I., & Fletcher, P. (2012). Food images engage subliminal motivation to seek food. *International Journal of Obesity*, 36(9), 1245.