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Valence, not utility, underlies reward-driven prioritization in human vision

Ludwig Barbaro, Marius V. Peelen and Clayton Hickey

Center for Mind/Brain Sciences, University of Trento, Italy

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Correspondence should be addressed to Clayton Hickey, Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068, Rovereto, Italy, clayton.hickey@unitn.it,

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Ludwig Barbaro, Marius V. Peelen, and Clayton Hickey

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Center for Mind / Brain Sciences, University of Trento, Italy

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Clayton Hickey

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Center for Mind / Brain Sciences

19

University of Trento

20

Corso Bettini 31, 38068, Rovereto, Italy

21

clayton.hickey@unitn.it

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Abstract

Objects associated with reward draw attention and evoke enhanced activity in visual cortex. What is the underlying mechanism? One possibility is that reward's impact on vision is mediated by unique circuitry that modulates sensory processing, selectively increasing the salience of reward-associated stimuli. Alternatively, effects of reward may be part of a more general mechanism that prioritizes the processing of any beneficial object, importantly including stimuli that are associated with the evasion of loss. Here, we test these competing hypotheses by having male and female humans detect naturalistic objects associated with monetary reward, the evasion of equivalent loss, or neither of these. If vision is economically normative, processing of objects associated to reward and evasion of loss should be prioritized relative to neutral stimuli. Results from fMRI and behavioural experiments show that this is not the case: while objects associated with reward were better detected and represented in ventral visual cortex, detection and representation of stimuli associated with the evasion of loss was degraded. Representations in parietal cortex reveal a notable exception to this pattern, showing enhanced encoding of both reward- and loss-associated stimuli. Experience-driven visual prioritization can thus be economically irrational, driven by valence rather than objective utility.

60 Significance Statement

61 Normative economic models propose that gain should have the same value as
62 evasion of equivalent loss. Is human vision rational in this way? Objects
63 associated with reward draw attention and are well-represented in visual cortex.
64 This is thought to have evolutionary origins, highlighting objects likely to provide
65 benefit in the future. But benefit can be conferred not only through gain, but also
66 through evasion of loss. Here we demonstrate that the visual system prioritizes
67 real-world objects presented in images of natural scenes only when these objects
68 have been associated to reward, not when they have provided the opportunity to
69 evade financial loss. Visual selection is thus non-normative and economically
70 irrational, driven by valence rather than objective utility.

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79 Introduction

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80 Visual stimuli associated with reward become salient and attention-drawing. As a
81 result, they are easy to find as targets of visual search but hard to ignore when
82 they act as task-irrelevant distractors (for review: Anderson, 2015; Le Pelley et
83 al., 2015). This selective bias sustains when it is counter-productive (Hickey,
84 Chelazzi, & Theeuwes, 2010a) and appears to rely at least in part on plasticity in
85 visual cortex (van Koningsbruggen, Ficarella, Battelli, & Hickey, 2016),
86 suggesting that it is a product of implicit attentional and perceptual learning rather
87 than explicit strategy. It may have evolutionary origins - facilitating the search for
88 food - and could underlie maladaptive selective behaviour observed in eating
89 disorders and addiction (Berridge, 1996; Robinson & Berridge, 1993).

90 This effect of reward on selection has been interpreted in two ways. On one hand
91 is the idea that reward may activate unique and specific brain mechanisms that
92 prioritize reward-predictive stimuli in visual processing (Roelfsema, van Ooyen, &
93 Watanabe, 2010; Hickey, Chelazzi, & Theeuwes, 2010a). This is in line with
94 ideas from the animal literature about approach behaviour and the function of
95 reward-related dopamine (Berridge & Robinson, 1998), and is reflected in a
96 recent computational model that proposes long-range neurochemical interactions
97 between the reward system and visual cortex (Roelfsema & van Ooijen, 2005).
98 But on the other hand is the equally-compelling idea that attentional bias to
99 reward-associated stimuli might constitute one instantiation of a broader
100 motivational mechanism in vision (Gottlieb, 2012; Le Pelley et al., 2016). Using a
101 term from economics, this would act to maximize objective utility - the absolute
102 quality or usefulness of outcome - by prioritizing any informative object that can

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103 be acted on to create a relative benefit, including stimuli that predict negative
104 outcome when this information can be used to evade greater loss or harm.

105 Here we test these accounts of reward's influence on visual selection. We
106 designed a visual search task in which participants could accumulate points with
107 cash value by correctly detecting examples of target categories in pictures of
108 natural scenes. A given category could be associated with rewarding outcome,
109 neutral outcome, or loss. Correct detection of an example of the reward-
110 associated category thus resulted in receipt of 150 points, but failure to detect
111 this target garnered only 50 points. In contrast, correct detection of an example
112 from the loss-associated category resulted in the forfeiture of 50 points, but
113 failure to detect this target resulted in the greater loss of 150 points. Finally,
114 detection of a neutral target garnered only 1 point and failure to detect this target
115 resulted in the loss of only 1 point. Accurate detection of both reward- and loss-
116 associated targets in our design therefore had a consistent benefit of 100 points
117 relative to incorrect performance, making them more valuable than neutral
118 targets, and participants were made explicitly aware of this fact.

119 If selective bias for reward-associated stimuli reflects a rational, utility-maximizing
120 mechanism, reward- and loss-associated targets should be prioritized equally in
121 our task. This motivates the set of predictions illustrated in Figures 1A and 1B,
122 which we refer to as the utility model. Targets should draw attention and be well
123 represented in visual cortex (Hickey, Chelazzi, & Theeuwes, 2010; Anderson,
124 Laurent, & Yantis, 2011), but reward- and loss-associated targets should draw

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125 attention with greater strength than neutral targets (Figure 1A). When these
126 objects act as task-irrelevant distractors, their salience will cause them to
127 interfere with search for other targets and they will need to be attentionally
128 suppressed (Hickey & Peelen, 2015, 2017; Sawaki, Luck, & Raymond, 2015;
129 Figure 1B). But if selective bias for reward-associated stimuli is not economically
130 rational, it presumably reflects an impact of the absolute valence of outcome. By
131 this valence model, targets that predict reward should be visually salient (Figure
132 1C), and reward-associated distractors should require strong attentional
133 suppression (Figure 1D). Targets predicting sub-optimal outcome, however, may
134 not only fail to draw attention, but be actively suppressed and poorly represented
135 in the visual system (Hickey, Chelazzi, & Theeuwes, 2010; Hickey & van Zoest,
136 2012; Hickey & Peelen, 2017; Figure 1C). If this is so, loss-associated distractors
137 may not interfere with search, thus requiring little inhibition (Figure 1D).

Materials and Methods

138
139 We conducted two experiments to test the predictions illustrated in Figure 1.
140 Experiment 1 relied on the use of multivariate pattern analysis (MVPA) of human
141 fMRI data to index the quality of visual representations in the brain. While in the
142 scanner, 23 participants searched for examples of real-world object categories in
143 images of city- and landscapes (Figure 2A). The target category – cars, trees,
144 buildings, or people – was indicated at the beginning of each block of trials, and
145 for each participant one object category was associated to reward when it acted
146 as target, one to loss, and the others to neutral outcome (Figure 2B). Importantly,

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147 when search was for one of the neutral categories, examples of the reward-
148 associated, loss-associated, and other neutral category appeared in the scenes
149 as irrelevant distractors.

150 To maximize our power to detect potentially-subtle effects on distractor
151 representations, Experiment 1 adopted a design where examples of all distractor
152 categories were present in every scene. We therefore conducted a second
153 behavioural experiment to determine how the association of reward or loss to
154 distractors impacted search behaviour. Here, 101 participants completed a
155 variant of the task in which outcome was manipulated independently of target
156 identity. Each block thus began with a cue indicating both target category and
157 pay scheme and scenes only occasionally contained outcome-associated
158 distractors. By looking at performance within each block we were able to
159 examine how outcome association impacted target detection, whereas by looking
160 across blocks we were able to see how examples from object categories that had
161 recently been associated with reward or loss came to interfere with detection of
162 neutral targets.

163 *Participants*

164 Twenty-four volunteers (9 female, 25 years \pm 4 SD) gave informed consent
165 before completing Experiment 1. One participant reported the target as present in
166 $>90\%$ of trials and was excluded from analysis. One hundred and five volunteers
167 gave informed consent before completing Experiment 2 (79 female, 23 years \pm
168 4 SD). Three participants were excluded because of low accuracy (>3 SD from

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169 group mean) and one because of inconsistent responses on a screening
170 questionnaire. For both experiments, sample size was guided by observed effect
171 sizes in our prior work employing similar methodology. All methods were
172 approved by the University of Trento ethical committee and adhered to the
173 Declaration of Helsinki.

174 *Experiment 1 – Object Selective Cortex Localizer*

175 The object-selective cortex (OSC) localizer involved 2 scanner runs of 317 s.
176 duration, each comprised of 16 blocks of 20 trials and 3 fixation blocks. Each run
177 started with a 15 s fixation period followed by a 2 s reminder of task instructions
178 and ended with a 15 s fixation period. Each trial began with fixation (400 ms)
179 followed by a central image of an isolated everyday object (e.g. telephone, alarm
180 clock, blender; 350 ms, n=20) or a pixel-scattered version of one of these
181 images. Participants monitored for image repetition, which occurred once per
182 block. Every 5th block was a fixation block, where for 15 s only the fixation cross
183 was presented.

184 *Experiment 1 - Category Pattern Localizer*

185 The category pattern localizer involved 2 scanner runs of 392 s. duration, each
186 comprised of 20 blocks of 20 trials and 4 fixation blocks. Each run started with a
187 15 s fixation period followed by a 2 s reminder of task instructions and ended with
188 a 15 s fixation period. In each block images of isolated examples of one of the
189 four relevant stimuli categories were presented (n=40 per category). Each trial
190 began with fixation (400 ms) followed by image presentation (350 ms). As in the

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191 OSC localizer, participants monitored for image repetition, which occurred once
192 per block, and every 5th block was a fixation block where for 15 s only the
193 fixation cross was presented. Note that localizer images of people were headless
194 because faces in the primary experimental task were commonly too small to
195 visually resolve. We did not want the localizer pattern to reflect the encoding of
196 faces if this was not possible in the experiment itself.

197 As an internal check, we conducted a split-half correlation analysis of category
198 patterns in OSC. This correlated the pattern for each category as derived from
199 half the data with the pattern for each category as derived from the other half of
200 the data. Patterns for the same categories were similar, and thus positively
201 correlated on average (0.73), whereas the patterns across categories were
202 dissimilar and thus negatively correlated (-0.23).

203 *Experiment 1 - Design*

204 The primary experiment involved 4 scanner runs of 590 s. duration, each
205 comprised of 8 blocks of 24 trials. Each run started and ended with a 15 s fixation
206 period. At the beginning of each block central text indicated the target category
207 for the coming block for 10 s (cars, trees, buildings, people) alongside the
208 number of points that had been accumulated to that point in the experiment. The
209 trial sequence is illustrated in Figure 2A. In half of the trials the scene contained
210 examples of all relevant object categories, while in remaining trials the target was
211 absent, and the order of target present and target absent trials was randomized
212 within each block. Participants reported the presence or absence of the target

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213 with the right index and middle fingers respectively. Late responses (>750 ms)
214 and missing responses were incorrect. When the target was present and
215 response was accurate, feedback was determined by the target category (see
216 Figure 2B). The association of specific categories to reward, loss, and neutral
217 outcome was counterbalanced across participants, and participants were
218 explicitly informed at the beginning of the experiment about the relationship
219 between each target category and its associated outcome. All participants
220 completed a short training procedure prior to entering the scanner and were able
221 to report this relationship before beginning the experiment itself. Participants
222 were paid based on the number of points they accumulated during the
223 experiment (€0.0018 / point) and each received between €25 and €40.

224 *Experiment 1 - fMRI Data Acquisition, Preprocessing, and Analysis*

225 Whole-brain Imaging was conducted using a Bruker BioSpin MedSpec 4T
226 scanner with an eight-channel head coil (functional data: T2*-weighted echo-
227 planar images, 31 slices with 0.45 mm gap, 3x3x3 mm voxel size, repetition time
228 [TR] = 2.2 s., echo time [TE] = 33 ms, flip angle = 76°; structural data: T1-
229 weighted MPAGE, 256 slices, 1x1x1 mm voxel size). Functional data were
230 motion corrected, slice time corrected, smoothed using a 6-mm full-width half-
231 max Gaussian kernel, high-pass filtered at 0.008 Hz, coregistered to the
232 structural image, and spatially normalized to the Montreal Neurological Institute
233 (MNI) template. Preprocessing and subsequent data analysis was conducted
234 with SPM12 (University College London, UK) and the CoSMo-MVPA toolbox

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235 (Oosterhof, Connolly, & Haxby, 2016).

236 A separate general linear model (GLM) was created for each of the OSC
 237 localizer, category localizer, and visual search task. In each GLM, all regressors
 238 of interest were convolved using the canonical hemodynamic response function
 239 implemented in SPM12 and all models contained six regressors of no interest
 240 obtained from the realignment procedure to account for head motion.

241 In the OSC localizer, the BOLD signal for each voxel was modeled using two
 242 regressors of interest, one for intact and one for scrambled objects. OSC was
 243 functionally defined in MNI space for each participant by contrasting responses
 244 evoked for the intact and scrambled images and identifying reliably activated
 245 voxels in occipital or temporal cortex ($p < 0.001$, uncorrected). Mean OSC size
 246 was 1491 voxels \pm 845 SD. In the category localizer, four regressors of interest
 247 were employed, reflecting the presentation of people, cars, houses or trees. In
 248 the visual search task, four regressors of interest were employed, reflecting the
 249 block target. All regressors of interest spanned whole experimental blocks.

250 *Experiment 1 - MVPA*

251 Category patterns were derived from the category localizer data by identifying the
 252 set of t-values elicited for each voxel in OSC by each of the four object
 253 categories. Similar patterns were isolated for each condition of interest in the
 254 visual search experiment. All voxel-wise t-values were normalized within each
 255 experiment by subtracting the mean t-value observed across experimental
 256 conditions from each conditional value (Haxby, Gobbini, Furey, Ishai, Schouten,

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257 & Pietrini, 2001). This removes voxel variance unrelated to experimental
258 manipulations while retaining conditional variance. OSC patterns observed in the
259 visual search experiment were subsequently correlated with OSC patterns
260 observed in the category localizer to generate a 4x4 correlation matrix. These
261 values were Fisher-transformed and organized in terms of category outcome
262 association and whether the category acted as target or distractor. As an internal
263 check, we determined that OSC patterns elicited by scenes correlated more
264 strongly with the benchmark pattern corresponding to the target (mean = 0.125)
265 than they did with the other benchmark patterns (-0.041; $p < 0.001$).

266 The correlation values computed in this way are on an interval rather than a ratio
267 scale, with a zero point that is not informative. This is the case because of the
268 normalization procedure (Haxby et al., 2001; Misaki et al., 2011). When all
269 pairwise correlations are calculated for the conditions of two individually
270 normalized datasets, the resulting set of normalized correlations are centered on
271 zero. Negative values are thus negative only in relationship to the mean of all
272 possible cross-correlations between the datasets. Raw, non-normalized
273 correlation values in Experiment 1 were consistently positive because scene and
274 localizer stimuli evoked a similar visual response in many OSC voxels. The
275 normalization procedure isolated conditional differences in this signal.

276 Each category type acted as distractor in three block types. For example, if a
277 category was associated with neutral outcome, it could act as distractor when the
278 target category was also neutral, when the target category was associated with

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279 reward, and when the target category was associated with evasion of loss.
280 However, in order to isolate changes in distractor representation that were
281 produced solely by the association of specific outcome to the distractor category,
282 we focussed analysis of distractor categories on results observed when the
283 target was associated with neutral outcome. The general pattern of distractor
284 information emerges in much the same way if analysis includes conditions where
285 the target could be associated with reward or evasion of loss.

286 *Experiment 1 - Regression Analysis*

287 To statistically assess the ability of the utility and valence models to account for
288 our OSC and searchlight results we conducted multiple linear regression
289 analyses for each participant dataset (and, in the case of searchlight analysis, for
290 each searchlight sphere). The first regressor described the difference in task
291 relevance between targets and distractors, positively weighting targets and
292 negatively weighting distractors (i.e. [1 1 1 -1 -1 -1]). The second described the
293 valence model, positively weighting reward-associated targets and loss-
294 associated distractors and negatively weighting loss-associated targets and
295 reward-associated distractors (i.e. [1 0 -1 -1 0 1]). The final regressor described
296 the utility model, positively weighting both reward- and loss-associated targets
297 and negatively weighting both reward- and loss-associated distractors (i.e. [1 -2 1
298 -1 2 -1]). Notice that each regressor vector is orthogonal to the others, has a
299 mean value of zero, and that distractor weights are an inverted version of target
300 weights. Regressor vectors were z-scored before linear regression was

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301 conducted. This analysis garnered a coefficient for each participant that was
302 positive in value when the regressor predicted dataset variance. The sets of
303 coefficient values observed across participants were tested against a null
304 hypothesis of zero.

305 *Experiment 1 - Correlation between univariate activity and information*

306 We approached the experiment with the idea that reactivity in the dopaminergic
307 midbrain might predict the quality of object representation in OSC (Hickey &
308 Peelen, 2015, 2017). To test this hypothesis, we began by conducting a separate
309 event-related GLM analysis with a predictor for the presence of reward-
310 associated, loss-associated, and neutral targets. We subsequently used a
311 probabilistic anatomical MRI atlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) to
312 define two midbrain regions of interest (ROIs), one describing the bilateral red
313 nuclei and the other the bilateral substantia nigrae (Figure 4a). We extracted
314 activity in each of these ROIs as observed when a reward-associated, loss-
315 associated, and neutral target was present in the scene. Following the logic of
316 our regression analysis of OSC category information, we conducted a regression
317 analysis of this univariate activity with predictors for the utility (ie. [+1 -2 +1]) and
318 valence models (ie. [+1 0 -1]).

319 This analysis - and the preceding GLM - was limited to activation elicited by the
320 presence of targets because all distractors were consistently present in each trial
321 in the design of Experiment 1. To maintain equivalence between univariate and
322 multivariate results, we calculated new regression coefficients for OSC category

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323 information with utility and valence predictors modelling the representation of
324 only targets (and thus ignoring variance in the representation of distractors). The
325 target-only univariate midbrain coefficients were then correlated with these
326 target-only category information coefficients (Figure 4B).

327 We conducted a whole-brain analysis based on the same logic as this ROI-based
328 analysis (Hickey & Peelen, 2015). For each voxel, coefficients for the valence
329 model were calculated based on univariate activity observed in that voxel in
330 response to scenes containing reward-associated, loss-associated, and neutral
331 targets. The resulting values were correlated across participants with target-only
332 category information coefficients. These correlation values were Fisher
333 transformed and assigned to the voxel location in a new brain volume.

334 *Experiment 1 - Whole-brain Searchlight Analysis*

335 Searchlight analysis began with the identification of brain regions where scene-
336 evoked patterns contained more information about targets than distractors. For
337 each voxel in the brain we defined a surrounding sphere with 21 mm diameter (7
338 voxels). We subsequently computed voxelwise correlations between scene-
339 evoked activity in each of these spheres and spatially-equivalent mean
340 benchmark patterns evoked in our category pattern localizer. These correlation
341 values were Fisher transformed and assigned to the center voxel of each sphere.
342 Target category information - i.e. the correlation between the scene-evoked
343 pattern and the benchmark pattern for the object category currently acting as
344 target in the scene - were subsequently contrasted with non-target category

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345 information - i.e. the correlation between the scene-evoked pattern and the
346 benchmark pattern for the object categories currently acting as distractors in the
347 scene. For each voxel, this difference was tested for statistical reliability across
348 participants.

349 Voxels showing selectivity at $p < 0.001$ were selected for further analysis when
350 they were part of a cluster with minimum size of 50 voxels. This identified three
351 clusters. Figure 5A illustrates OSC, as identified in our OSC localizer experiment.
352 The first and second clusters identified in this searchlight analysis are illustrated
353 in Figure 5B, and are roughly equivalent in size and location to bilateral OSC.
354 The third cluster was located in posterior parietal cortex and is illustrated in
355 Figure 6A.

356 Further analysis was constrained to the parietal cluster, where we examined
357 variance in category information in each sphere as a function of outcome-
358 association. To test the degree to which category information for each sphere
359 followed the utility or valence model we isolated category information for reward-
360 associated, loss-associated, and neutral category examples when these were the
361 target of search, and for reward-associated, loss-associated, and neutral
362 category examples when these were distractors and the target of search was an
363 example of one of the two outcome-neutral object categories. We conducted
364 multiple linear regression for category information at each voxel using the same
365 regressor weights described above. All regression coefficient values
366 corresponding to voxels falling within the parietal ROI were mean averaged to

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367 generate a single value describing the explanatory power of the task relevance,
368 utility, and valence models for information in the parietal cluster as a whole.
369 These values were subsequently tested across participants against a null
370 hypothesis of zero.

371 *Experiment 2 - Design*

372 As in Experiment 1, the stimulus set for Experiment 2 consisted of a set of black
373 and white pictures of natural scenes (n=384). However, the set of images
374 employed in Experiment 2 only partially overlapped with the set of images
375 employed in Experiment 1. This is the case because, in Experiment 1, scenes
376 contained examples of either 3 or 4 of the possible target categories. In
377 Experiment 2, scenes contained examples of either 2 or 3 of the categories. Four
378 groups of scenes (n=48) each contained all possible combinations of three
379 categories. Six more groups of scenes contained all possible combinations of two
380 categories. Of these six groups, we had trouble finding life-like examples of
381 car/tree and people/house combinations in the absence of the other categories.
382 As a result, these groups of images contained only 24 examples; all other groups
383 contained 32 images. Scenes were masked using the same images as employed
384 in Experiment 1.

385 Experiment 2 took place in a quiet room and was comprised of 48 blocks of 16
386 trials. Each block began with a text cue indicating both the target category for the
387 coming block and the pay scheme. This means that, in contrast to the design of
388 Experiment 1, the association of outcome to object categories could be

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389 counterbalanced within participants in Experiment 2. For each participant, two
390 object categories (cars and trees) were paired with each of the possible
391 outcomes in an equal number of experimental blocks, with the order of pairing
392 counterbalanced across participants. Two other target categories (people and
393 buildings) were consistently associated with neutral feedback. Blocks were
394 organized in pairs, such that blocks in which participants searched for one of the
395 two outcome-varying categories (cars or trees) were always followed by blocks
396 where they searched for one of the two always-neutral categories (people or
397 buildings). In these neutral-target test blocks, examples of the target category
398 from the immediately preceding block could appear as task irrelevant distractors.

399 All blocks contained 8 target present and 8 target absent trials. In target present
400 trials, in addition to the target the scenes contained an example of 1 of the 3 non-
401 target categories in half of the trials and examples from 2 of the 3 non-target
402 categories in the remainder. In target absent trials, the scenes contained
403 examples of 2 of the 3 non-target categories in half of the trials and examples
404 from all 3 non-target categories in the remainder. This was manipulated such that
405 examples of each non-target category were present and absent an equal number
406 of times in both target-present and target-absent conditions, allowing us to
407 determine how the presence of each distractor type impacted performance in the
408 neutral test blocks. The trial sequence in Experiment 2 was as illustrated in
409 Figure 2A but with different latencies. Fixation (833 ms) was followed by
410 presentation of the scene (40 ms), a mask (260 ms), the reappearance of fixation
411 (300 ms), and feedback (533 ms).

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412 For 54 participants in Experiment 2 the payoff scheme was identical to that
413 employed in Experiment 1. For 47 participants detection of reward-associated
414 targets garnered 100 points and failure to detect resulted in 0 points, detection of
415 neutral targets resulted in 1 point and failure to detect resulted in the loss of 1
416 point, and detection of loss-associated targets resulted in 0 points and failure to
417 detect resulted in the loss of 100 points. Payoff for target absent trials remained
418 as in Experiment 1. Statistical analysis demonstrated no difference in
419 performance across these groups (for all effects involving this difference, $p >$
420 0.211). Participants were paid based on the number of points they accumulated
421 during the experiment (€0.0011 / point) and each received between €7 and €12.

422 *Experiment 2 - Analysis*

423 Blocks with varying-outcome targets (cars and trees) were analyzed separately
424 from blocks with consistent-outcome targets (people and buildings), with the
425 former focusing on variance as a function of target association (i.e. accuracy for
426 reward- vs. loss-associated targets) and the latter focusing on variance as a
427 function of distractor association (i.e. accuracy for neutral targets in the presence
428 of distractors that served as reward-, neutral- or loss-associated targets in the
429 preceding block).

430 Behavioural results from Experiment 2 were analyzed using the same regression
431 approach employed in Experiment 1. Detection accuracy was identified for
432 conditions where the target was associated with reward, loss, or neutral
433 outcome, and also for conditions where the target was associated with neutral

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434 outcome, but the distractor was associated with reward, loss, or neutral outcome.
435 These six values were regressed to predictors representing the utility and
436 valence models for each participants, and the resulting beta coefficients were
437 tested against a null hypothesis of zero.

438 *Statistics*

439 All statistics reported in the paper are a product of permutation analysis with two
440 exceptions: the GLM models used to generate parametric fMRI maps and the
441 whole-brain correlation analysis. For permutation tests against the null
442 hypothesis of zero, data-driven distributions were generated by randomly
443 sampling from the relevant dataset 10^6 times with replacement. The likelihood of
444 observed data given the null was calculated in comparison to these distributions.
445 Tests of multi-factor results were conducted by randomly relabeling conditional
446 data over 10^4 iterations to create a data-driven distribution of F values for each
447 main effect and interaction. The likelihood of observed F values given the null
448 was calculated in comparison to these distributions. Tests of correlation were
449 conducted using a Studentized bootstrap analysis (with 10^4 iterations in the outer
450 loop and 100 permutations in the inner loop).

451 Results

452 *The impact of reward and loss on stimuli representations in OSC and behaviour*

453 Our first aim was to determine if the association of reward or loss impacted the
454 visual representation of experimental stimuli in a manner predicted by the utility

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455 or valence models. We began by analyzing fMRI results from Experiment 1,
456 deriving measures of category information from voxel-wise patterns in object
457 selective visual cortex (OSC). To do this, we first isolated OSC by comparing
458 cortical responses to objects versus scrambled versions of these objects. We
459 then correlated voxel-wise patterns evoked in this area during scene viewing with
460 benchmark patterns identified in a separate localizer experiment (in which
461 participants viewed isolated examples of our relevant object categories; Figure
462 2C). The degree to which the scene-evoked OSC pattern matched each of the
463 individual category benchmarks provided a measure of the strength with which
464 each of these categories was represented in ventral visual cortex (Peelen, Fei-
465 Fei, & Kastner, 2009; Seidl, Peelen, & Kastner, 2012).

466 As illustrated in Figure 3, category information was greater for targets than
467 distractors, even though targets were only present in half of the trials while all
468 distractors were present in every trial. The effect is evident in a scale shift in
469 category information in comparison of Figures 3A and 3B. This strong modulation
470 by top-down set replicates prior studies using this technique to investigate
471 naturalistic visual search (Seidl, Peelen, & Kastner, 2012; Peelen, Fei-Fei, &
472 Kastner, 2009; Hickey & Peelen, 2015). Variance in category information as a
473 function of outcome-association closely followed the valence model: OSC carried
474 more information about reward-associated targets than loss-associated targets
475 (Figure 3A), but this pattern reversed for distractors, with OSC carrying less
476 information about reward-associated distractors than loss-associated distractors
477 (Figure 3B).

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478 Behavioural analysis was focused on target detection accuracy when the target
479 was present in the scene (ie. hit rate) as an analogue of the target OSC
480 information effect described above. As illustrated in Figure 3C, hit rate paralleled
481 the pattern observed in target category information, and thus also closely
482 followed predictions from the valence model. Importantly, no corresponding effect
483 was observed in accuracy observed when targets were absent from the scene
484 (ie. correct rejects; 69%, 72%, and 71% accuracy respectively), suggesting that
485 outcome association impacted the ability to detect the target rather than
486 increasing the overall propensity that the target would be reported as present.

487 To statistically assess the ability of the valence and utility models to predict our
488 results we conducted linear regression analyses. In analysis of imaging data,
489 these had 3 factors: the first predicted that category information for task relevant
490 stimuli would be greater than for distractors (Seidl, Peelen, & Kastner, 2012;
491 Peelen, Fei-Fei, & Kastner, 2009; Hickey & Peelen, 2015), the second that
492 results would follow the utility model (as illustrated in Figures 1A and 1B), and the
493 third that results would follow the valence model (as illustrated in Figures 1C and
494 1D). This garnered 3 regression coefficients for each participant reflecting the
495 degree to which the data varied according to each of these hypotheses. The
496 coefficients corresponding to the task-relevance model were significantly
497 positive, $p < 10^{-6}$, as were the coefficients corresponding to the valence model, p
498 $= 0.003$, demonstrating that these factors reliably predicted our results. However,
499 coefficients for the utility model did not differ from zero, $p = 0.789$. Follow-up
500 contrasts revealed that OSC carried more information about reward-associated

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501 targets than loss-associated targets, $p = 0.002$, but less information about
502 reward-associated distractors than loss-associated distractors, $p = 0.018$. In
503 OSC, the valence model better characterized the pattern of category information
504 than did the utility model.

505 Because all distractor types were present in every scene, analysis of behavioural
506 data from Experiment 1 was limited to the effect of outcome association with
507 target stimuli. Regression analysis therefore had 2 factors: the first predicted that
508 hit rate would follow the utility model (as illustrated in Figure 1A) and the second
509 that it would follow the valence model (as illustrated in Figure 1C). Coefficients
510 corresponding to the valence model were significantly positive, $p = 0.002$, but
511 coefficients for the utility model did not differ from zero, $p = 0.360$. Follow-up
512 analysis demonstrated that the effect of target-outcome association on hit rate
513 reliably differed from its effect on correct rejects (interaction $p = 0.017$). As was
514 the case in analysis of OSC category information, the valence model better
515 characterized detection accuracy than did the utility model.

516 To gain further perspective on the relationship between brain activity and
517 behaviour we examined individual differences in how the valence and utility
518 models fit OSC category information and behaviour. Our expectation was that
519 those participants showing a strong fit of the valence model in brain activity
520 should also show a strong fit of the model in behaviour. To test this hypothesis,
521 we Pearson correlated the valence model coefficients derived from brain data
522 (Figures 3A and 3B) with the valence model coefficients derived from hit rate

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523 data (Figure 3C). As illustrated in Figure 3D, a reliable relationship emerged ($r =$
 524 0.439 , $p = 0.002$). No corresponding relationship was evident when utility model
 525 coefficients for OSC category information and behaviour were correlated ($r =$
 526 0.075 , $p = 0.351$). Expression of the valence pattern in brain activity therefore
 527 predicted a valence pattern in behaviour, demonstrating a close relationship
 528 between brain activity and behaviour.

529 *Midbrain activity as a predictor of representational quality in OSC*

530 Our study was motivated in part by theories of dopamine's role in attentional
 531 selection and approach behaviour (Berridge & Robinson, 1998; Ikemoto &
 532 Panksepp, 1999), alongside results relating reward's impact on selection to
 533 activity in the dopaminergic midbrain (Hickey & Peelen, 2015; 2017) and the
 534 release of dopamine in the striatum (Anderson et al., 2016). To test the
 535 relationship between midbrain activity and OSC representations in the current
 536 data we used an MRI atlas to define a ROI describing the bilateral SN (Figure
 537 4A). The dorsal aspect of this SN ROI – encompassing pars compacta and
 538 including voxels projecting into the ventral tegmental area – contains
 539 dopaminergic neurons that project to the striatum and frontal cortex (Williams &
 540 Goldman-Rakic, 1993; Haber, Fudge, & McFarland, 2000). As a functionally
 541 distinct proximal control area, we additionally isolated the bilateral red nuclei,
 542 which are located slightly medial and rostral to the SN but do not contain
 543 dopaminergic cells and have different connectivity than the SN (Figure 4A;
 544 Nioche, Cabanis, & Habas, 2009).

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545 Our expectation was that participants showing greater responsivity in SN to
546 reward- vs. loss-associated targets would also show increased category
547 information for these stimuli in OSC. To test this, we conducted a univariate
548 regression analysis of voxel activation in the SN and red nuclei ROIs with
549 predictors representing the utility and valence models. The parameter values
550 identified in this univariate analysis of SN and red nucleus were subsequently
551 correlated with valence model coefficients from multivariate analysis of target
552 information in OSC. As illustrated in Figure 4B, participants showing a valence
553 pattern in the SN also showed this pattern in OSC category information, $r =$
554 0.387 , $p = 0.030$. This relationship was not evident for the red nucleus, $r = 0.054$,
555 $p = 0.397$, and correlation of utility model coefficients for OSC information and
556 SN activity identified no relationship, $r = -0.019$, $p = 0.538$. These findings
557 demonstrate that when the valence pattern discretely expressed in the SN, it also
558 expressed in OSC category information.

559 We conducted an additional whole-brain analysis employing this analytic
560 approach. Here, coefficient values were extracted for each participant based on
561 univariate activation of each voxel in brain space and subsequently correlated
562 with category information coefficients. After FDR correction for multiple
563 comparisons (Benjamini & Hochberg, 1995), this analysis revealed a set of small
564 voxel clusters where a good fit of the valence model to univariate activity
565 predicted a good fit of the valence model to OSC category information.
566 Supporting the ROI analysis detailed above, a set of voxels was identified in the
567 midbrain (Figure 4C). These were located bilaterally in the substantia nigra (left:

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568 2 voxels; peak: -9, -25, -11; right: 1 voxel; 12, -25, -11) and in the vicinity of the
 569 ventral tegmental area (1 voxel; 0, -29, -15). Other clusters emerged in the
 570 posterior cingulate cortex (Figure 4D; 15 voxels; peak: -9, -46, 16), left superior
 571 frontal gyrus (Figure 4E; 10 voxels; peak: -21, -1, 65), and left medial frontal
 572 gyrus / dorsal anterior cingulate (Figure 4F; 3 voxels; peak: -6, 5, 58). The
 573 superior frontal, anterior cingulate, and midbrain clusters are similar to those that
 574 we have identified using similar methodology in earlier investigation of incentive
 575 salience (Hickey & Peelen, 2015).

576 *Beyond OSC: whole-brain analysis of category information*

577 In the imaging analyses described to this point we have measured
 578 representational quality based on consideration of voxel patterns in OSC, which
 579 constitutes a large portion of ventral visual cortex spanning the occipital and
 580 temporal lobes (Figure 5A). However, other brain areas are known to also carry
 581 multivoxel information about naturalistic visual stimuli and their task relevance
 582 (Konen & Kastner, 2008; Jeong & Xu, 2016). To test the ability of the valence
 583 and utility models to describe variance in the quality of object representation
 584 outside OSC we conducted a whole-brain searchlight analysis of the fMRI data
 585 (Kriegeskorte, Goebel, & Bandettini, 2006).

586 This began with the identification of brain areas that carried more information
 587 about the target of visual search than about task-irrelevant distractors, such that
 588 category information in these areas could be subsequently examined for the
 589 effect of outcome association. We defined spheres around each voxel in the

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590 brain, testing whether the pattern of voxel-wise activity in each area correlated
591 with corresponding values from benchmark data generated in our localizer task.
592 This identified three areas that carried more information about targets than
593 distractors. Two of these were in the bilateral ventral visual cortex, roughly
594 equivalent in location and size to OSC as discussed above (see Figure 5).
595 Consistent with other recent work (Jeong & Xu, 2016; Bettencourt & Xu, 2016) a
596 third cluster emerged in right posterior parietal cortex, notably containing aspects
597 of the intra-parietal sulcus and superior parietal lobule (Figure 6A; cf. Peck et al.,
598 2009).

599 We constrained subsequent analysis to this parietal cluster, extracting category
600 information for targets and distractors as a function of outcome association. In a
601 reversal of the pattern we observed in OSC, mean category information here
602 paralleled the utility rather than valence model: category information was equal
603 for reward- and loss-associated targets, in both cases larger than for neutral
604 targets (Figure 6B), but this reversed in analysis of distractor information, with
605 parietal cortex carrying less information about both reward- and loss-associated
606 distractors than neutral distractors (Figure 6C).

607 We once again used linear regression to statistically assess these results. For
608 each participant and searchlight sphere we modelled category information with
609 predictors for task relevance, the utility model, and the valence model. We
610 subsequently generated a set of mean coefficients for each participant that
611 described the degree to which information in the parietal cluster was

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612 characterized by our models. The parietal cluster was defined based on its
613 sensitivity to task relevance, so coefficients corresponding to the task relevance
614 predictor were unsurprisingly positive, $p < 10^{-6}$. Utility model coefficients were
615 also positive, $p = 0.002$, demonstrating the explanatory power of this model, but
616 valence model coefficients did not differ from zero, $p = 0.511$.

617 Follow-up contrasts revealed that parietal cortex trended toward carrying more
618 information about a reward-associated target than a neutral target, $p = 0.108$,
619 and about a loss-associated target than a neutral target, $p = 0.143$. Equivalent
620 analyses of distractor information garnered more reliable effects, with less
621 information about a reward-associated distractor than a neutral distractor, $p =$
622 0.015 , and less information about a loss-associated distractor than a neutral
623 distractor, $p = 0.010$.

624 Personality as a predictor of representational quality in OSC.

625 We have previously found that selective biases to reward-associated stimuli, as
626 evident in behaviour (Hickey, Chelazzi, & Theeuwes, 2010b) and OSC category
627 information (Hickey & Peelen, 2015; Hickey & Peelen, 2017), can vary across
628 individuals as a function of personality traits related to reward-sensitivity. With
629 this in mind, we approached the current study with the idea that personality traits
630 related to the valuation of reward and loss might predict the degree to which
631 representations in OSC followed the utility and valence models, and participants
632 in Experiment 1 completed a native-language version of the BIS / BAS
633 personality scale (Carver & White, 1994; Leone, Pierro, & Mannetti, 2002)

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634 immediately after the scanning session. This scale generates two primary values:
635 a behavioural inhibition score (BIS), reflecting sensitivity to punishment, and a
636 behavioural activation score (BAS), reflecting sensitivity to reward.

637 We correlated BIS and BAS scores across participants with OSC coefficients for
638 the valence model. This identified a negative correlation between BIS and OSC
639 valence coefficients (Figure 4G), $r = -0.501$, $p = 0.021$, and a non-significant
640 relationship with BAS, $r = -0.122$, $p = 0.294$. It is important to point out, however,
641 that the significance of the relationship between BIS and OSC valence
642 coefficients did not sustain when the single participant with a BIS score of 13 was
643 removed from analysis ($r = -0.370$, $p = 0.056$). This finding suggests that the
644 overall propensity for stronger OSC representation of reward-associated rather
645 than loss-associated targets (and vice versa for distractors) may be reduced in
646 participants with high sensitivity to negatively-valenced outcome. But the pattern
647 should be interpreted with caution given the marginal statistics.

648 The impact on behaviour of reward and loss associations to distractors

649 Experiment 1 identified a difference in detection accuracy for reward- and loss-
650 associated targets. However, because all distractor categories were present in
651 every trial, there was no opportunity to determine how distractors impacted task
652 performance. We accordingly conducted a second behavioural experiment to
653 further examine the effect of reward- and loss-associated distractors on search
654 behaviour. In Experiment 2 each block began with a cue indicating both the
655 target category and pay scheme for the coming trials. Blocks were organized in

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656 pairs such that blocks involving reward-associated, loss-associated, or neutral
657 targets were consistently followed by a block where the target was neutral. In
658 these test blocks examples of the target category from the immediately preceding
659 block could appear as task-irrelevant distractors, allowing us to determine how
660 distractors recently associated to reward or loss impacted search for the neutral
661 target.

662 As illustrated in Figures 7A and 7B, response accuracy in Experiment 2
663 paralleled the pattern of OSC information observed in Experiment 1, thus also
664 closely following predictions from the valence model. Once again, per-participant
665 regression analyses were used to assess the predictive power of the models.
666 Coefficients corresponding to the valence model were positive, $p < 10^{-4}$, but
667 coefficients corresponding to the utility model were negative, $p = 0.036$, reflecting
668 an inverse relationship between the model and experimental results (and thus a
669 very bad fit). Follow-up contrasts demonstrated that detection of reward-
670 associated targets was better than of loss-associated targets, $p < 10^{-4}$, but that
671 detection of neutral targets was degraded more by a reward-associated distractor
672 than by a loss-associated distractor, $p = 0.045$.

673 More detailed analyses of behaviour are presented in Figure 8. Our prior work
674 with reward-associated stimuli has demonstrated that non-strategic reward-
675 driven prioritization expresses in accuracy, response latency, or both measures,
676 depending on task confines (Hickey & Peelen, 2015; Hickey, Chelazzi, &
677 Theeuwes, 2010a), but is short-lived and can be followed by attentional

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678 suppression (Hickey & Peelen, 2015; Hickey & van Zoest, 2012). With this in
679 mind, participants in Experiment 2 were required to respond within 600 ms of
680 stimulus onset. This created two types of task error: explicit errors, when
681 participants incorrectly reported the presence or absence of the target, and time-
682 out errors, where they failed to respond in the critical interval. Separating these,
683 we found that participants made fewer explicit errors when scenes contained a
684 reward-associated rather than loss-associated target (Figure 8A). This did not
685 reflect a response bias: if participants were simply more likely in the reward
686 condition to report the target present, they would have made many errors when
687 the target was in fact absent. But participants were also nominally more accurate
688 in reporting the absence of a reward-associated target (Figure 8B). Accordingly,
689 signal detection analysis shows a greater d' in the reward condition than in the
690 loss condition (Figure 8C) with no concomitant change in criterion (Figure 8D).
691 When participants responded within the time-limit, they were slower to do so for a
692 loss-associated target rather than a reward-associated target (Figure 8E), and
693 the cost in accuracy created by the presence of a reward-associated distractor
694 (Figure 7B) was not a product to speed-accuracy tradeoff, as target responses
695 were not any faster under this circumstance (Figure 8F). Consistent with the RT
696 slowing, participants were less likely to respond within the time limit in this loss
697 condition (Figure 8G). This effect on time-out errors was significantly greater
698 when the target was present than when it was absent (Figure 8H; interaction, $p =$
699 0.004), suggesting that this reflects a difficulty in target processing rather than a
700 more general slowing of response in the loss condition.

701

Discussion

702 Economically rational preferences are defined by their logical consistency: they
703 remain the same across irrelevant changes to circumstance and context (Arrow,
704 1982; Tversky & Kahneman, 1989; Glimcher, 2010). Here we ask whether
705 selective bias for visual stimuli associated with economic benefit meets this
706 criterion. We designed a naturalistic visual search task in which participants
707 earned points with cash value by detecting examples of object categories in
708 images of scenes. Detection of reward-associated targets resulted in a gain of
709 150 points with misses garnering 50 points, whereas detection of loss-associated
710 targets resulted in the forfeiture of 50 points but saved participants from the
711 greater loss of 150 points. Correct detection of both reward- and loss-associated
712 targets therefore had a benefit of 100 points, but this was couched in the
713 irrelevant context of absolute gain or loss.

714 If the ability of reward-associated stimuli to draw attention reflects a normative
715 visual preference for objects that can be used to maximize utility, this design
716 should cause reward-associated and loss-associated stimuli to draw attention
717 equally well. But results from analysis of category information in OSC
718 (Experiment 1) and task performance (Experiment 2) show no hint of this pattern.
719 Consistent with prior work, reward-associated stimuli were easy to detect and
720 well represented in OSC (Hickey & Peelen, 2015). But loss-associated stimuli
721 were not prioritized in the same way. Selective bias for reward-associated object
722 categories in natural scenes thus appears to reflect an irrational visual

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723 preference for objects associated to positive-valence outcome, not a rational
724 sensitivity for stimuli that maximize utility.

725 This bias in visual representation parallels known effects in economic decision-
726 making. Tversky and Kahneman (1981) famously showed that the perceived
727 utility of a choice is sensitive to the context in which the options are presented,
728 with change in this 'choice frame' strongly impacting decision-making and
729 behaviour. As a result, people are more likely to choose an option presented in a
730 positive frame than a negative frame, even when the value of outcome does not
731 change. This has been interpreted as reflecting the use of simplifying heuristics,
732 like reliance on emotional content, that forego effortful reasoning and valuation of
733 options (Lowenstein, Weber, Hsee, & Welch, 2001).

734 By framing the benefit of correct performance in the irrelevant context of absolute
735 loss, we may therefore have caused participants to devalue this outcome
736 altogether. However, results from whole-brain searchlight analysis of our fMRI
737 data argue against this possibility. This identified rational, utility-maximizing
738 stimuli representations in the intraparietal sulcus and superior gyrus of the
739 parietal lobe. This is broadly consistent with existing neurophysiological and fMRI
740 studies suggesting IPS may code the true value of environmental stimuli (eg.
741 Kahnt et al., 2014; Leathers & Olson, 2012). But in the current results these
742 utility-driven representations did not influence encoding in OSC and did not drive
743 task performance.

744 One possibility is that development of these parietal representations was slower

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745 than the impact of valence and thus could not influence the representation of
746 stimuli before the preparation and execution of response. The idea that valence
747 may have an earlier impact on attentional control than does strategy is consistent
748 with existing work using time-sensitive measures (Hickey, Chelazzi, & Theeuwes,
749 2010; Hickey & van Zoest, 2012; Buschschulte, Boehler, Strumpf, Stoppel,
750 Heinze, Schoenfeld, & Hopf, 2014) and in line with the broad idea that
751 prioritization of reward-related stimuli may reflect long-term plasticity in visual
752 cortex triggered by neuromodulatory signals (Roelfsema, van Ooyen, &
753 Watanabe, 2010; Hickey & Peelen, 2015, 2017). Our results further support the
754 idea that OSC representations may be influenced by neuromodulatory systems
755 by showing that these representations vary as a function of signalling in midbrain
756 nuclei known to contain dopaminergic cells.

757 At first glance, our results appear at odds with a literature demonstrating
758 attentional bias toward negatively-valenced stimuli associated to threat or pain
759 (Tamietto & De Gelder, 2010; Pessoa & Adolphs, 2010). However, this bias is
760 thought to be unique, perhaps relying on a distinct subcortical route for visual
761 information (Tamietto & De Gelder, 2010). There are relatively few studies
762 investigating attentional bias to stimuli associated with economic loss, and these
763 have garnered mixed results (Schacht, Adler, Chen, Guo, & Sommer, 2012;
764 Wentura, Müller, & Rothermund, 2014; Wang, Yu, & Zhou, 2013). Studies
765 employing disgusting images, however, show that these are rapidly suppressed
766 and subsequently ignored (eg. Zimmer, Keppel, Poglitsch, & Ischebeck, 2015).
767 The emotion evoked by stimuli associated with small, unavoidable economic loss

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768 strikes as potentially more similar to disgust than fear, and it is perhaps
769 reasonable that the visual representation of our loss-associated objects is similar
770 to that of stimuli associated to disgust.

771 In conclusion, we show an economically irrational influence of prior experience
772 on search for naturalistic environmental stimuli and the encoding of these stimuli
773 in ventral visual cortex. Normative models of economic behaviour propose that
774 human preferences are consistent and rational, but results from studies of
775 decision-making and behavioural economics show that this is commonly not the
776 case (Glimcher, 2010). Here we demonstrate that this economic irrationality in
777 human cognition begins as early as during perceptual encoding of our
778 environment.

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Figure Captions

Figure 1. Predictions from the utility and valence models. (A) By the utility model, reward- and loss-associated targets should draw selective resources, and thus be better represented than neutral targets. (B) During search for neutral targets, reward- and loss-associated distractors should require the same degree of attentional suppression, and thus be poorly represented relative to neutral distractors. (C) By the valence model, reward-associated targets should draw selective resources, while loss-associated targets may be actively suppressed and poorly represented in the visual system. (D) Reward-associated distractors should require attentional suppression, but loss-associated distractors should not.

Figure 2. (A) Schematic illustration of the trial sequence. Participants reported the presence of examples of the cued category in briefly presented scenes. Of four possible target categories, one was associated to reward, one to loss, and two to neutral outcome. Image and font sizes are not to scale, and the block cue here indicates only the target category for the coming trials, whereas in the experiment itself the total number of points earned to that point in the experiment was also presented. (B) Feedback schedule. The association of category to outcome in the actual experiment was counterbalanced across participants. Note that feedback indicated here was for target-present trials. Correct performance in target-absent trials garnered a single point in neutral blocks and 0 points in reward and loss blocks. Incorrect performance in target-absent trials resulted in the loss of a single point in neutral blocks and the loss of 50 points in reward and loss blocks. (C) Analytic approach. Scene-evoked activity patterns in OSC were correlated with benchmark patterns. High correlation indicates increased information for that category in visual cortex during scene perception.

Figure 3. Results from Experiment 1. (A) In line with the valence model, reward-associated targets are better represented in OSC than loss-associated targets. (B) During search for neutral targets, OSC carried less information about reward-associated distractors than loss-associated distractors, indicative of attentional suppression. Note that our normalization procedure causes these values to be represented on an interval scale with an uninformative zero point. As such, negative values do not imply the presence of information in the form of negative correlation (see Materials and Methods for details). (C) Accuracy in detecting the target when it was present in the scene. (D) The relationship between coefficients from a fit of the valence model to OSC category information, as illustrated in panels A and B, and coefficients from a fit of the valence model to hit rate data, as illustrated in panel C. Error bars reflect within-participant standard error (Cousineau, 2005).

Figure 4. (A) Anatomically defined ROIs characterizing the SN and RN. (B) Relationship between inter-individual variance in the valence coefficient of the SN ROI and the valence coefficient of category information in OSC. (C) Midbrain voxels identified in whole-brain correlational analysis. Note that the single 3mm voxel on the midline actually begins one slice inferior to the illustrated horizontal section (beginning at $z = -14$). (D-F) Other clusters identified in whole-brain correlational analysis, see text for

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951 details. (G) Relationship between inter-individual variance in BIS and the valence
952 coefficient of category information in OSC.

953

954 Figure 5. (A) OSC as defined in the OSC localizer. Voxels identified here were present in
955 the OSC of 16 or more of the 23 participants in Experiment 1. (B) Results from the
956 searchlight contrast of information for targets vs. distractors. Voxels identified here
957 constitute the center of spheres that carried more information for targets than distractors
958 at $p < 0.001$ with a cluster threshold of 50 voxels.

959

960 Figure 6. (A) Parietal cluster identified in searchlight analysis. This brain region was
961 defined by contrasting information content for targets vs. distractors. Centroid: +9, -73,
962 +43, MNI space. (B) Results from analysis of outcome association in the parietal cluster.
963 Error bars reflect within-participant standard error (Cousineau, 2005).

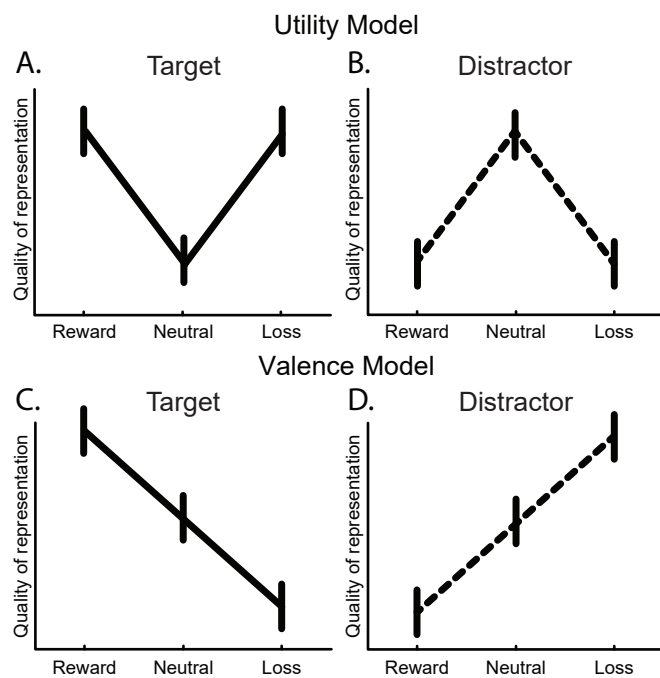
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965 Figure 7. Results from Experiment 2. (A) In line with the valence model, accuracy is
966 better for reward-associated targets than loss-associated targets. (D) Search for a
967 neutral target is more strongly disrupted by a reward- vs. loss-associated distractor.

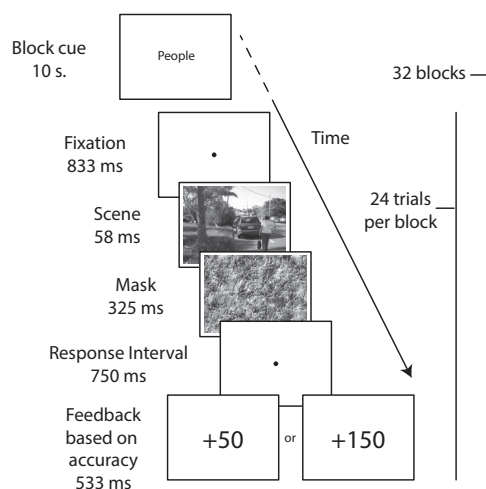
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969 Figure 8. Further analysis of results from Experiment 2. (A) Explicit accuracy in target-
970 present trials as observed when a response was made within the time limit. (B) Explicit
971 accuracy in target-absent trials. (C) Perceptual sensitivity for targets. (D) Response
972 criterion. Participants tended to report the target as present, resulting in a negative
973 criterion, but this did not differ across reward and loss conditions. (E) Reaction times for
974 target-present and target-absent trials as a function of target association. (F) Reaction
975 times for target-present and target-absent trials where the target had neutral
976 association, as a function of whether a reward-, loss-, or neutral-associated distractor
977 was present in the scene. (G) Number of time-out trials when target was present, as
978 proportion of total per condition. (H) Number of time-out trials when target was absent.
979 Error bars reflect within-participant standard error (Cousineau, 2005).

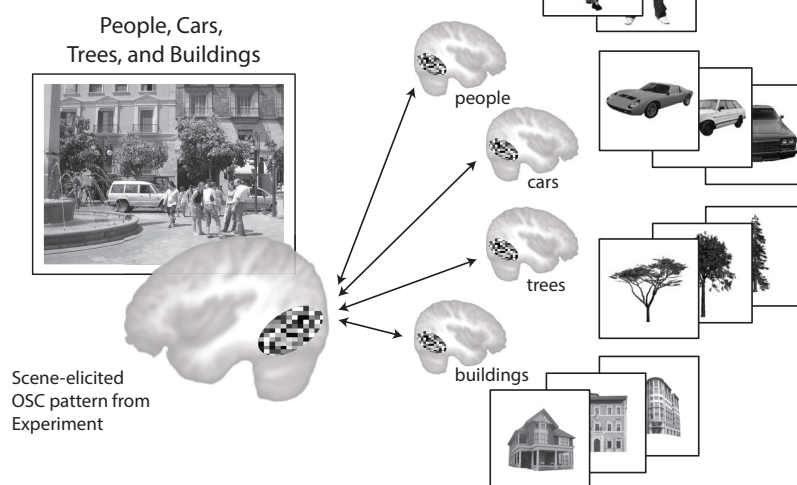
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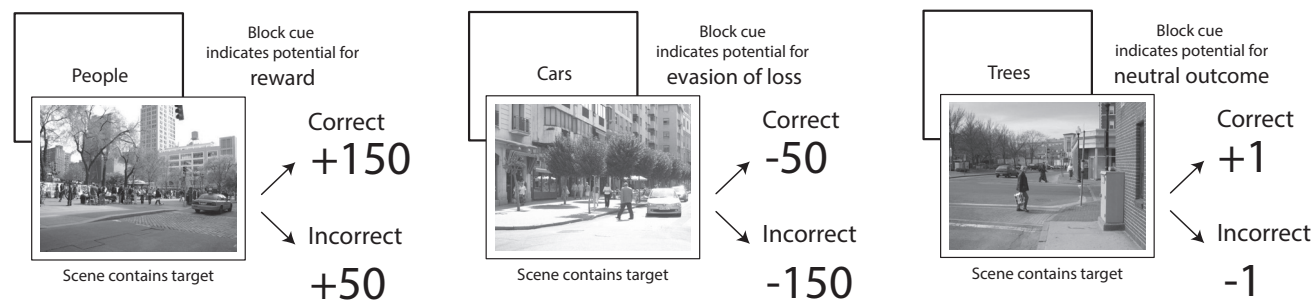
A. Experiment 1: Visual search in natural scenes



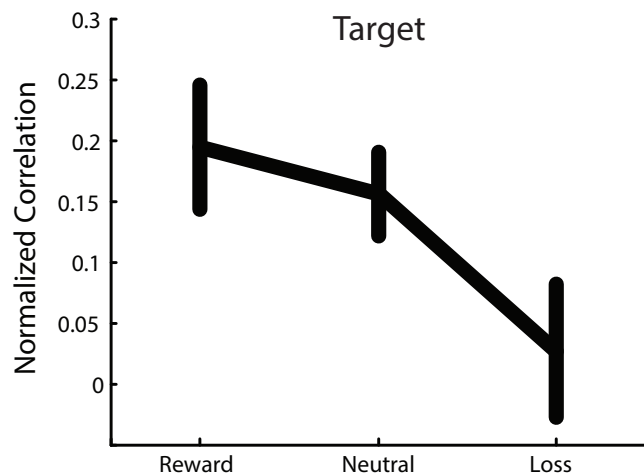
C. Correlate Scene-elicited OSC Patterns To Patterns from Category Localizer



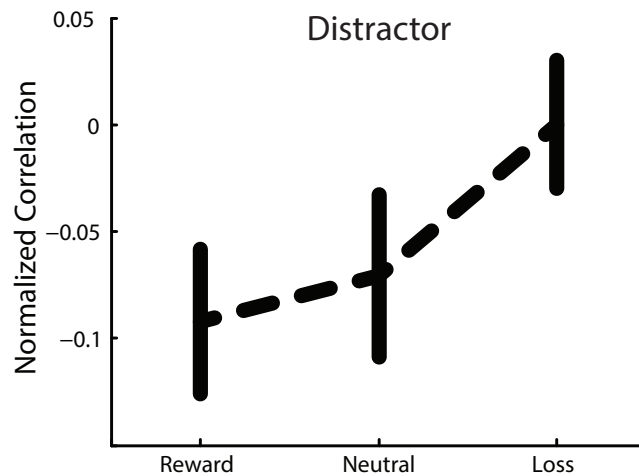
B. Feedback Schedule



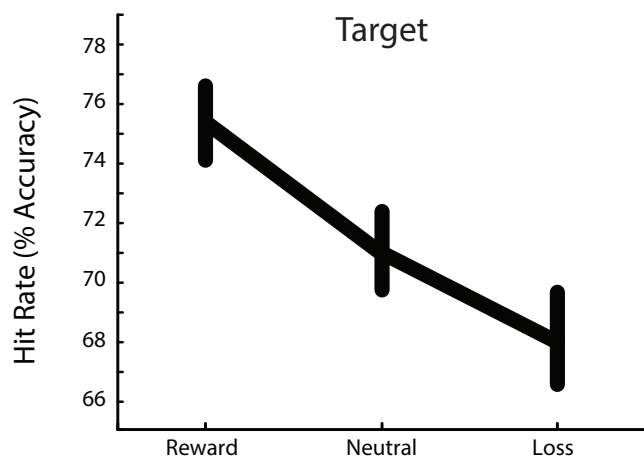
A.



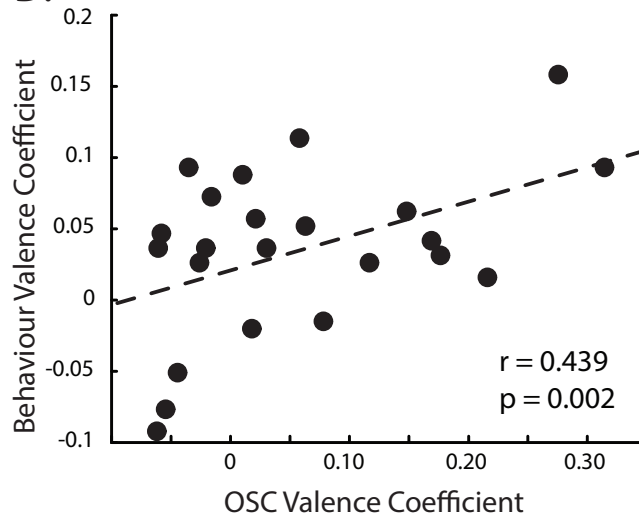
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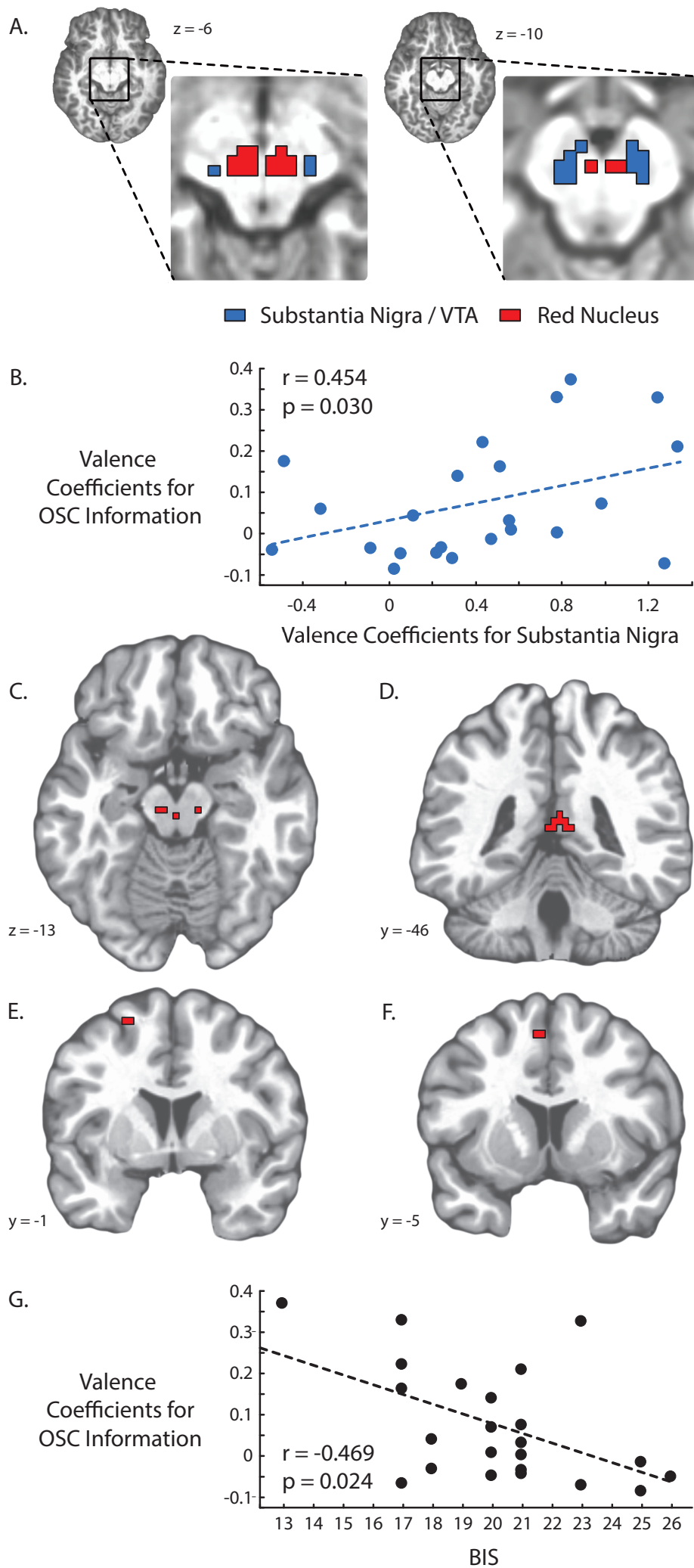


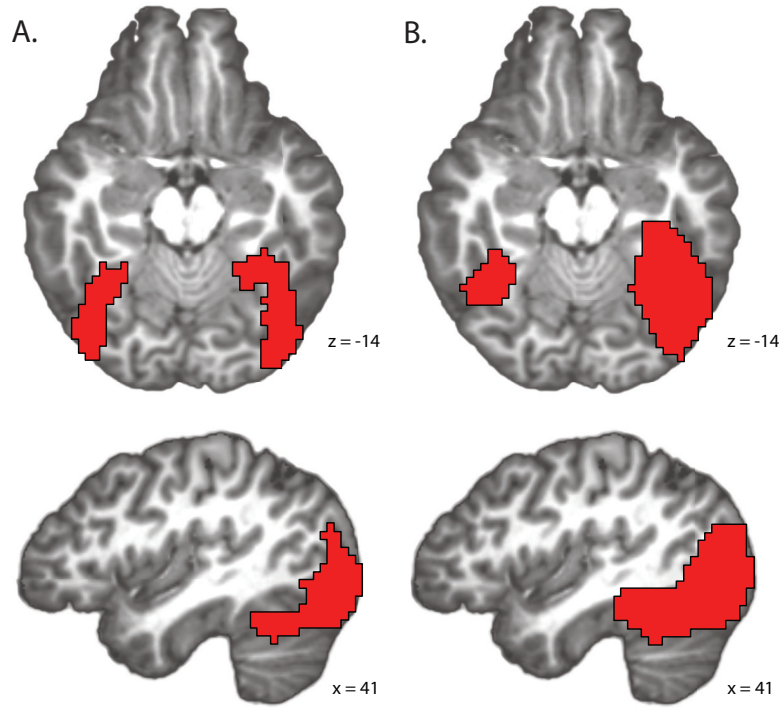
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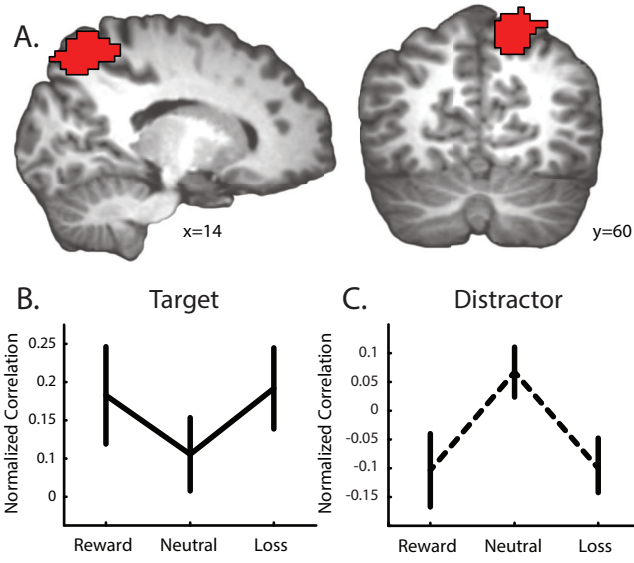


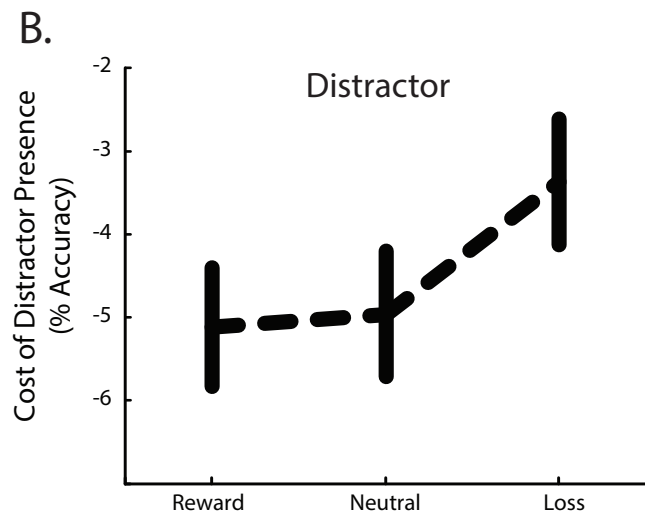
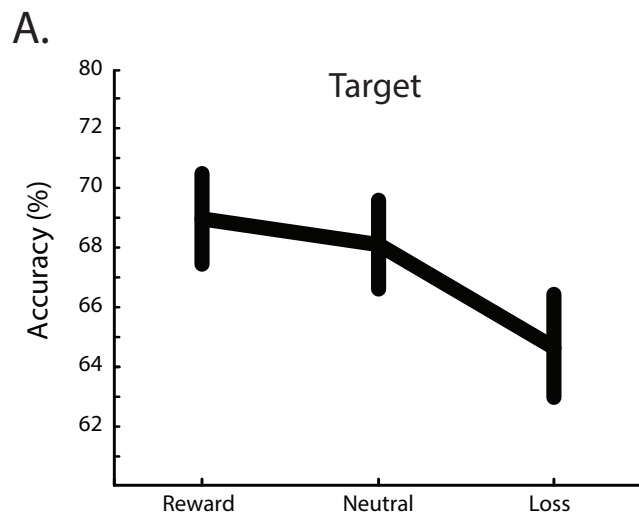
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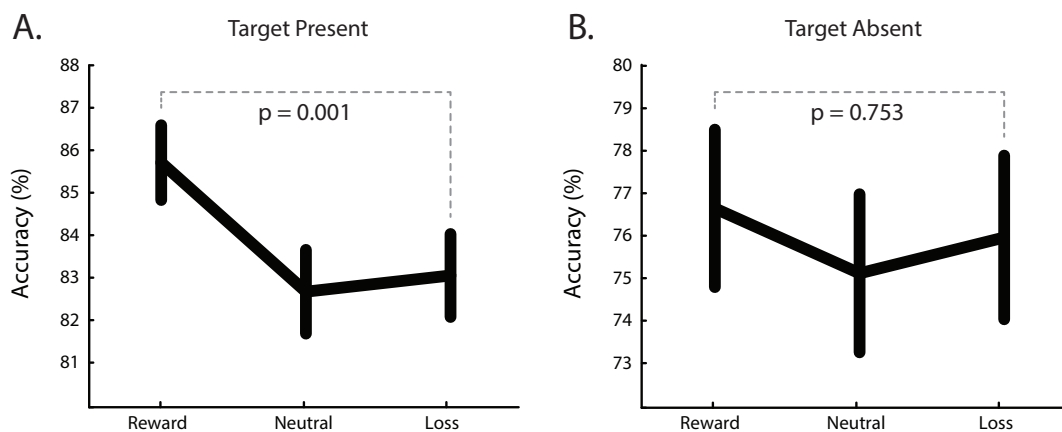




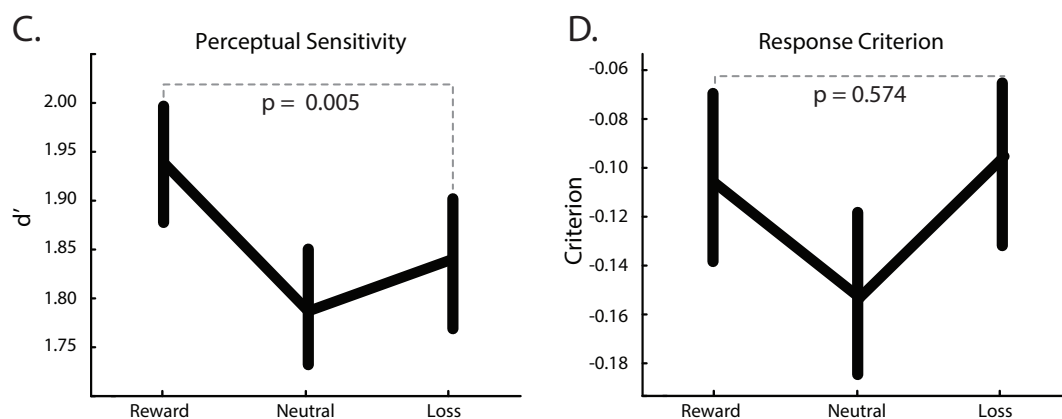




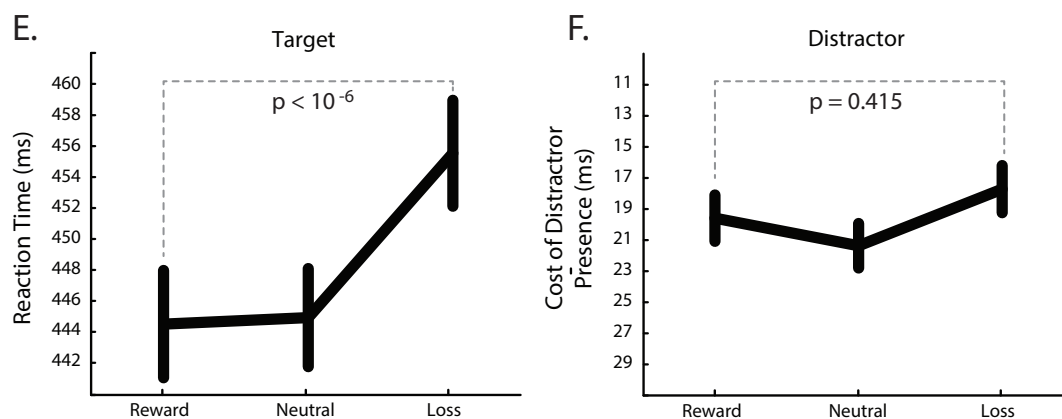
Accuracy - Response made



Signal Detection - Response made



Reaction Times - Response made



Time-outs - No response made

