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Dynamic interplay between reward and voluntary attention determines stimulus processing in the visual cortex

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Abstract

Reward enhances stimulus processing in the visual cortex, but the mechanisms through which this effect occurs remain unclear. Reward prospect can both increase the deployment of voluntary attention, and increase the salience of previously neutral stimuli. In this study we orthogonally manipulated these two factors while human participants performed a global motion detection task. We recorded steady-state visual evoked potentials (SSVEPs) to simultaneously measure the processing of attended and unattended stimuli linked to different reward probabilities, as they compete for attentional resources. The processing of the high rewarded feature was enhanced independently of voluntary attention, but this gain diminished once rewards were no longer available. Neither the voluntary attention, nor the salience account alone can fully explain these results. Instead, we propose how these two accounts can to be integrated to allow for the flexible balance between reward-driven increase in salience and voluntary attention.

Introduction

30   Maximizing rewards and avoiding punishments are one of the main determinants of human

32 behavior. In order to increase reward probability, reward-related information needs to be

33 prioritized. Selective attention is crucial for adaptive behavior as it facilitates processing of relevant

34 and suppression of irrelevant information in our environment (Chun, Golomb, & Turk-Browne,

35 2011; Desimone & Duncan, 1995). This process depends on our current goals (e.g., searching for

36 our keys) and the physical salience of stimuli (e.g., a loud noise; Corbetta & Shulman, 2002;

37 Posner, 1980; Theeuwes, 2010). Recent research has indicated that motivation can influence

38 selective attention by impacting both of these factors. Reward expectation can enhance voluntary

39 selective attention, and reward associations can increase the salience of previously neutral stimuli.

40 In most situations, attention is guided by the combination of both voluntary allocation of attention

41 and reward history of stimuli (Awh, Belopolsky, & Theeuwes, 2012). For example, while we are

42 searching for keys (goal-relevant target) our attention can be captured by a cake (goal-irrelevant

43 distractor). These two ways in which rewards influence selective attention have been commonly

44 studied in isolation and the neural mechanisms through which they jointly guide attention remain

45 unclear. Specifically, it remains unclear how voluntary selective attention and reward history

46 interact to determine the processing of goal-relevant and irrelevant stimuli in the visual cortex.

47   Voluntary selective attention is thought to be enhanced when individuals anticipate that

48 they can earn rewards for good task-performance (Botvinick & Braver, 2015; Krebs & Woldorff,

49 2017; Pessoa, 2015). A number of fMRI and EEG studies found reward-based enhancements in

50 preparation for upcoming target stimuli driven by enhanced activity in frontoparietal regions

51 involved in attentional control (Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Pessoa &

52 Engelmann, 2010; Schevernels, Krebs, Santens, Woldorff, & Boehler, 2014) and by enhanced task-

53   set representations in these regions (Etzel, Cole, Zacks, Kay, & Braver, 2016; Wisniewski,

54   Reverberi, Momennejad, Kahnt, & Haynes, 2015). While these studies suggest that reward

55   influences attentional control via modulations in the frontoparietal network, it remains unclear how

56   such modulations translate to affect the processing of attended and unattended stimuli in visual

57   cortex.

58   Within a largely independent research line, a set of studies has focused on the processing

59   of stimuli associated with earning rewards. These studies have demonstrated that stimuli currently

60   or previously associated with rewards capture attention in an automatic fashion, and even in cases

61   when this conflicts with the current goals (Anderson, 2016; Awh, Belopolsky, & Theeuwes, 2012;

62   Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Failing & Theeuwes, 2017). Behavioral

63   studies have demonstrated that stimuli predictive of rewards capture attention, and that they can do

64   so in subsequent trials when rewards are no longer present (Anderson, Laurent, & Yantis, 2011;

65   Della Libera & Chelazzi, 2009; Failing & Theeuwes, 2014). At the neural level it has been shown

66   that stimuli related to rewards receive increased sensory processing (Serences, 2008). Studies

67   focusing specifically on attention have shown that attentional capture by rewarding stimuli can be

68   related to changes in the early processing of such stimuli in the visual cortex (i.e., increase in the

69   P1 component; Donohue et al., 2016; Hickey, Chelazzi, & Theeuwes, 2010; Luque et al., 2017;

70   MacLean & Giesbrecht, 2015). However, other studies have not found evidence for such early

71   modulations in the visual cortex, and instead reported changes at later stages of stimulus processing

72   (increased N2pc component and improved decoding in later processing stages; Qi, Zeng, Ding, &

73   Li, 2013; Tankelevitch, Spaak, Rushworth, & Stokes, 2019). One fMRI study (Hickey & Peelen,

74   2015) provided evidence for the simultaneous enhancement in representation of reward-related

75   stimuli and suppression of stimuli devoid of a specific motivational value. More specifically, using

76   a multivoxel pattern analysis and decoding technique, these authors found a gain increase in object-

77   selective visual cortex for stimuli paired with rewards, while those not associated with this

78   incentive were suppressed.

79   Importantly, the effects of reward history and voluntary attention are often difficult to

80   dissociate, and they are commonly confounded in cognitive tasks (Maunsell, 2004). Thus the open

81   question is whether the reward-related changes in stimulus processing in visual cortex occur as a

82   consequence of voluntary selective attention, changes in stimulus salience, or a combination of

83   both. One option (the *voluntary selective attention view*) is that rewards influence the processing

84   of stimuli by increasing the amount of voluntary attention deployed toward these stimuli. This

85   hypothesis can be derived from the models which are focused on the role of motivation in the

86   allocation of attention and cognitive control (Brown & Alexander, 2017; Holroyd & McClure,

87   2015; Shenhav, Botvinick, & Cohen, 2013; Verguts, Vassena, & Silvetti, 2015). These models

88   propose that the amount of attention allocated toward stimuli is dependent on the amount of rewards

89   which can be earned by doing so. Another possibility (*the salience view*) is that rewards increase

90   the salience of stimuli, and thus capture attention automatically, independently of voluntary

91   attention. This view can be derived from theoretical models focused on the role of reward history

92   in guiding selective attention (Anderson, 2016; Awh et al., 2012; Chelazzi et al., 2013; Failing &

93   Theeuwes, 2017). These models propose that the processing of stimuli related to high rewards is

94   facilitated, while the processing of other stimuli is suppressed, and that this effect is long lasting,

95   even when rewards are no longer available.

96   In this study, we orthogonally manipulated voluntary attention and reward probability in

97   order to test the predictions of these models within a single paradigm. To this end, participants

98   performed a continuous global motion discrimination task (Andersen, Muller, & Hillyard, 2009;

99   Andersen & Müller, 2010). On each trial, two superimposed random dot kinematograms (RDKs)

100   of different color (red and blue), were presented concurrently and participants were cued on a trial-

101   by-trial basis to attend to one of them. Thus, these two RDKs served as goal-relevant (attended)

102   and goal-irrelevant (unattended) stimuli, respectively. Critically, after a baseline period used as

103   control condition, these two colors were systematically associated with a low or high probability

104   of earning a reward in a training phase. We subsequently examined the influence of the previous

105   reward history in the test phase in which rewards were no longer available. The two RDKs flickered

106   at different frequencies, thereby driving separate steady-state visual evoked potentials (SSVEPs).

107   SSVEPs offer the unique advantage of simultaneously tracking the processing of multiple stimuli

108   as the specific oscillatory response of each stimulus can be extracted (frequency tagging), and the

109   two resulting signals can be compared to each other (Andersen & Müller, 2010; Kashiwase,

110   Matsumiya, Kuriki, & Shioiri, 2012; Müller, Teder-Sälejärvi, & Hillyard, 1998). Voluntary

111   attention is known to increase SSVEP amplitudes of attended stimuli (Morgan, Hansen, & Hillyard,

112   1996). Further, SSVEP amplitudes are highly sensitive to changes in the physical salience of

113   stimuli and are increased for more salient stimuli (Andersen, Muller, & Martinovic, 2012). Hence,

114   analyzing SSVEPs in this design provided us with the ability to simultaneously track the visual

115   processing of attended and unattended stimuli related to high or low rewards respectively. This

116   design thus enabled us to dissociate the effects of voluntary attention and reward, which are often

117   difficult to distinguish (Maunsell, 2004).

118   We tested predictions arising from the theoretical models developed to account for the

119   effects of rewards on cognitive control (Brown & Alexander, 2017; Holroyd & McClure, 2015;

120   Shenhav et al., 2013; Verguts et al., 2015) and the effects of reward history on attention (Anderson,

121   2016; Awh et al., 2012; Chelazzi et al., 2013; Failing & Theeuwes, 2017) respectively. The first

122 class of models predict that reward influences sensory processing through voluntary attention

123 (Figure 1A), and the second class of models predict that rewards directly influence the salience of

124 stimuli (Figure 1B). Both groups of models predict behavioral improvements and enhanced

125 processing (higher SSVEP amplitudes) of the stimuli related to high rewards. However, the

126 salience view predicts that the processing of the high reward stimuli will be enhanced irrespective

127 of voluntary attention, while the voluntary attention view predicts that the processing of the high

128 reward stimuli will be enhanced only when they are attended. The salience view also predicts the

129 suppressed processing of the low reward stimuli, while the voluntary attention view predicts that

130 the processing of these stimuli will be suppressed only when they are not attended. Finally, the

131 salience view predicts that these effects will persist when rewards are no longer available (test

132 phase), while the voluntary attention view predicts that the processing of both high and low reward

133 stimuli will retreat to baseline levels.

A

Reward enhances voluntary attention

High reward

Low reward

B

Reward enhances salience

High reward

Low reward

Baseline   Training   Test

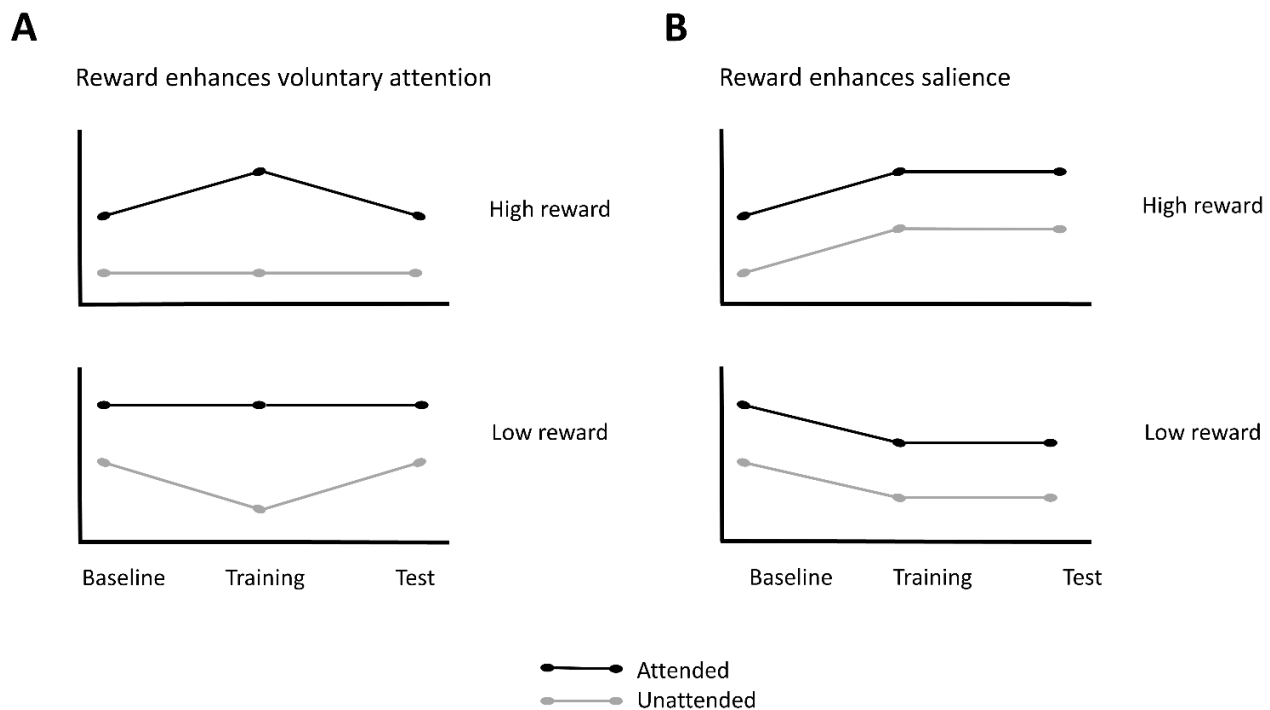Baseline   Training   Test

●———● Attended
●———● Unattended

Figure 1. Predictions from the salience and voluntary selective attention views. A. If rewards influence the processing of stimuli through changes in voluntary attention, the processing of the high reward stimulus will be enhanced when it is attended, while the processing of the low reward stimulus will be suppressed when it is unattended (training phase). The processing of the stimuli related to high and low rewards will retreat back to baseline once the rewards are no longer available (test phase). **B.** If rewards increase salience of a stimulus independently of voluntary attention, the processing of the high reward stimulus will be enhanced and the processing of the low reward stimulus will be suppressed in both the attended and unattended condition (training phases). Further, this effect will persist even when rewards are no longer available (test phase).

<div style="text-align:center">

Methods

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135 **Participants**

136   We tested 48 participants with normal or corrected-to-normal vision and no history of

137 psychiatric or neurological disorders. Four participants were excluded due to technical problems

138 during EEG recording and one person was excluded due to noisy EEG data. Thus, the final data

139 set consisted of 43 participants (39 females, 14 males; median age = 22). Participants received a

140 fixed payoff of 20 €, plus up to 6 € depending on task performance (on average 25.5 €). The study

141 was approved by the ethics committee of Ghent University.

142   **Stimuli and task**

143   We used the coherent motion detection task (Andersen & Müller, 2010; *Figure 1A*), in which

144   participants were presented with two overlapping circular RDKs of isoluminant colors (red and

145   blue) on a grey background. Viewing distance was fixed with a chinrest at 55 cm from the 21-inch

146   CRT screen (resolution of 1024 x 768 pixels, 120 Hz refresh rate). At the beginning of each trial,

147   participants were instructed which of the two RDKs to attend by a verbal audio cue: "red" (241

148   ms) or "blue" (266 ms). The two RDKs had a diameter corresponding to 20.61 degrees of visual

149   angle and consisted of 125 randomly and independently moving dots each (0.52 degrees of visual

150   angle per dot). The two RDKs flickered at different frequencies (10 or 12 Hz). One-third of trials

151   contained one, two, or three coherent motion intervals, occurring with equal probability in the

152   attended and unattended color RDK. During these intervals, dots in one of the RDKs moved with

153   75% coherence in one of four cardinal directions (up, down, left, or right) for 300 ms. Participants

154   had to detect the occurrence of coherent motion in the attended RDK as fast as possible by pressing

155   the space key on a standard AZERTY USB keyboard while ignoring such coherent motion in the

156   unattended RDK. Responses occurring between 200 ms and 1500 ms after coherent motion onset

157   of the attended or unattended dots were counted as hits or false alarms, respectively. Correct

158   responses were followed by a tone (200 ms sine wave of either 800 or 1,200 Hz, counterbalanced

159   across participants). Late or incorrect responses were followed by an error sound (200 ms square

160   wave tone of 400 Hz).

161   The experiment started with 4 practice blocks of 60 trials in each block. After each block,

162   participants received feedback on their performance. After finishing the practice phase, participants

163   completed 12 blocks (each consisting of 50 trials) divided into 3 phases (*baseline*, *training*, and

164   *test*; *Figure 1B*) of 4 blocks each. Each phase contained 100 trials on which participants were

165   instructed to attend to the red color and 100 trials in which they were instructed to attend to the

166   blue color. Out of those 100 trials, 40 trials contained no dot motion, while 60 trials contained one,

167   two, or three dot motions (20 of each). The trials in which participants attended one or the other

168   color, and the trials with different number of motions were intermixed. Participants did the coherent

169   motion detection task, as described above, throughout all three phases (baseline, training, and test).

170   In the training phase, participants could earn additional monetary rewards (up to 6 €) based on their

171   actual performance. They were instructed that one of the colors would be paired with high

172   probability (80%) and the other color with low probability (20%) of earning 10 extra cents for each

173   correct motion detection. The mapping between color and reward probability was counterbalanced

174   across participants. Receipt of the reward was signaled by a new tone that replaced the usual correct

175   tone. If the correct tone was a sine wave of 800 Hz, the reward tone was a sine wave of 1,200 Hz

176   and vice versa. At the end of each of 4 training blocks, participants received feedback regarding

177   both their performance and the amount of reward earned within the block. The third phase (test)

178   was identical to baseline (i.e., no monetary rewards assigned). The entire task lasted for

179   approximately 50 minutes, including short breaks in between blocks. After finishing the task,

180   participants completed two questionnaires aimed at assessing reward sensitivity (BIS-BAS;

181   Franken et al., 2005) and depression levels (BDI-II; Van der Does, 2002). The collection of the

182   questionnaire data is not reported here as it was collected for exploratory purposes in order to form

183   a larger database of neural and self-report measures of reward processing. This experiment was

184   realized using Cogent 2000 developed by the Cogent 2000 team at the FIL and the ICN and Cogent

185   Graphics developed by John Romaya at the LON at the Wellcome Department of Imaging
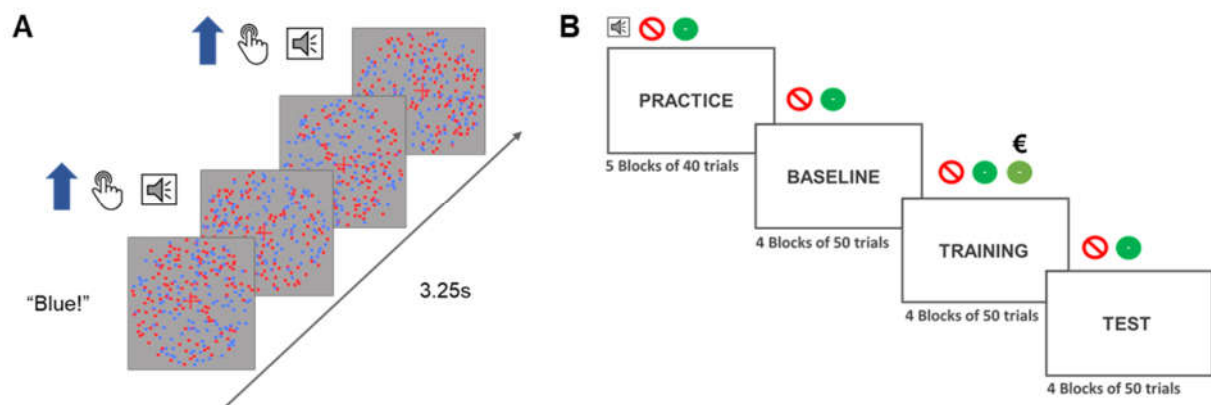
186   Neuroscience.

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Figure 1. Depiction of a single trial and the phases of the experiment. A. Each trial started with an audio cue ("Blue" or "Red") which instructed participants which color to attend to in that trial. The trial lasted for 3.25 seconds during which dots of either of the colors could move from 0 to 3 times in total. If the participants were instructed to attend to the blue dots and the blue dots moved coherently, they had to press the response button. In that case they would hear the auditory feedback signaling the correct detection of the motions. **B.** The experiment started with a practice and a baseline block in which the participants heard an audio cue at the beginning of the trial and two types of feedback sounds (incorrect or correct). In the training block a third sound was introduced to signal that the participants were both correct and received a reward for that response. They would still at times hear the old correct feedback which would signal that they were correct, but not rewarded. The test phase was the same as the baseline phase.

188

EEG recording and pre-processing

189

190   Electroencephalographic activity (EEG) was recorded with an ActiveTwo amplifier (BioSemi,

191   Inc., The Netherlands) at a sampling rate of 512 Hz. Sixty-four Ag/AgCl electrodes were fitted into

192   an elastic cap, following the international 10/10 system (Chatrian, Lettich, & Nelson, 1985). The

193   common mode sense (CMS) active electrode and the driven right leg (DRL) passive electrode were

194   used as reference and ground electrodes, respectively. Additional external electrodes were applied

195   to the left and right mastoids, as well as on the outer canthi of each eye and in the inferior and

196   superior areas of the left orbit (to record horizontal and vertical electrooculogram, EOG).

197   Data pre-processing was performed offline with custom MATLAB scripts and functions

198   included in EEGLAB v14.1.1b (Delorme & Makeig, 2004). After subtracting the mean value of

199   the signal (DC offset), the continuous EEG data were epoched between 0 and 3,250 ms,

200   corresponding to the beginning and end of the trial, respectively. After referencing to *Cz*, FASTER

201   v1.2.3b (Nolan, Whelan, & Reilly, 2010) was used for artifact identification and rejection using

202   the following settings: (i) over the whole normalized EEG signal, channels with variance, mean

203   correlation, and Hurst exponent exceeding $z = \pm 3$ were interpolated via a spherical spline procedure

204   (Perrin, Pernier, Bertrand, & Echallier, 1989); (ii) the mean across channels was computed for each

205   epoch and, if amplitude range, variance, and channel deviation exceeded $z = \pm 3$, the whole epoch

206   was removed; (iii) within each epoch, channels with variance, median gradient, amplitude range,

207   and channel deviation exceeding $z = \pm 3$ were interpolated; (iv) grand-averages with amplitude

208   range, variance, channel deviation, and maximum EOG value exceeding $z = \pm 3$ were removed; (v)

209   epochs containing more than 12 interpolated channels were discarded. Subsequently, automated

210   routines were used to reject all trials with blinks or horizontal eye-movements exceeding 25

211   microvolt. For details, see our commented code at https://osf.io/kjds3/. After pre-processing, the

212   average number of interpolated channels was 3.61 ($SD = 1.23$, range $1 - 6$) and the mean percentage

213   of rejected epochs was 8.77% ($SD = 6.71$, range $0 - 27.78$). After re-referencing to averaged

214   mastoids, trials in each condition were averaged separately for each participant, resulting in the

215   following averages: (i) baseline, red attended; (ii) baseline, blue attended; (iii) training, red

216   attended; (iv) training, blue attended; (v) test, red attended; (vi) test, blue attended.

217   After removing linear trends, SSVEP amplitudes were computed as the absolute of the complex

218   Fourier coefficients of the trial averaged EEG in a time-window from 500 ms (to exclude the

219   typically strong phasic visual evoked response to picture onset) to 3,250 ms after stimulus onset.

220   Electrodes with maximum SSVEP amplitudes were identified by calculating isocontour voltage

221   maps based on grand-averaged data collapsed across all conditions. Based on this, a cluster

222   consisting of the four electrodes Oz, O2, POz, and Iz was chosen for further analysis. SSVEP

223   amplitudes were normalized (rescaled) for each participant and frequency (10 and 12 Hz)

224   separately by dividing amplitudes by the average amplitude of the two conditions in the baseline.

225   **Statistical analyses**

226   Behavioral and EEG data were analyzed using Bayesian multilevel regressions. We fitted and

227   compared multiple models of varying complexity to predict observer sensitivity (d′, i.e.

228   participants' ability to distinguish between target and distractor coherent motion), reaction times

229   for correct responses, and SSVEP amplitudes. For the behavioral data, mean reaction times of

230   correct detections (hits) and sensitivity (d′) were analyzed. Sensitivity index d′ (Macmillan &

231   Creelman, 2004) was calculated with adjustments for extreme values (Hautus, 1995) using the

232   *psycho* R package (for the method see: Pallier, 2002).

233   Each of the fitted models included both constant and varying effects (also known as fixed and

234   random). Participant-specific characteristics are known to affect both behavioral performance (e.g.,

235   response speed) and EEG signal (e.g., skull thickness, skin conductance, hair); therefore, we

236   decided to model this variability by adding varying intercepts in our models. Additionally, the

237   studied effects (i.e., selective attention and reward sensitivity) are known to vary in magnitude over

238   participants, so we opted for including varying slopes in our models[1].

239   Models were fitted in R using the *brms* package (Bürkner, 2016) which employs the

240   probabilistic programming language *Stan* (Carpenter et al., 2016) to implement Markov Chain

241   Monte Carlo (MCMC) algorithms in order to estimate posterior distributions of the parameters of

242   interest (details about the fitted models can be found in the data analysis scripts). Each of the

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[1] Due to the simultaneous estimation of group-level and participant-level parameters, multilevel models display a property called shrinkage. In brief, estimates that strongly deviate from the mean (e.g., a participant performing the task much worse than the average of the total sample) will be pulled toward the group mean (McElreath, 2016). This advantageous property prevents extreme values from having large effects on the results.

243   models were fitted using weakly informative prior distributions (described below) and Gaussian

244   likelihood. Four MCMC simulations ("chains") with 6,000 iterations (3,000 warmup) and no

245   thinning were run to estimate parameters in each of the fitted models. Further analyses were done

246   following the recommendations for Bayesian multilevel modeling using *brms* (Bürkner, 2016,

247   2017; Nalborczyk & Bürkner, 2019). We confirmed that all models converged by examining trace

248   plots, autocorrelation, and variance between chains (Gelman-Rubin statistic; Gelman & Rubin,

249   1992). We compared models based on their fit to the actual data using the Bayesian R^2 (Gelman,

250   Goodrich, Gabry, & Ali, 2017), and their out-of-sample predictive performance using the Widely

251   Applicable Information Criterion (WAIC; Watanabe, 2010). The best model was selected and the

252   posterior distributions of conditions of interest were examined. Differences between conditions

253   were assessed by computing the mean and the 95% highest density interval (HDI) of the difference

254   between posterior distributions of the respective conditions (Kruschke, 2014). Additionally, we

255   calculated the evidence ratios (ERs) for our hypotheses as the ratios between the percentage of

256   posterior samples on each side of the zero of a difference distribution between two conditions. ERs

257   can be interpreted as the probability of a hypothesis (e.g. "Condition A is larger than condition B")

258   against its alternative ("Condition B is larger than condition A").

259   Behavioral data
260

261   We fitted three models to predict sensitivity (d′) and reaction times (in milliseconds) separately

262   (*Figure 2* for the raw data and *Supplementary Table 1* for the descriptive statistics). First, we fitted

263   the *Null model* with a constant and varying intercepts across participants. This model was fitted in

264   order to explore the possibility that the data would be best explained by simple random variation

265   between participants. To investigate the effect of reward phase (baseline, training, test), we fitted

266   the *Reward phase* model which included only reward phase as the constant predictor, as well as

267   varying intercepts and slopes across participants for this effect. To investigate the possible

268   interaction between reward phase and reward, we fitted the *Reward phase × Reward Probability*

269   model including the intercepts and slopes of these two effects and their interaction as both constant

270   and varying effects. All models had a Gaussian distribution as the prior for the intercept (for

271   sensitivity: centered at 1.8 with a standard deviation of 1; for reaction times: centered at 500 with

272   a standard deviation of 200). The models with slopes also included a Gaussian distribution as prior

273   for the slopes (for sensitivity: centered at 0 with a standard deviation of 2; for reaction times:

274   centered at 0 with a standard deviation of 200). The means for the priors for the intercepts were

275   selected based on the previous study with the same task (Andersen & Müller, 2010). The standard

276   deviations of all of the prior distributions were chosen so that the distributions are very wide and

277   thus only weakly informative. Note that there are two additional models that, although possible to

278   fit, are not plausible in the context of our experiment. Specifically, the model including only the

279   effect of reward probability overlooks the fact that this effect would necessarily be most

280   pronounced in the training phase, thus interacting with the effect of reward phase. The same logic

281   applies to the model with additive effects of reward phase and probability (i.e., these effects could

282   not act independently in our experimental design).

283

284   SSVEP amplitudes
285

286   We fitted seven models to predict the trial-averaged SSVEP amplitudes (in a.u. due to the

287   normalization) across conditions (*Figure 2C, Figure 2D,* and *Supplementary Table 2*). The *Null*

288   *model* included one constant and multiple varying intercepts across participants. The *Attention*

289   *model* included the constant effect of attention; the *Reward Phase model* included the constant

290   effect of reward phase; the *Reward Phase + Attention* model included the additive effects of reward

291   phase and attention; and the *Reward Phase × Attention* model also included the interaction between

292   reward phase and attention. The *Reward probability × Reward phase + Attention* model consisted

293   of the constant effects of reward and phase, their interaction, and the independent effect of

294   attention. The last model was the *Reward probability × Reward phase × Attention* model which

295   included all constant effects and their interaction. All models, except for the *Null model*, included

296   varying intercepts and slopes across participants for all of the constant effects. All models included

297   a Gaussian distribution as the prior for the intercept (centered at 1 with a standard deviation of 1).

298   The mean across both attended and unattended conditions is approximately 1 in this paradigm

299   (Andersen & Müller, 2010), while the normalized amplitudes are in the 0-2 range (the normalized

300   amplitude of 2 for the attended stimulus would equal the physical removal of the unattended

301   stimulus) which is why we opted for the standard deviation of 1 for the prior distributions. In

302   addition, the models with slopes included a Gaussian distribution as the prior for the slopes

303   (centered at 0 with a standard deviation of 1). As was the case for the behavioral data, several

304   models were not fitted because they were not plausible in the context of our experiment (e.g.,

305   models that include both reward phase and probability, but not their interaction, are implausible

306   because reward probability cannot affect the baseline phase).

307   **Results**

308   **Behavioral results**

309   Sensitivity d′
310

311   Of all the tested models, the *Reward phase × Reward probability* model best predicted

312   sensitivity (*Table 1*). The posterior distributions of the interaction model (*Figure 2A* and *Table 2*)

313   revealed that sensitivity improved in the training phase compared to the baseline for both the low

314 reward (M = 0.14; 95% HDI [0.01, 0.27]; ER = 57.82) and the high reward color (M = 0.04; 95%

315 HDI [-0.08, 0.17]; ER = 3.10). This improvement was more pronounced for low compared to high

316 reward (M = 0.10; 95% HDI [-0.08, 0.27]; ER = 6.25). Conversely, there was no evidence for a

317 difference between training and test phases in the low reward condition (M = 0.00; 95% HDI [-

318 0.13, 0.13]; ER = 1.09), and a small reduction in sensitivity in the high reward condition (M = -

319 0.08; 95% HDI [-0.20, 0.05]; ER = 8.52). These results suggest a higher sensitivity for coherent

320 motion detection in the training phase compared to baseline, that was more pronounced for the low

321 relative to the high reward color. There was also very little evidence of a change in sensitivity from

322 the training to the test phase.

Table 1

Mean and standard errors (in parenthesis) of WAIC and Bayesian R^2 for each model predicting sensitivity and reaction times.

Model	WAIC (SE)	Bayesian R^2 (SE)
Sensitivity		
Null	533.3 (26.5)	0.27 (0.05)
Reward phase	541.0 (26.5)	0.27 (0.05)
Reward phase × Reward probability	202.7 (19.1)	0.84 (0.01)
Reaction times		
Null	2,500.2 (31.6)	0.50 (0.04)
Reward phase	2,483.0 (35.3)	0.56 (0.04)
Reward phase × Reward probability	2,322.5 (30.0)	0.82 (0.02)

323

Table 2

Means and 95% HDIs of the posterior distributions of reaction times and sensitivity in each condition.

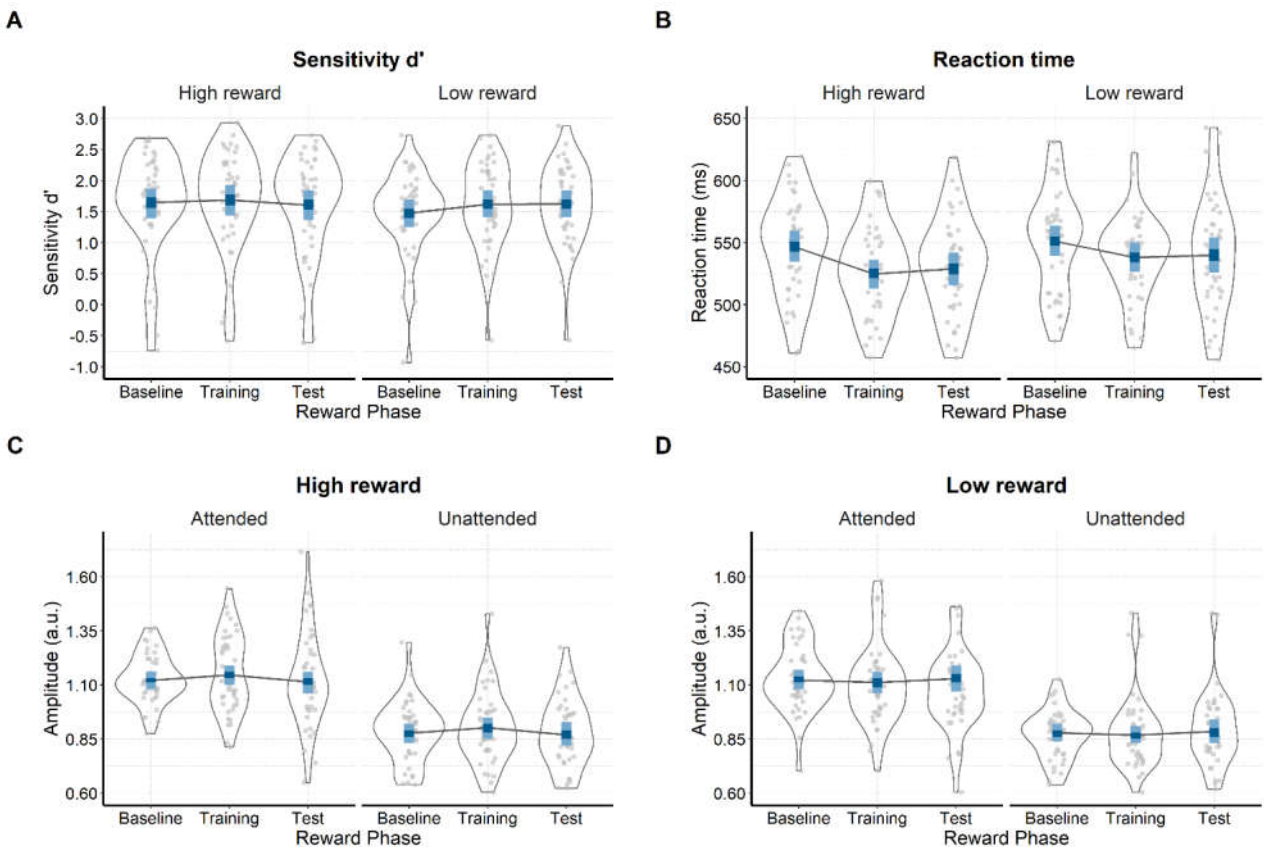| Reward phase	Reward probability	Sensitivity (d′)	Reaction times (milliseconds)
Baseline	High	1.64 [1.39, 1.87]	546.54 [534.33, 559.30]
Baseline	Low	1.48 [1.25, 1.69]	551.13 [539.34, 563.50]
Training	High	1.69 [1.44, 1.93]	524.91 [512.94, 536.30]
Training	Low	1.62 [1.41, 1.84]	537.99 [526.48, 550.32]
Test	High	1.61 [1.36, 1.84]	528.97 [515.90, 541.99]
Test	Low	1.62 [1.41, 1.84]	539.85 [525.63, 554.34]

324

325

Figure 2. Raw and modelled data. Violin plots displaying raw data for each participant (grey dots), separately for each condition. Results from the winning models are presented in blue (dark blue – 50% HDIs and light blue – 95% HDIs). **A.** Sensitivity (d′) **B.** Reaction times (ms) **C.** SSVEP amplitudes (arbitrary units) in response to the color related to high reward on trials in which it is attended or unattended. **D.** SSVEP amplitudes for the color linked to low reward on trials when it was attended or unattended.

326   Reaction times

327   The *Reward phase × Reward probability* model also best predicted the reaction times (*Figure*

328   *2B* and *Table 1*). In the training, compared to the baseline phase, participants were reliably faster

329   in detecting the motions of both the high (M = -21.60; 95% HDI [-29.90, -12.80]; ER > 12,000.,

330   i.e. the whole posterior distribution was below zero thus the ER is larger than the total number of

331   posterior samples) and the low reward colors (M = -13.10; 95% HDI [-21.70, -4.69]; ER = 999).

332   Moreover, this difference between baseline and training was larger for detecting motions of the

333   high relative to low reward color (M = -8.49; 95% HDI [-18.60, 2.06]; ER = 17.18). We found less

334   evidence for changes in reaction times between the training and the test phase. There was a very

335   small increase in the reaction times in the test compared to training phase for the high reward color

336   (M = 4.07; 95% HDI [-4.52, 13.10]; ER = 4.40), and no difference for the low reward (M = 1.87;

337   95% HDI [-6.93, 10.70]; ER = 1.98). These results indicate that participants were faster in detecting

338   coherent motions in the condition in which they could earn rewards (training), and more so for high

339   than low reward color. Also, there was a very small increase in the reaction times for the high

340   reward condition and no difference in the low reward condition when the rewards were no longer

341   available (test). Supplementary analyses carried out to assess possible training effects indicated

342   some evidence for the presence of training effects in sensitivity and scant evidence for such effects

343   in reaction times (*Supplementary materials*).

344   **SSVEP amplitudes**

345   As shown in *Figure 3* SSVEP amplitudes averaged over conditions peaked at central occipital

346   channels (i.e., *Oz*, *POz*, *O2*, *Iz*). Also, the amplitude spectra showed the expected peaks at the
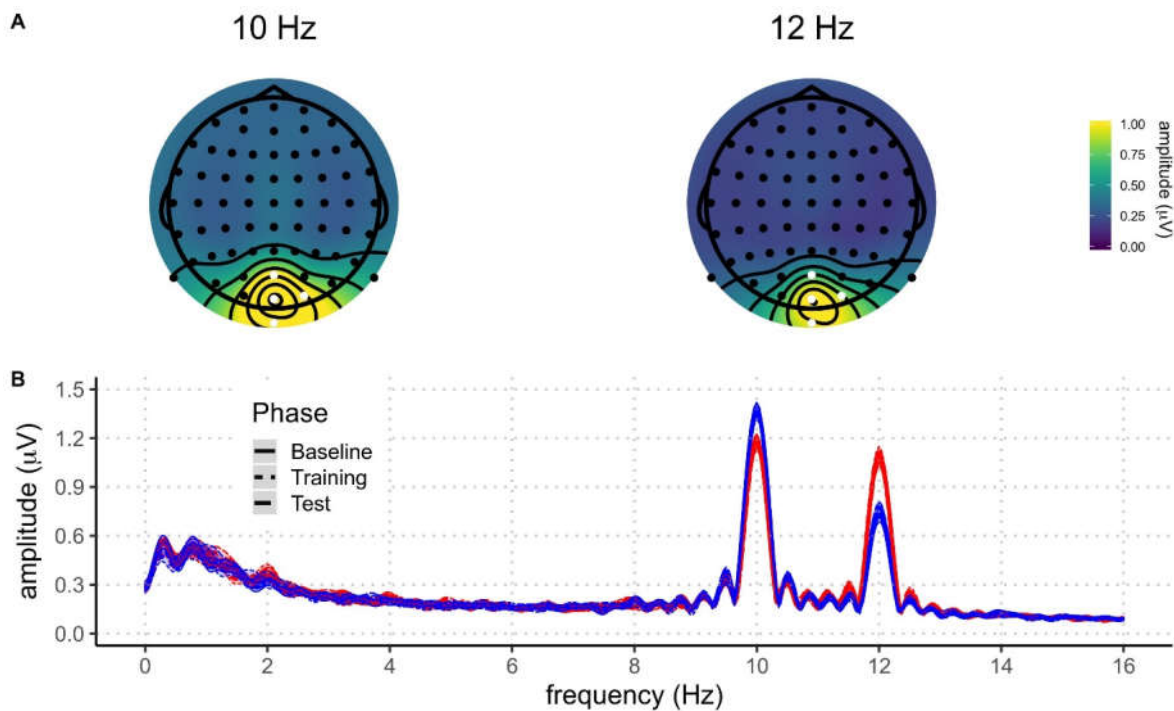
347   frequencies of 10 and 12 Hz.

348

Figure 3. A) Topographies of SSVEP amplitudes, averaged across all participants and conditions, at 10 Hz and 12 Hz. Electrodes selected for the analysis are highlighted in white. **B)** Grand average amplitude spectra (zero-padded to 8 times the length of the data for plotting purpose) derived from EEG signals at best four-electrode cluster plotted for the different experimental conditions (blue: attended; red: unattended; solid: baseline phase; dotted: rewarded phase; dashed: non-rewarded phase). The shaded areas around the means indicate 95% confidence intervals.

349   The *Reward probability × Reward phase + Attention* model best predicted SSVEP amplitudes

350   across conditions (*Table 3*). However, the *Reward probability × Reward phase × Attention* was

351   only slightly worse than the winning model. Here we draw inferences from the winning model, but

352   note that the conclusions do not substantially change when analyzing the model which includes the

353   three-way interaction. The analysis of the posterior distributions of the winning model (*Figure 2*

354   and *Table 3*) revealed a strong effect of voluntary selective attention: in all conditions, SSVEP

355   amplitudes were higher when the eliciting stimulus was attended compared to when it was

356   unattended. In the winning model, this effect did not interact with the other factors in the model,

357   i.e. the magnitude of selective attention was unaffected by reward probability and reward phase.

358   The posterior distribution of the difference between attended and unattended stimuli did not include

359   zero, thus resulting in infinite probability that the attended stimuli would elicit higher SSVEP

360   amplitudes compared to the unattended ones ($M = 0.24$; 95% HDI [0.20, 0.29]; ER > 12,000).

361   These results reveal a very robust effect of voluntary selective attention across all experimental

362   conditions: the SSVEP response was systematically larger when the driving stimulus was attended.

Table 3

Model comparison indices for EEG results

Model	WAIC (SE)	Bayesian R^2 (SE)
Null	-22.3 (56.2)	0.01 (0.01)
Reward phase	-31.8 (55.0)	0.05 (0.01)
Attention	-436.5 (66.4)	0.37 (0.02)
Reward phase + Attention	-464.7 (64.9)	0.40 (0.02)
Reward phase × Attention	-461.3 (65.2)	0.41 (0.02)
Reward probability × Reward phase + Attention	-696.1 (71.9)	0.55 (0.02)
Reward probability × Reward phase × Attention	-690.4 (71.9)	0.55 (0.02)

363

Table 4

Means and 95% HDIs of the posterior distributions of the SSVEP amplitudes for each condition.

Attention	Reward phase	Reward probability	Amplitudes (a.u.)
Attended	Baseline	High	1.12 [1.08, 1.16]
Attended	Baseline	Low	1.12 [1.07, 1.17]
Attended	Training	High	1.15 [1.10, 1.19]
Attended	Training	Low	1.11 [1.07, 1.16]
Attended	Test	High	1.11 [1.06 ,1.17]
Attended	Test	Low	1.13 [1.07, 1.19]
Unattended	Baseline	High	0.88 [0.83, 0.92]
Unattended	Baseline	Low	0.88 [0.84, 0.92]
Unattended	Training	High	0.90 [0.85, 0.95]
Unattended	Training	Low	0.87 [0.82, 0.91]
Unattended	Test	High	0.87 [0.82, 0.92]
Unattended	Test	Low	0.88 [0.83, 0.94]

364

365   The winning model also included the interaction between reward phase and reward probability,

366 but this interaction remained the same for both attended and unattended stimuli. SSVEP amplitudes

367 were higher in the training phase than at baseline for the high reward color ($M = 0.02$; 95% HDI [-

368 0.01, 0.06]; ER = 9.53), both when it was attended and unattended. However, there was no evidence

369 of difference for the change in SSVEP amplitudes from baseline to training for the low reward

370 color ($M = 0.01$; 95% HDI [-0.03, 0.05]; ER = 2.58). Comparing the training to the test phase, the

371 amplitudes of the high reward color were reduced ($M = -0.03$; 95% HDI [-0.07, 0.01]; ER = 13.71),

372 while the amplitudes of the low reward color did not change ($M = -0.02$; 95% HDI [-0.06, 0.02];

373 ER = 3.72). To summarize, visual processing of the high reward color stimulus was enhanced in

374 the phase in which participants could earn monetary rewards and returned to baseline in the

375   subsequent test phase without rewards. Thus, change occurred irrespective of whether that color

376   was attended or not. Finally, visual processing of the low reward color remained constant across

377   the three phases of the experiment.

Discussion

379   In this study we investigated the neural mechanisms through which voluntary selective

380   attention and reward history jointly guide visual processing. We compared the processing of

381   attended and unattended stimuli of different reward probabilities on a continuous global motion

382   discrimination task. Compared to baseline, the introduction of rewards speeded up task

383   performance, especially for the higher reward stimuli, which was accompanied by enhanced

384   processing of these stimuli in the visual cortex (higher SSVEPs). This sensory gain was present

385   both when the high reward stimulus was attended and unattended, thus indicating that rewards

386   influenced visual processing independently of voluntary selective attention. When rewards were

387   no longer available, sensory processing of high reward stimuli returned to baseline levels, but

388   participants were still faster to detect coherent motions of high reward stimuli.

389   The introduction of rewards improved behavioral performance on the task and facilitated

390   the visual processing of stimuli associated with high rewards. This effect on SSVEP amplitudes is

391   likely localized in the V1-V3 areas of the visual cortex, as reported in the previous studies using

392   the same task (Andersen et al., 2009; Andersen & Müller, 2010; Andersen, Hillyard, & Müller,

393   2008). Crucially, this effect was the same both when the high reward stimulus was attended and

394   unattended. Thus, this effect was independent of the effect of voluntary selective attention as

395   reflected in the enhanced processing of the attended compared to unattended stimuli (Andersen &

396   Müller, 2010). This pattern of results suggests that the effect of reward acted independently of

397   visual selective attention. This finding supports the predictions of the models which propose that

398   the effect of reward history on visual processing is independent from voluntary attention

399   (Anderson, 2016; Awh et al., 2012; Chelazzi et al., 2013; Failing & Theeuwes, 2017). Further, this

400   finding can help refine the existing models which are focused on the role of rewards in the

401   allocation of cognitive control. These models (Brown & Alexander, 2017; Holroyd & McClure,

402   2015; Shenhav et al., 2013; Verguts et al., 2015) are largely focused on the activity in the

403   frontroparietal regions, for example the dorsolateral Prefrontal Cortex and the Anterior Cingulate

404   Cortex, which are known to increase their activation in anticipation of rewards (Krebs, Boehler,

405   Roberts, Song, & Woldorff, 2012; Pessoa & Engelmann, 2010; Schevernels, Krebs, Santens,

406   Woldorff, & Boehler, 2014). However, these models are not explicit about their predictions of how

407   the top-down signals from these areas modulate the processing of stimuli at the level of the visual

408   cortex. Our findings suggest that increased rewards act to enhance the processing of the stimuli

409   related to high rewards independently of other top-down voluntary attention effects, which is

410   similar to the way in which physical salience of stimuli acts in the same paradigm we used

411   (Andersen et al., 2012). Interestingly, this is in contrast with the recent finding showing that a

412   flagship cognitive control effect, post-error adjustments, operates through enhancement of

413   voluntary selective attention as measured by SSVEPs in the adapted version of the task used here

414   (Steinhauser & Andersen, 2019). This indicates a possible dissociation between the effects of

415   reward and other cognitive control effects on selective attention. Such dissociation between the

416   cognitive control and reward effects are an important question which should be further addressed

417   both theoretically and empirically.

418   In the test phase, the behavioral data displayed similar patterns as in the training phase.

419   Individuals were faster to detect motions of the dots in color related to high compared to low

420   reward. This finding follows the reward-history effects reported in several paradigms (Anderson,

421   Laurent, & Yantis, 2011; Della Libera & Chelazzi, 2009; Failing & Theeuwes, 2014). However,

422   our SSVEP results show that the visual processing of the high reward stimuli returned to baseline

423   levels, diverging from the behavioral pattern of results. This result indicates that the longer lasting

424   effect of reward history was not mediated by the prolonged gain enhancement in sensory processing

425   as measured by the SSVEPs, contrary to the predictions of the models accounting for the effects of

426   reward history on attention (Anderson, 2016; Awh et al., 2012; Chelazzi et al., 2013; Failing &

427   Theeuwes, 2017). This result is predicted by the models which relate cognitive control and reward,

428   as they predict that the reward-related enhancements should retreat to baseline levels when rewards

429   are no longer available (Brown & Alexander, 2017; Holroyd & McClure, 2015; Shenhav et al.,

430   2013; Verguts et al., 2015). This finding suggest that visual processing can be adapted in a much

431   more flexible way than predicted by the models focused on the reward-history effects on attention.

432   Of note, it is possible that our SSVEP measure captures the more general aspect of feature

433   processing in the visual cortex, while the effects of reward history could be specifically locked to

434   the onset of the rewarded stimulus (Donohue et al., 2016; Hickey et al., 2010; Luque et al., 2017;

435   MacLean & Giesbrecht, 2015). However, there are at least two studies which have not found

436   evidence for the effects of reward history on early visual processing (Qi et al., 2013; Tankelevitch

437   et al., 2019). This leaves open the possibility that the effects of reward history are not necessarily

438   driven purely by gains in sensory processing. One interesting possibility, which should be explored

439   in future studies, is that rewards initially improve performance by enhancing stimulus salience, but

440   later rely on more direct stimulus-response mappings. Finally, it is important to note that our

441   paradigm involves a cue on every trial which induces a direct goal, while this is not the case in

442   most of the studies assessing the influence of reward-history on attention. Further research using

443   SSVEPs in tasks designed to explicitly address the reward-history effects could help disentangle

444   between the possible explanations of our findings.

445   Our paradigm allowed us to simultaneously measure the processing of stimuli linked to

446   both high and low value. Some initial evidence for the suppression of the stimuli linked to low

447   compared to high rewards has been found at the behavioral and neural level (Hickey & Peelen,

448   2015; Padmala & Pessoa, 2011). Suppression of the features linked to low or no rewards has also

449   been proposed as one of the potential mechanisms through which incentives impact attention

450   (Chelazzi et al., 2013; Anderson, 2016; Failing & Theeuwes, 2018). On the contrary, in this study

451   we found no evidence for this proposal. Suppression was neither observed when the low value

452   color was attended, nor when it was unattended. The amount of attention allocated toward this

453   feature remained unchanged throughout the experiment. There are two features of our experiment

454   which could explain this finding. First, in our experiment both colors were related to rewards, but

455   they differed in reward value. For example, the study which showed evidence for the suppression

456   of the non-rewarded feature did so in the context in which suppression occurred for the

457   representations of objects which were never rewarded (Hickey & Peelen, 2015). In our paradigm

458   it could be beneficial for participants not to suppress the low value color because correct responses

459   to the motions of this color would still earn them a reward on 20% of trials. Second, while the

460   attended color changed trial-by-trial in our experiment, the experiment of Hickey and Peelen

461   consisted out of small blocks of 16 trials in which the attended object was always the same (e.g.,

462   searching for a car in a complex picture). When searching for one object or feature across a number

463   of future trials, it is possible that the optimal solution for the cognitive system is to suppress the

464   processing of the other features or objects (i.e., goal-irrelevant stimuli). However, if the attended

465   feature is likely to change on each trial, as in our experiment, the suppression of the low rewarded

466   feature could be maladaptive as it would carry a cost of reconfiguring the control signals on every

467   trial (for a computational implementation of a reconfiguration cost see: Musslick, Shenhav,

468   Botvinick, & Cohen, 2015).

469   The design of this study and the use of the SSVEPs allowed us to independently assess the

470   influence of voluntary attention and reward on sensory processing in the visual cortex. This enabled

471   us to directly compare the magnitudes of the two effects on sensory processing. While both of these

472   factors displayed an effect on visual processing, it is important to note that the effect of voluntary

473   attention on visual processing (30% increase for the attended vs. the unattended stimuli) was an

474   order of magnitude stronger than the effect of reward (3% increase from baseline to training for

475   the high reward stimuli). Thus, even though reward associations can influence processing in

476   opposition to voluntary attention, the magnitude of this effect is very small compared to the effect

477   of voluntary attention. Most theoretical models to date have focused on how top-down and reward-

478   driven attention jointly guide stimulus processing (Awh et al., 2012), but how much each of these

479   processes contribute to stimulus processing still has to be incorporated into the theoretical models.

480   This finding is especially important in the light of recent studies investigating the relevance of

481   reward-driven automatic biases in attention in clinical disorders such as addiction (Anderson, 2016)

482   and depression (Anderson, Leal, Hall, Yassa, & Yantis, 2014). While it is possible that more

483   automatic biases in attention play a role in these disorders, it is also important to focus on the

484   influence of more goal-directed processes which are likely to have a bigger impact on cognition in

485   clinical disorders (Grahek, Shenhav, Musslick, Krebs, & Koster, 2019).

486   In conclusion, in this study we directly assessed how voluntary attention and reward jointly

487   guide attention. Our findings provide a novel insight into the flexible dynamics of visual processing

488   based on these two factors. They demonstrate that rewards can act independently of voluntary

489   attention to enhance sensory processing in the visual cortex. However, sensory processing is

490   flexibly readjusted when rewards are no longer available. This result points to the dynamical

491   interplay between top-down and reward effects in the visual cortex which needs to be accounted

492   for in theoretical models of motivation-cognition interactions. The effect can be flexibly removed

493   as soon as the reward structure in the environment changes.

494   **Supplementary materials**

495   **Means of the raw behavioral and SSVEP data**

Supplementary Table 1

Means and 95% HDIs (in square brackets) of the raw data for sensitivity and reaction times

Reward phase	Value	Sensitivity (d′)	Reaction times (milliseconds)
Baseline	High	1.64 [-0.04, 2.68]	546.59 [485.64, 619.34]
Baseline	Low	1.47 [0.04, 2.30]	551.10 [490.50, 631.36]
Training	High	1.69 [0.29, 2.73]	524.99 [467.12, 599.49]
Training	Low	1.62 [0.46, 2.68]	537.94 [465.32, 584.63]
Test	High	1.60 [-0.20, 2.73]	528.98 [457.08, 599.83]
Test	Low	1.62 [0.74, 2.88]	539.75 [455.80, 623.21]

496

Supplementary Table 2

Means and 95% HDIs of the raw data for the recorded SSVEP amplitudes in each condition

Attention	Reward phase	Value	Amplitudes (a.u.)
Attended	Baseline	High	1.13 [0.92, 1.52]
Attended	Baseline	Low	1.13 [0.86, 1.52]
Attended	Training	High	1.16 [0.80, 1.60]
Attended	Training	Low	1.13 [0.76, 1.71]
Attended	Test	High	1.13 [0.61, 1.61]
Attended	Test	Low	1.13 [0.59, 1.84
Unattended	Baseline	High	0.87 [0.47, 1.17]
Unattended	Baseline	Low	0.87 [0.49, 1.11]
Unattended	Training	High	0.91 [0.54, 1.38]
Unattended	Training	Low	0.89 [0.50, 1.28]
Unattended	Test	High	0.88 [0.48, 1.23]
Unattended	Test	Low	0.91 [0.44, 1.42]

497

Additional analyses to assess possible training effects

499   In order to assess potential training effects on behavioral performance, we split each reward

500   phase into two halves (*Supplementary Figure 1* and *Supplementary Table 3*). If training effects

501   were influencing the behavioral outcome, we could expect performance improvement through

502   baseline and training. To investigate this possibility, we fitted the *Reward phase × Value* model

503   that was identical to the one described in the results section. We then compared behavioral

504   performance between the first and the second part of the baseline phase, and between the second

505   part of baseline and the first part of training phase.

506

Supplementary Table 3

Means and 95% HDIs of the raw data for sensitivity and reaction times across six phases of the experiment

| Reward phase	Value	Sensitivity (d′)	Reaction times (milliseconds)
Baseline1	High	1.48 [-0.36, 2.62]	548.84 [479.43, 613.76]
Baseline1	Low	1.32 [0.09, 2.35]	548.43 [458.26, 610.63]
Baseline2	High	1.60 [-0.27, 2.56]	544.34 [454.56, 620.36]
Baseline2	Low	1.47 [0.08, 2.33]	554.01 [479.48, 632.80]
Training1	High	1.54 [-0.08, 2.65]	521.40 [437.90, 587.57]
Training1	Low	1.59 [0.47, 2.45]	542.34 [463.65, 593.47]
Training2	High	1.59 [0.08, 2.56]	528.74 [462.00, 598.58]
Training2	Low	1.48 [0.00, 2.62]	533.94 [479.38, 618.25]
Test1	High	1.48 [-0.07, 2.47	528.58 [457.88, 596.17]
Test1	Low	1.50 [0.36, 2.50]	536.54 [444.89, 621.00]
Test2	High	1.49 [-0.38, 2.49]	529.30 [448.24, 606.00]
Test2	Low	1.55 [0.65, 2.55]	543.01 [450.11, 617.44]

507

508   The posterior distributions for sensitivity (*Supplementary Figure 1A* and *Supplementary Table*

509   *4*) revealed performance improvement from the first to the second part of the baseline for both high

510   (*M* = 0.12; 95% HDI [-0.05, 0.28]; ER = 11.05) and low (*M* = 0.15; 95% HDI [0.01, 0.32]; ER =

511   36.04) value conditions. When comparing the second part of baseline to the first part of training,

512   there was only a very small improvement in sensitivity in the high value condition (*M* = 0.06; 95%

513   HDI [-0.11, 0.22]; ER = 2.94), and a much bigger one in the low value condition (*M* = 0.11; 95%

514   HDI [-0.04, 0.28]; ER = 10.90). These results indicate that participants improved not only

515   throughout the baseline phase, but also from the end of baseline to the first part of the training

516   (albeit for low rewarded color only). This might indicate some presence of training effects in the

517   sensitivity data.

518   The posterior distributions of reaction times (*Supplementary Figure 1B* and *Supplementary*

519   *Table 2*) revealed only a very small difference between the first and the second part of baseline for

520   high (M = -4.52; 95% HDI [-15.0,0 5.77]; ER = 4.21) value condition, while the low value

521   condition was somewhat slower in the second part of the baseline (M = 5.60 95% HDI [-4.76,

522   16.20]; ER = 5.71). The comparison between the second part of baseline and the first part of

523   training revealed a very reliable speeding in both high (M = 22.90; 95% HDI [12.60, 33.80]; ER >

524   6000) and low (M = 11.60; 95% HDI [0.70, 22.10]; ER = 57.82) value conditions. These results

525   clearly point to the absence of large training effects in the reaction time data.

526   Taken together, these results indicate that our effects were not driven by the improved

527   performance over the course of the task. Although there is some evidence that sensitivity was

528   improving during the baseline phase, reaction times clearly indicate that the main shift in

529   performance happens in the beginning of training, when rewards are introduced. Importantly, the

530   strongest behavioral effects in our study were found on reaction time data, as indicated in the results

531   section.

532   Similar analyses could not be performed for the EEG data, because splitting the number of trials

533   in each phase would significantly affect the signal-to-noise ratio. However, our EEG results point

534   to changes in SSVEP amplitudes in only one of the value conditions. If amplitude changes were

535   mainly driven by training effects, the differences across reward phases would be expected for both

536   value conditions. This observation, combined with the lack of strong training effects in behavior,

537   suggests that our EEG results are not driven by training effects.

A
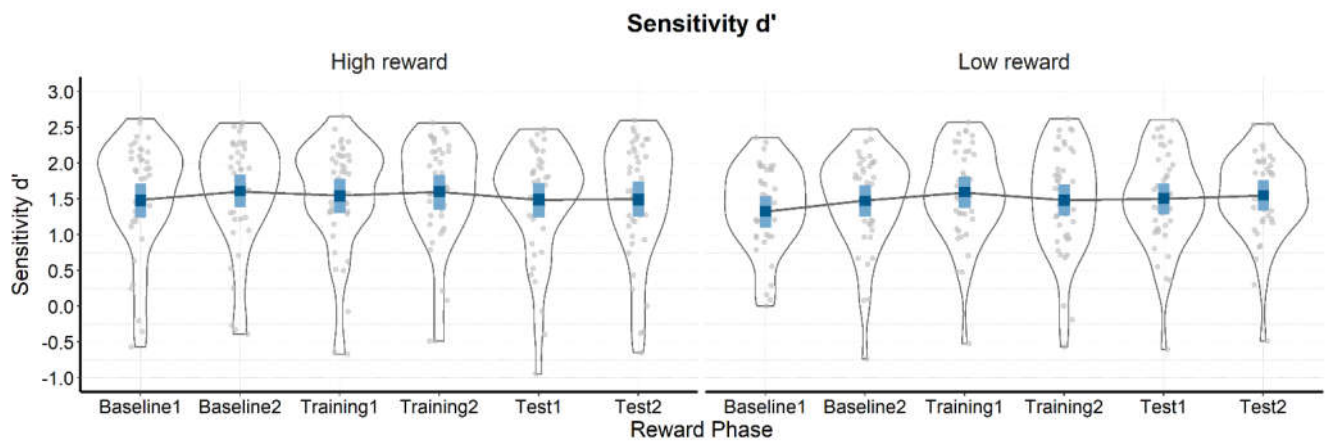
B
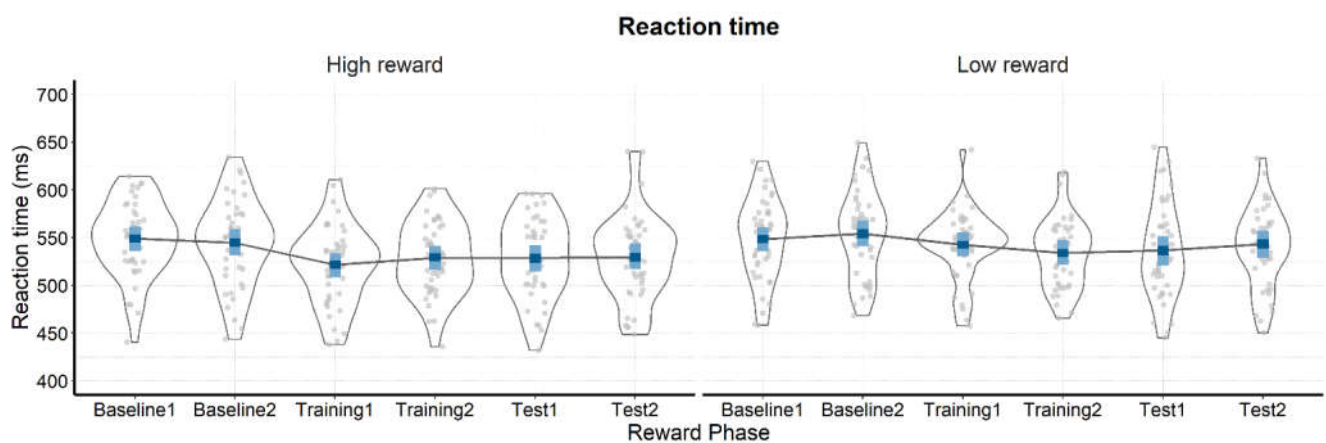
Supplementary Figure 1. Raw and modelled behavioral data in each half of each phase of the experiment. On both plots raw participant data is represented with grey dots and their distribution. The winning model is presented in blue (dark blue – 50% HDIs and light blue – 95% HDIs). **A.** Sensitivity (d′) across the phases of the experiment for the conditions in which the attended color is linked to either high or low value. **B)** Reaction times (ms) in the six phases when the attended stimulus is related to high or low reward probability.

538

539

Supplementary Table 4

Means and 95% HDIs of sensitivity and reaction times across six phases of the experiment

Reward phase	Value	Sensitivity (d′)	Reaction times (milliseconds)
Baseline 1	High	1.48 [1.24, 1.71]	548.86 [535.97, 561.35]
Baseline 1	Low	1.32 [1.09, 1.53]	548.38 [535.83, 560.97]
Baseline 2	High	1.60 [1.38, 1.84]	544.34 [531.22, 558.49]
Baseline 2	Low	1.47 [1.25, 1.69]	553.98 [540.67, 567.69]
Training 1	High	1.54 [1.30, 1.78]	521.42 [508.48, 533.66]
Training 1	Low	1.59 [1.37, 1.81	542.35 [530.05, 555.45]
Training 2	High	1.60 [1.35, 1.83]	528.74 [515.92, 541.36]
Training 2	Low	1.48 [1.26, 1.70]	533.91 [521.41, 547.24]
Test 1	High	1.49 [1.24, 1.72]	528.64 [514.39, 542.24]
Test 1	Low	1.50 [1.28, 1.71]	536.51 [520.49, 551.37]
Test 2	High	1.49 [1.25, 1.74]	529.32 [516.53, 543.70]
Test 2	Low	1.55 [1.33, 1.76]	543.01 [528.56, 557.28]

540

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552 and Dr. Inez Greven for help with data collection.

Author contributions

554 Author contributions are coded according to the CRediT taxonomy (Allen, Scott, Brand, Hlava, &

555 Altman, 2014).

556 **Conceptualization**: IG, AS, EHWK, SKA. **Data curation**: IG, AS. **Formal analysis**: IG, AS.

557 **Funding acquisition**: IG, AS, EHWK, SKA. **Investigation**: IG, AS. **Methodology**: IG, AS, SKA.

558 **Project administration**: IG, AS. **Resources**: EHWK, SKA. **Software**: SKA, IG, AS.

559 **Supervision**: AS, SKA. **Validation**: IG, AS. **Visualization**: IG, AS. **Writing – original draft**: IG,

560 AS. **Writing – review & editing**: IG, AS, EHWK, SKA.

Competing interests

562 The authors have no competing interests to report.

Data availability

564 Raw and pre-processed data, materials, and analysis scripts are available at: https://osf.io/kjds3/.

Software for data visualization and analysis

566 Visualization and statistical analyses were performed using R v3.4.4 (R Core Team, 2017) via

567 RStudio v1.1.453 (RStudio Team, 2015). We used the following packages (and their respective

568 dependencies):

569 • data manipulation: tidyverse v1.2.1 (Wickham, 2017);

570 • statistical analyses: Rmisc v1.5 (Hope, 2013), brms v2.3.1 (Bürkner, 2016);

571   •   visualization: cowplot v0.9.2 (Wilke, 2016), yarrr v0.1.5 (Phillips, 2016), viridis v0.5.1

572   (Garnier, 2018), eegUtils v0.2.0 (Craddock, 2018), BEST (Kruschke & Meredith, 2017);

573   •   report generation: pacman v0.4.6 (Rinker & Kurkiewicz, n.d.), knitr v1.20 (Xie, 2018);

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