How Learning and Motivational Shifts Determine the Incentive Salience of Reward Cues: a Human Behavioral Perspective

by

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ABSTRACT

Reward cues acquire distinctive incentive properties from their association with motivationally significant outcomes. These incentive properties are manifest in an augmented salience that provides reward cues with the capacity to attract attention, also in contexts where pursuing the reward is not relevant. I will first examine the unresolved debate concerning the learning parameters that define the cue-reward association and eventually modulate attention. Specifically, whether the cue attentional salience is governed by reward expectancy or uncertainty. I will then study another incentive property of reward cues, that is the ability to strengthen the performance of a separately learned instrumental action exerted to obtain an outcome, a phenomenon known as Pavlovian-Instrumental transfer (PIT). Since the motivational value of reward is altered when reward is devalued, an interesting question is whether the incentive properties of reward cues change accordingly, both in the attentional and in the operant domain. Therefore, I will investigate the effects of motivational shifts on the incentive properties of reward cues, by means of reward devaluation. In the context of the ability of a cue attentional salience to update in accordance with the altered outcome value, I will further analyze the influence of incentive learning (i.e. the possibility to re-associate the cue with the devalued outcome). The procedures adopted through the experiments share two main phases: a learning phase in which human thirsty participants learned cue-beverage reward associations involving different contingencies, and a test phase in which no reward was delivered. During the learning phase, participants accumulated the beverage reward that acted as an incentive, since it was not consumed through this phase. This allowed a controlled devaluation procedure by consummatory satiation (i.e.

a motivational shift) that was administered at different moments during the experiments depending of the hypothesis at test. Results showed that the cues that better predicted the reward during learning were the stimuli preferentially attended at test, and the stimuli that invigorated more the instrumental action for the outcome. These incentive attributes persisted despite reward devaluation: the attentional bias and the PIT effect emerged unaltered after participants quenched their thirst. Reward cues persisted in capturing attention after reward devaluation even when participants were given the chance for incentive learning by means of an additional learning phase. Taken together, the evidence that emerged indicates that the incentive properties of reward cues, once acquired, can surprisingly and irrationally outlast reward devaluation and can resist incentive learning, suggesting that some incentive properties of the cue can become independent from those of the reward. These results may provide important implications for the understanding of the psychological mechanisms underlying different types of addiction.

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CHAPTER 1

INTRODUCTION

Everyday our cognitive system is bombarded with a multitude of stimuli that recall us or allude to rewarding goods or experiences. In most societies at present, it is hard not to encounter a marketing sign on a daily basis. Those signs (or *cues*) are often not only shimmering in colors and sophisticated in design, but also well-conceived to evoke hedonic memories, desires or symbolic values in the attempt to spur the consumption of rewarding products. So, for example, seeing the sign of a pizza can make us hungry, even if a moment before we were not thinking of food. At the same time, a luxury car brand can call to mind beliefs, attitudes, and even personality traits - a set of concepts that have nothing in common with the mechanics of a motor vehicle. The psychological mechanism, whereby some stimuli are capable to evoke certain qualities of the associated reward, and to trigger its pursuit, is a form of associative learning known as Pavlovian conditioning (Bindra, 1978; Toates, 1986). Crucially, conditioned incentive stimuli are powerful attractors that grab our attention and incite action, a fact that is beautifully captured by the etymology of the word “advertising”, which comes from the Latin *ad vertere*, namely "to turn toward". Conditioning and other learning mechanisms play a fundamental role in determining the organism consumption of food and other substances, and provide a perspective for understanding maladaptive motivational behaviors such as compulsive food seeking and addiction.

FROM REINFORCES TO INCENTIVES

The traditional view posits that the main function of reward is to reinforce the association between two stimuli (S-S, Pavlovian conditioning), or between stimulus and response (S-R, Instrumental conditioning). However, since the original studies of Bindra (1978) and Toates (1986), an additional view have been proposed to account for the type of learning that occur in conditioning. According to this particular view, the main role of reward is to provide *incentive motivation* rather than to reinforce or “stamp in” the S-S or the S-R association (Berridge, 2001; Kringelbach & Berridge, 2016). Within this theoretical framework, the conditioned stimulus (CS) can acquire the motivational properties of the unconditioned stimulus (US), by means of Pavlovian learning. Hence, once conditioning has taken place, the CS works not only as a predictor of the US occurrence, but, importantly it can also trigger the desire of the associated US (Berridge, 2012). Therefore, the cue is salient not only because it generates an expectation about the arrival of the reward, but because the cue itself becomes an incentive stimulus with motivational properties. The incentive theory of reward provided a theoretical framework to explain apparently irrational phenomena like *autoshaping* and operant *stereotypies*, which were commonly observed in animal studies. In the autoshaping phenomenon, indeed, the animal approaches and tries to consume the reward cue itself (i.e. the CS), a behavior that might appear irrational and bizarre, and that reveals that the animal’s attention is totally captured by the reward cue, even in the extreme case of the (reward) omission contingency (Schwartz & Williams, 1972).

THE INCENTIVE-SENSITIZATION THEORY OF ADDICTION

The ability of some Pavlovian cues to attract attention and to trigger the pursuit of their associated reward or US has been described in the framework of the incentive-sensitization theory of addiction (Berridge & Robinson, 1998, 2016, T. E. Robinson & Berridge, 1993, 2008). In this framework, a particular type of implicit *"wanting"* (or *incentive salience*), well distinguishable from learning or explicit cognitive desires (Berridge & Robinson, 2003), is defined as a type of wanting for reward triggered by Pavlovian cues and by the unconditioned reward itself. Crucially, the notion of incentive salience rests on two key psychological processes, attention and motivation. Hence, a cue with a great incentive salience can trigger a "wanting" for the associated US, a form of visceral and irrational desire that motivates the organism to obtain the reward, but that differs from the explicit *wanting*, which is a rational cognitive wish (Berridge & Robinson, 2003). At the same time, the cue incentive salience engages the organism's attention, so that the Pavlovian cue behaves like an attentional magnet or attractor, while also promoting the action to obtain the corresponding reward or US. Mesocorticolimbic brain systems and dopamine neurotransmission, previously thought to be responsible for hedonic pleasure (Wise, 2004) and then for learning about rewards (Schultz, 1998), might instead mediate this type of "wanting" (Badiani, Berridge, Heilig, Nutt, & Robinson, 2017; Berridge, 2012). According to the theory, "wanting" is often correlated with *"liking"* (i.e. the hedonic component of reward), but dissociable under some circumstances (Tindell, Smith, Berridge, & Aldridge, 2009). The theory posits that a cue for reward can trigger a desire to seek that reward, but not only that. The behavioral attractiveness is therefore a hallmark of "wanting" or incentive salience.

Accordingly, the attentional system of humans and other animals seems to be biased towards cues that predict motivationally significant outcomes (Chelazzi, Perlato, Santandrea, & Della Libera, 2013). The responsiveness of the attentional system towards valuable stimuli has been largely investigated in the last decade, and a great bulk of evidence has accumulated showing that reward-predicting cues attract covert and overt attention. The evolutionary benefits of this attentional bias are evident. Reward cues act like motivational magnets: they automatically and involuntarily attract eye-fixation (Chen, Cheng, Zhou, & Mustain, 2014; Pool, Brosch, Delplanque, & Sander, 2014; Theeuwes & Belopolsky, 2012) and deviate ocular movements (Hickey & Van Zoest, 2012). Stimuli that have been trained in association to a reward become distractive for the motivational value they acquire, independently of their physical salience or their relevance to the task (Anderson, Laurent, & Yantis, 2011). The ability of some cues to grab attention and to trigger the desire for their associated reward can be so powerful to become in some cases pathologic, as in drug addiction. Indeed, drug addicts are often inevitably attracted by drug cues, which in turn trigger compulsory drug craving and consumption (Berridge & Robinson, 2016).

THE PRESENT WORK

The aim of the present work is to investigate the behavioral attributes of incentive salience of reward cues in humans, by looking at how human perception and behavior is affected by the presence of stimuli that formerly predicted an incentive outcome. In Chapter 2 and 3, the focus is to determine the learning mechanism that governs the relation between a cue and a reward, and that is responsible of endowing a reward cue with the behavioral attributes of incentive salience. By further manipulating the physiological state that underlies different motivational states, in Chapter 4 and 5 I examine how the incentive salience of reward cues can be modulated, and what are the factors that might influence such modulation. In Chapter 6, the aim is to explore how time and learning can alter the motivational properties acquired by reward cues.

CHAPTER 2

ATTENTIONAL BIAS:

THE UNCERTAINTY FACTOR

A LEARNED ATTENTIONAL BIAS

The debate on how reward predicting stimuli attain the capacity to bias attention arose decades ago in the field of associative learning (for a review see Le Pelley, 2004) and fostered a line of research investigating how nonhuman animals attend to the environment as a result of conditioning (Pearce & Bouton, 2001). Independently from the associative learning tradition, a more recent line of research has suggested that learning influences the capacity of stimuli to capture attention in visual search tasks (e.g., Anderson, Laurent, & Yantis, 2011). Recently, these two research areas have been considered together in order to broaden the understanding of the relation between learning and attention (Le Pelley, Mitchell, Beesley, George, & Wills, 2016). The present chapter aims at further exploring the relation between attention and reward in the context of associative learning.

EXPECTANCY VS. UNCERTAINTY

The literature addressing the influence of learning on attention is dominated by two main views. One view, advocated by Mackintosh (1975), claims that attention is preferentially allocated towards the relatively best reward predictor, and therefore the cue's salience would increase with the strength of the cue-reward association. The idea that the cue attentional salience is proportional to the reliability of the information regarding the outcome prediction is exemplified by the *predictiveness principle*. Analogously, the *learned value* encapsulates the idea that the cue attentional salience is proportional to the motivational significance of the outcome prediction. It has already been proposed that the predictiveness principle and the learned value are intimately related (Le Pelley et al., 2016); therefore, here I shall refer to them as the *expectancy* hypothesis. Alternatively, Pearce and Hall (1980) proposed that attentional salience should be greatest for cues followed by uncertain consequences, probably because *uncertainty* does not allow to develop an automatic response to the cue, and therefore a continuous monitoring of the cue-outcome relation is required. The role of this monitoring process has been acknowledged in a recent attempt to reconcile two apparently opposite views (Beesley, Nguyen, Pearson, and Le Pelley. 2015). According to the authors, the uncertainty hypothesis is reflected in the attentional *exploration* of potential useful cues, whereas the attentional *exploitation* of cues with the goal of maximizing the information benefit would be associated to the expectancy hypothesis.

Existing evidence provides support in favor of both the expectancy and the uncertainty hypothesis. However, when the human literature is reviewed altogether, there seems to be stronger evidence in favor of the expectancy hypothesis than the uncertainty hypothesis (Le Pelley et al., 2016). That said, the debate is not yet resolved.

Indeed, while there are data in support of a hybrid model describing effects consistent with both views (Beesley et al., 2015; Luque, Vadillo, Le Pelley, & Beesley, 2016), a more thorough examination of the uncertainty condition seems advisable. More specifically, it has been suggested that a Pearce-Hall type of processing might emerge when it is necessary to explore several sources of information providing uncertain predictions about the outcome, a condition that has not been fully investigated yet. In other words, procedures in which the role of attention was to exploit the information given by highly reliable cues have produced evidence in favor of the expectancy hypothesis. However, procedures in which there is the need to unveil the causal role of multiple uncertain cues have been overlooked, and might instead provide evidence in line with the uncertainty principle.

THE PREDICTION ERROR PERSPECTIVE

The difference between the Mackintosh view and Pearce and Hall view can also be described in terms of prediction error (Pearce & Bouton, 2001; Rescorla & Wagner, 1972; Schultz, 2006), with the former view claiming that attention is preferentially driven by cues associated with a small prediction error, and the latter view claiming instead that attention is summoned by cues associated with a large prediction error. It is worth noting that a common methodological feature characterizes previous studies establishing that attention is preferentially allocated toward cues that are more likely associated with a fixed amount of reward, or toward cues that predict the largest amount of reward. All those studies have employed a procedure in which expectancy is high and uncertainty is low or zero (e.g., Chen et al., 2014, 2013; Failing & Theeuwes, 2014). Reward expectancy increases monotonically as the reward probability (p) goes from 0 to 1, whereas reward uncertainty is minimal for extreme probabilities and maximal for a probability of .5. Therefore, when for instance a p = .8 reward cue is compared with a p = .2 reward cue, the results from human studies showed that the best reward predictor (p = .8) gains the largest attentional salience (Anderson et al., 2011; Anderson & Yantis, 2012; Theeuwes & Belopolsky, 2012; Wang, Duan, Theeuwes, & Zhou, 2014). It should be noted, however, that human and animal studies directly comparing uncertainty and expectancy have used extreme values of probability: namely, p = .5 to induce the maximum uncertainty, and p = 1 to induce the maximum expectancy. Within this procedure, the results showed that unreliable cues (p = .5) seem to attract more attention than reliable ones (p = 1) (Hogarth, Dickinson, Austin, & Brown, 2008; M. J. F. Robinson, Anselme, Fischer, & Berridge, 2014; M. J. F. Robinson, Anselme, Suchomel, & Berridge, 2015).

Therefore, an interesting question is how a combination of reward expectancy and reward uncertainty would affect the cue's attentional priority when both conditions generate a non-zero reward prediction error, a frequent condition in the real life. To put it formally, the question is whether a p = .5 cue is more salient than a p = .8 cue, a comparison that, to my knowledge, has never been conducted before. Contrasting a p = .5 vs. a p = .8 cue-reward contingency could be highly informative because, according to a recent study, any reward cue must be associated with a certain level of reward prediction error to develop attentional priority (Sali, Anderson, & Yantis, 2014).

It follows that to evaluate the impact of expectancy and uncertainty on the cue attentional salience one should exclude the experimental condition in which the reward prediction error is zero. Consequently, the following experiments tested the attentional capture triggered by a reward cue for three levels of cue-outcome probability (.2, .5, and .8). In such uncertain scenario, a strategy of attentional exploration of the cue-outcome relation is strongly encouraged, which would favor the possibility to observe that the major factor controlling the reward cue attentional salience is uncertainty rather than expectancy.

In Experiment 1, thirsty participants first performed an instrumental conditioning task in which they had to decide whether or not to respond to a colored stimulus (i.e., the reward cue) to obtain a liquid reward, with a given level of probability. Then, in the following extinction phase, participants were engaged in a visual search task, where target and distractor letters were presented inside the previous reward cues, now irrelevant for the task (see Figure 2). In Experiment 2, the cues selection history was equalized (Awh, Belopolsky, & Theeuwes, 2012) during the conditioning task, in order to control that the potential attentional bias emerged in the test phase was a genuine effect of the cue's predictability and not of its selection history (Chapman, Gallivan, & Enns, 2014). By adapting a procedure of omission contingency from Le Pelley and colleagues for conditioning (Failing, Nissens, Pearson, Pelley, & Theeuwes, 2015; Le Pelley, Pearson, Griffiths, & Beesley, 2015; Pearson, Donkin, Tran, Most, & Le Pelley, 2015), Experiment 3 tested the attentional bias towards cues that had never been task relevant, not even during the conditioning phase. Experiment 3 is crucial in two aspects. First, it separates definitively any potential attentional modulation due to prior conditioning from the influence of selection history, even at a conceptual level. Second, it implements for the first time a hybrid approach based on a training phase and a separate test phase, in which the reward cues are always task irrelevant (Anderson & Halpern, 2017).

EXPERIMENT 1

METHODS

Participants

Thirty undergraduate students (M_{age} = 22.1 years, 20 females) took part in the experiment after providing informed consent. They were asked not to drink for about 4 hours prior to the experimental session. They received €5 compensation for their participation.

Apparatus

Participants were seated in a dimly illuminated room with their head supported by a chin rest located at 60 cm from the monitor (1920x1080 resolution, 100 Hz). The generation and presentation of the stimuli was controlled by using Matlab and Psychtoolbox-3 (Pelli, 1997), running on Windows 7. A liquid delivery apparatus was placed on the right side of the monitor and was triggered by the computer. Each delivery consisted of 2 ml of water dropping into a visible cup (see Figure 1).

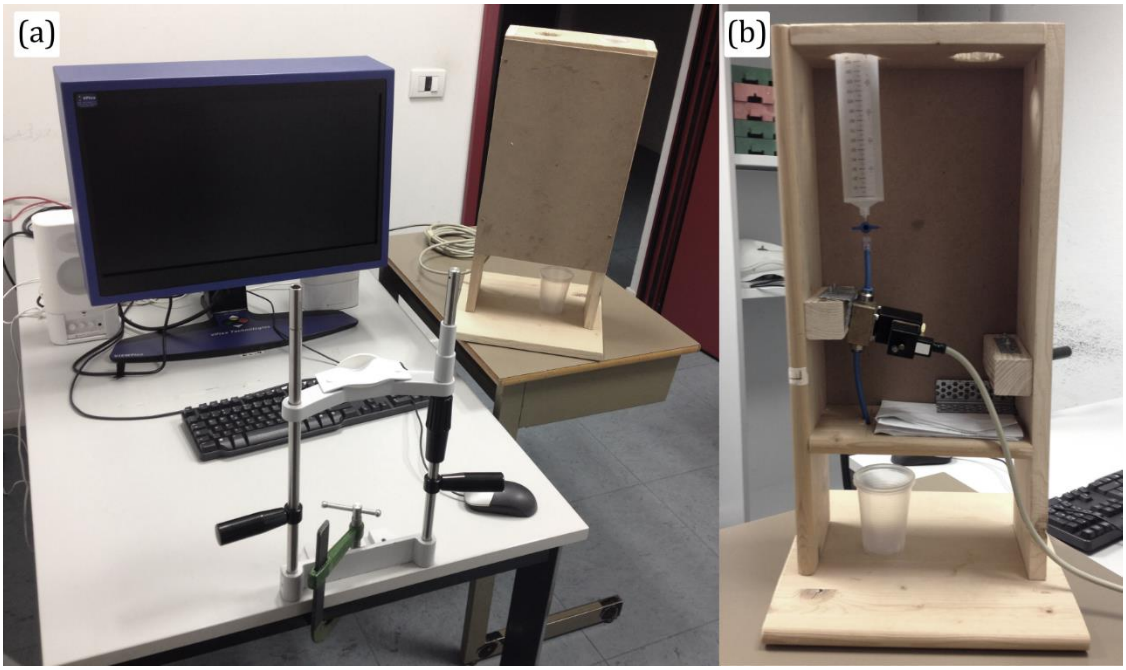

Figure 1. Apparatus of Experiment 1.

(a) General setting. (b) Detail of the liquid delivery apparatus.

Stimuli

Conditioning phase

The cue was an outlined colored ring (2° in diameter, 0.25° thick) with two gaps, one on the left and the other on the right side. The two gaps had different sizes, one large (0.6°) and one small (0.3°). Depending on the cue-reward contingency, the cue could have one of three equiluminant (28 cd/m^2) colors: green, red or cyan. The cue appeared in a random angular position on an imaginary circle with a radius of 5° from the center of the screen (see Figure 2, panel a). A fixation cross, inscribed in a circle with 0.5° diameter, appeared in the center of the screen. The background luminance was set at 13 cd/m^2. Reward delivery was accompanied by the on-screen simulation of a liquid dropping into a glass.

Visual Search

The stimuli consisted of two Ls and one T (1.8° x 1.8°), which appeared randomly tilted to the left or to the right, each one inside a colored ring used as reward cue during the conditioning phase (see Figure 2, panel b). The three compound stimuli were presented simultaneously and equally spaced (120°) on an imaginary circle (5° radius) centered on the screen. A fixation cross, inscribed in a circle with 0.5° diameter, appeared in the center of the screen.

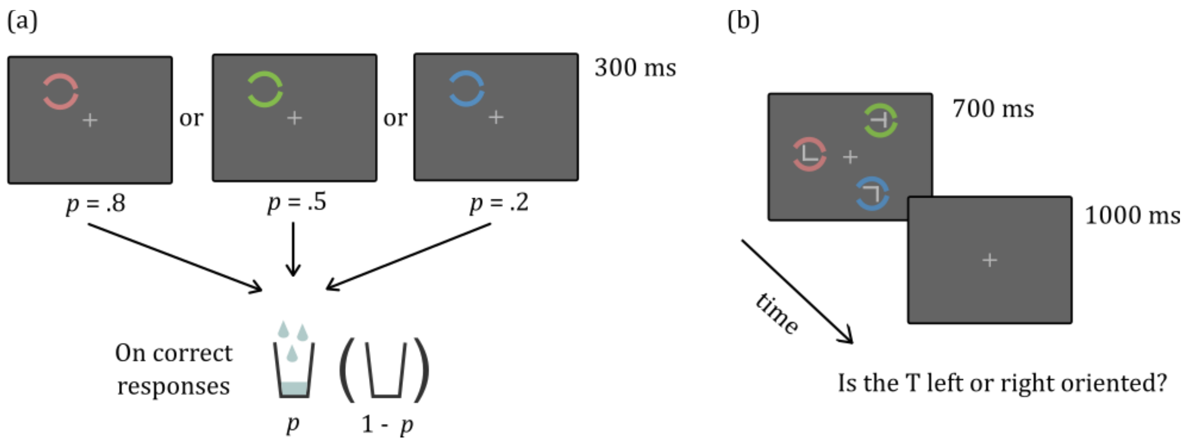

Figure 2. A schematic representation of the experimental procedure of Experiment 1.

(a) Conditioning task. (b) Visual search task.

Procedure

Participants' level of thirst was assessed verbally at the beginning of the experiment. To increase the level of thirst, participants were offered salty food that could be eaten at pleasure. They were also shown a variety of fresh beverages (from water to well-known sugary drinks) and were asked to select their preferred one as reward. The amount of liquid reward that dropped into the glass depended on their responses during the conditioning phase. Before starting the experiment, participants performed a few practice trials using a gray cue with the 0.5 cue-reward contingency. The experiment was divided into two phases, and overall lasted about 50 min. Participants were allowed to drink only at the end of the experiment.

Conditioning

Each trial started with a central fixation cross presented for 1000 ms, then the cue appeared for 300 ms. Participants' task was to detect the side (left vs. right) of the larger gap in the ring by pressing the right or left arrow on the computer keyboard. Participants were informed that each color was associated with a different reward probability and that the number of trials in which a response could be provided was less than the total number of trials. Therefore, they had to decide how to distribute their response as a function of the cue's color in order to maximize the amount of reward (Figure 2). They were also informed that the task could end early if all the available responses were used. However, both the total number of trials in the experiment (300) and the number of available responses (200) were unknown to the participants, who were also not informed about the three cue-reward contingencies. For each participant, the reward probability associated with a given color was randomly determined. In this way, I prevented participants from using the strategy of responding indifferently to all the cues. By contrast, the most effective strategy was to differentiate the response rates between the cues. After the cue appearance, participants had 1300 ms to respond. When delivered, the liquid dropped into a glass (see Figure 2 for details).

After completion of the two conditioning blocks, participants were asked to assess the cue-reward contingencies on a 10-point scale, with 0 meaning that the reward "never" followed the cue, and 9 that it "always" did.

Visual search

Participants performed a visual search task immediately after the conditioning phase. Each trial started with the appearance of a fixation cross for 1000 ms, and then the search display appeared for 700 ms. Participants had to report the orientation of the target letter as quickly as possible (see Figure 2 panel b). A minimal accuracy of 70% was required for obtaining the amount of beverage accumulated during the conditioning task. Participants were informed that no reward was delivered during this task and that the color of the previous reward cue stimuli was not predictive of the target location. Although their gaze was not controlled, participants were instructed to keep their eyes on the fixation cross during the task. From the onset of the display, the maximum time allowed for responding was 1700 ms, whereas the inter-trial interval was 1000 ms. Error feedback was provided. The visual search consisted of 180 trials, divided into 2 blocks of 90 trials. The target appeared within each colored ring in an equal number of trials.

RESULTS

All participants reported to be thirsty at the beginning of the experiment. I tested two contrasting hypotheses about the capacity of reward-predicting cues to capture attention. According to the "uncertainty hypothesis", response times (RTs) in the visual search task should be represented by a U-shaped function, with the minimum RT corresponding to the maximum level of uncertainty (.5). By contrast, the "expectancy hypothesis” would predict a decreasing trend in RTs as a function of increasing stimulus-reward contingencies (Figure 3 panel a). In this and the following experiments, outliers (here <2% of the correct trials) were identified and excluded from the analysis using the procedure suggested by Cousineau (2010). Because it has been shown that the awareness of the cue-outcome relation is critical for the expression of learned behavior in human conditioning studies (Hogarth et al., 2008; Lovibond, 2003; Lovibond & Shanks, 2002), I analyzed participant’s assessments of the cue-reward contingency. Participants ranking the cue-reward contingency in the right order, namely $p = .2$ cue < $p = .5$ cue < $p = .8$ cue, were classified as “aware” ($n = 22$), and the remaining participants as “unaware” ($n = 8$). I shall refer to this division method as the “correct ranking criterion”. I performed a repeated measures ANOVA on visual search RTs for correct responses (overall accuracy in detecting target orientation was 87.3%) including all ($n = 30$) participants with Contingency (.2, .5, and .8) as a within-subject factor and Group (aware and unaware) as a between subject factor. Results showed a significant interaction between Contingency and Group $F(2, 56) = 4.25$, $p = .019$, $\eta_p^2 = .132$, and no significant main effects of Contingency and Group ($p = .146$ and $p = .315$ respectively). I then focused the analysis on the group of “aware” participants. The accuracy in detecting target orientation for the remaining participants ($n = 22$) was 86.6%. A one-way repeated measures ANOVA on visual search RTs showed a significant main effect of Contingency (.2, .5, and .8), $F(2, 42) = 8.79$, $p = .001$, $\eta_p^2 = .295$. Data significantly fitted a linear trend, $F(1, 21) = 12.11$, $p = .002$, $\eta_p^2 = .366$, but not a quadratic trend ($p = .434$), thus favoring the “expectancy hypothesis” (Figure 3 panel c). Pairwise comparisons (one-tailed *t* test) showed that RTs in the $p = .8$ condition were significantly shorter than RTs in the $p = .5$ and $p = .2$ conditions, $t(21) = 2.59$, $p = .017$, $d = 0.552$, and $t(21) = 3.48$, *p*

= .002, *d* = 0.741 respectively. As shown in Figure 3 panel a, this RT-pattern is consisted only with the "expectancy hypothesis".

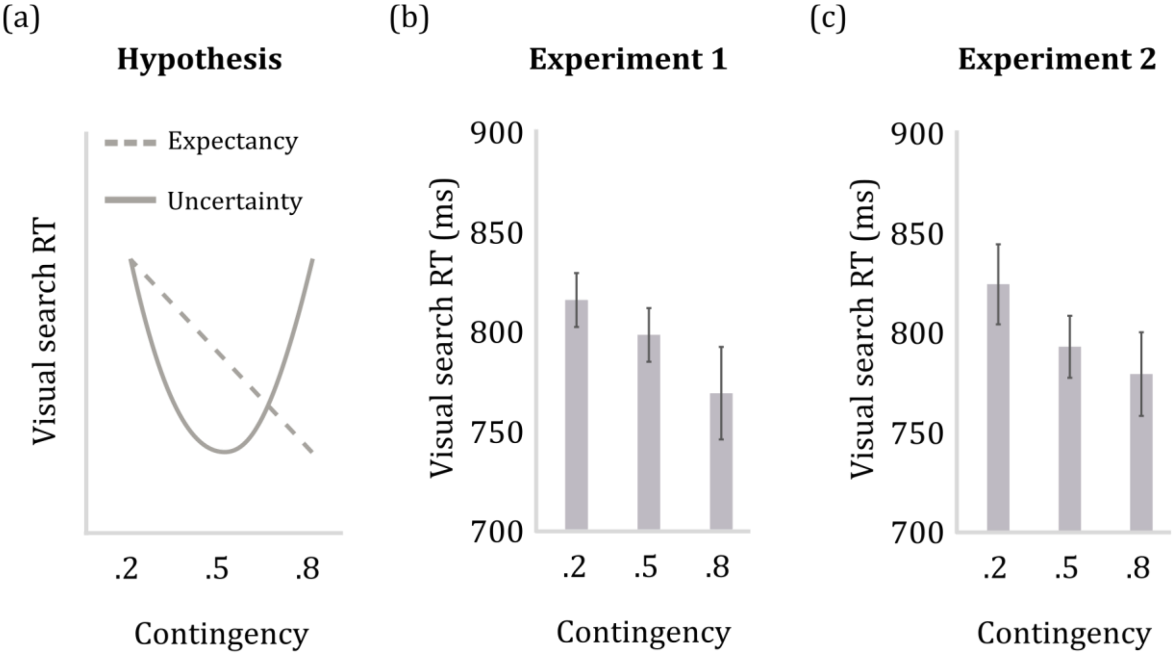

Figure 3. Hypothesis and results of Experiment 1 and 2.

(a) Theoretical RT-pattern predicted by the "expectancy hypothesis" and "uncertainty hypothesis". While the "expectancy hypothesis" predicts decreasing RTs with increasing contingency, the "uncertainty hypothesis" predicts a U-shaped trend, with similar RTs at the extremes and shorter RTs at maximal uncertainty (.5). (b) Visual search RTs in Experiment 1 plotted as a function of cue-reward contingencies. (c) Visual search RTs in Experiment 2 plotted as a function of cue-reward contingencies. Error bars represent 95% confidence intervals for within-subjects designs (Cousineau, 2005).

I analyzed the accuracy in the visual search task, also for detecting possible speed-accuracy trade off effects. A one-way repeated measures ANOVA on visual search accuracy showed a significant main effect of Contingency (.2, .5, and .8), *F*(2, 42) = 3.63, *p* = .035, η_p^2 = .147. Data significantly fitted a linear trend, *F*(1, 21) = 111.36, *p* = .011, η_p^2 = .271, indicating that during the test phase participants were more accurate at responding to targets enclosed in the cues associated to the highest probability of reward. In other words, participants in the test phase were both faster and more accurate in responding to targets enclosed to cues as a function of the cue-reward contingency.

I also analyzed the RTs for correct responses during conditioning, as the speed of responding to a reward cue has been shown to be a good index of conditioning (Pool et al., 2014; Talmi, Seymour, Dayan, & Dolan, 2008). The overall accuracy during the conditioning phase for the "aware" participants was 98.5% and outliers were less than 2%. RTs were entered into a one-way repeated measures ANOVA with the same factor as before, which revealed a main effect of Contingency $F(2, 42) = 21.92$, $p < .001$, $\eta_p^2 = .511$. Data significantly fitted a linear trend, $F(1, 21) = 33.49$, $p < .001$, $\eta_p^2 = .615$, thus indicating that during the conditioning phase participants were faster at responding to cues associated to the highest probability of reward (see Figure 6, panel c).

I also analyzed the rate of instrumental responses associated with the different colors. A one-way repeated measures ANOVA showed a significant main effect of Contingency (.2, .5, and .8), $F(1.41, 29.66) = 65.87$, $p < .001$, $\eta_p^2 = .758$ (Greenhouse-Geisser corrected). Data significantly fitted a linear trend, $F(1, 21) = 86.99$, $p < .001$, $\eta_p^2 = .806$, indicating that participants responses increased with the cue-reward contingency.

Poorly conditioned vs. highly conditioned: a conditioning level criterion

Because it seems reasonable to expect that the attentional bias towards a conditioned stimulus depends on the level of conditioning that has been acquired, I used this information to define two subgroups from the whole $n = 30$ participants: highly conditioned and poorly conditioned, divided by a "conditioning level criterion". To obtain an index of conditioning, I analyzed the rate of instrumental responses associated with the different colors. Intuitively, the degree of conditioning increases as the difference between the response rates increases. Therefore, I computed the response rate for each participant and each color by dividing the number of responses given to a specific color by the total number of available responses for that color. I then calculated the difference between the two extreme rates as follows:

$$\Delta_{\text{RATE}} = \text{RR}_{0.8} - \text{RR}_{0.2}$$

where $\text{RR}_{0.8}$ and $\text{RR}_{0.2}$ were the response rates for the color associated with 0.8 and 0.2 contingency respectively. Moreover, to obtain an index of conditioning awareness I analyzed how each participant assessed the cue-reward contingencies. I defined $\Delta_{\text{AWARENESS}}$ as the discrepancy between the observed ratings and the theoretical values:

$$\Delta_{\text{AWARENESS}} = |\text{T}_{0.2} - \text{O}_{0.2}| + |\text{T}_{0.5} - \text{O}_{0.5}| + |\text{T}_{0.8} - \text{O}_{0.8}|$$

where T and O were the theoretical and the observed values for color-associated contingencies respectively. By definition, the lower is the $\Delta_{\text{AWARENESS}}$, the higher is the participant's degree of knowledge about the reward contingencies, and consequently the higher is the probability of observing a robust conditioning. To summarize, the amount of conditioning increases as Δ_{RATE} increases, but decreases as $\Delta_{\text{AWARENESS}}$ increases. The opposite trends of Δ_{RATE} and $\Delta_{\text{AWARENESS}}$ were corroborated by a significant negative correlation between the two indices (Pearson's $r(30) = -.485$, $p = .007$, see Figure 5 panel a).

An index of the attentional bias for each participant was calculated as follows:

$$\Delta_{\text{RT}} = (M_{\text{RT}0.8} - M_{\text{RT}0.2})$$

where $M_{RT0.8}$ and $M_{RT0.2}$ were the mean RTs for the color associated with 0.8 and 0.2 contingency respectively. As expected, this value correlated negatively with Δ_{RATE} $r(30) = -.381$, $p = .038$, indicating that the more participants differentiated their responses during the conditioning, the larger the attentional bias for colors in visual search (Figure 4, panel a). Moreover, Δ_{RT} correlated positively with $\Delta_{AWARENESS}$, $r(30) = .465$, $p = .010$, indicating that the more a participant understood the color-contingency relation, the stronger the impact of the cues' color on visual search (Figure 4, panel b).

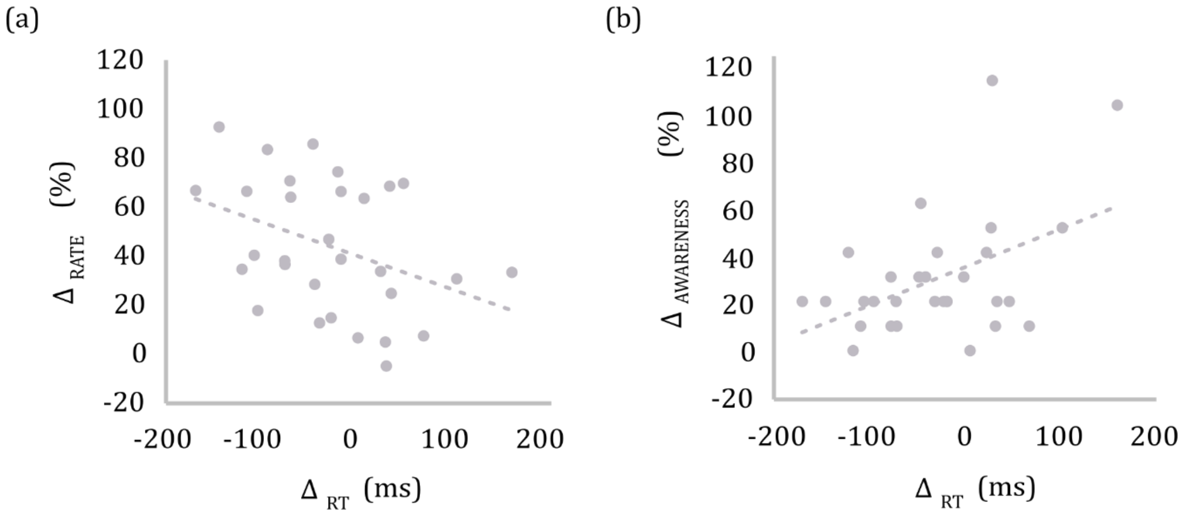

Figure 4. Correlations between conditioning variables in Experiment 1.

(a) Correlation between Δ_{RATE} and Δ_{RT}. The correlation shows that the larger the degree of conditioning (high values of Δ_{RATE}), the stronger the attentional bias in favor of the best reward-predicting cue (negative values of Δ_{RT}). A value of $\Delta_{RT} = 0$ indicates a lack of attentional bias according to the expectancy hypothesis. (b) Correlation between $\Delta_{AWARENESS}$ and Δ_{RT}. The correlation shows that the more participants were aware of the cue-reward contingency (low values of $\Delta_{AWARENESS}$), the more they paid attention to the best reward-predicting cue (negative values of Δ_{RT}). Regression lines are showed.

As suggested by these correlations, I combined Δ_{RATE} and $\Delta_{AWARENESS}$ to define the conditioning level criterion for dividing participants into two groups, depending on the level of conditioning. First, I ranked participants in ascending order according to Δ_{RATE}, and then I plotted $\Delta_{\text{AWARENESS}}$ and Δ_{RATE} together on the same graph (Figure 5, panel b). Because of their negative correlation, the regression lines of Δ_{RATE} and $\Delta_{\text{AWARENESS}}$ crossed each other, and the point of intersection (corresponding to Δ_{RATE} = 34%) was taken as a criterion for defining two groups: highly conditioned (Δ_{RATE} > 34%, *n* = 19) and poorly conditioned (Δ_{RATE} < 34%, *n* = 11).

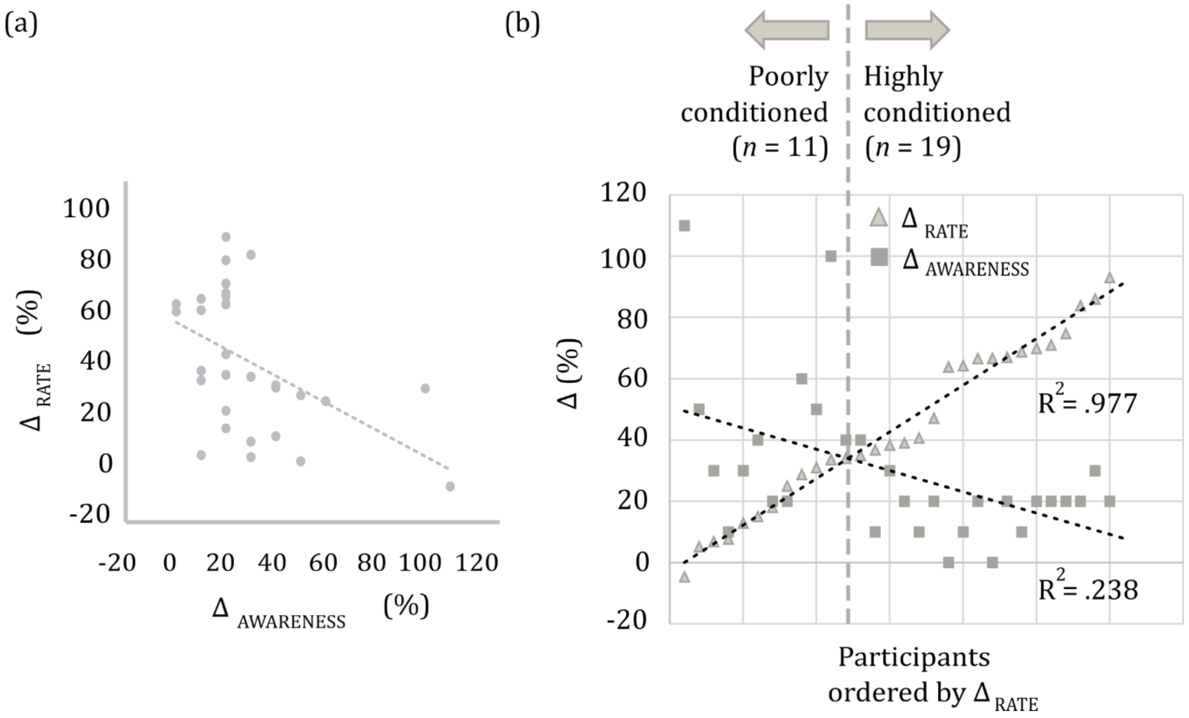

Figure 5. Correlation and conditioning level division criterion in Experiment 1.

(a) Correlation between Δ_{RATE} and $\Delta_{\text{AWARENESS}}$. High values of Δ_{RATE} reflect a markedly different response behavior for the cues during the conditioning phase. Low values of $\Delta_{\text{AWARENESS}}$ indicate that the participants' ratings of the cue-contingency association were accurate. Regression line is showed. (b) Conditioning level criterion. Δ_{RATE} and $\Delta_{\text{AWARENESS}}$ are plotted together, with Δ_{RATE} ranked in ascending order. Regression line and fitting value are shown for each series. The point of intersection of the two regression lines (corresponding to Δ_{RATE} = 34%) was used to divide participants into two groups: the highly conditioned (on the right; *n* = 19) and the poorly conditioned (on the left; *n* = 11).

Response rates were entered into an ANOVA with Contingency (0.2, 0.5, and 0.8) as within-subject factor, and Group (highly conditioned vs. poorly conditioned) as between-subject factor. The main effect of Contingency $F(1.475,41.3) = 66.4$, $p <.001$, $\eta_p^2 =.703$, Group $F(1,28) = 7.74$, $p =.010$, $\eta_p^2 =.217$, and their interaction $F(1.475,41.3) = 21.4$, $p <.001$, $\eta_p^2 =.433$ (Greenhouse-Geisser corrected), were all significant. As shown in Figure 6 panel f, the cue-reward contingency had a larger impact on the response rate of the highly-conditioned group.

For a validation of the conditioning level criterion, I analyzed conditioning RTs for the correct responses (overall accuracy was 98.7% and outliers less than 2%). An ANOVA on RTs with the same factors as before revealed a significant main effect of Contingency $F(2, 56) = 15.2$, $p <.001$, $\eta_p^2 =.351$, and a significant Contingency x Group interaction $F(2, 56) = 14.0$, $p <.001$, $\eta_p^2 =.334$. As depicted in Figure 6, panel d, RTs differed as a function of cue-reward contingency only in the group of highly-conditioned participants $F(2,36) = 32.4$, $p <.001$, $\eta_p^2 =.643$.

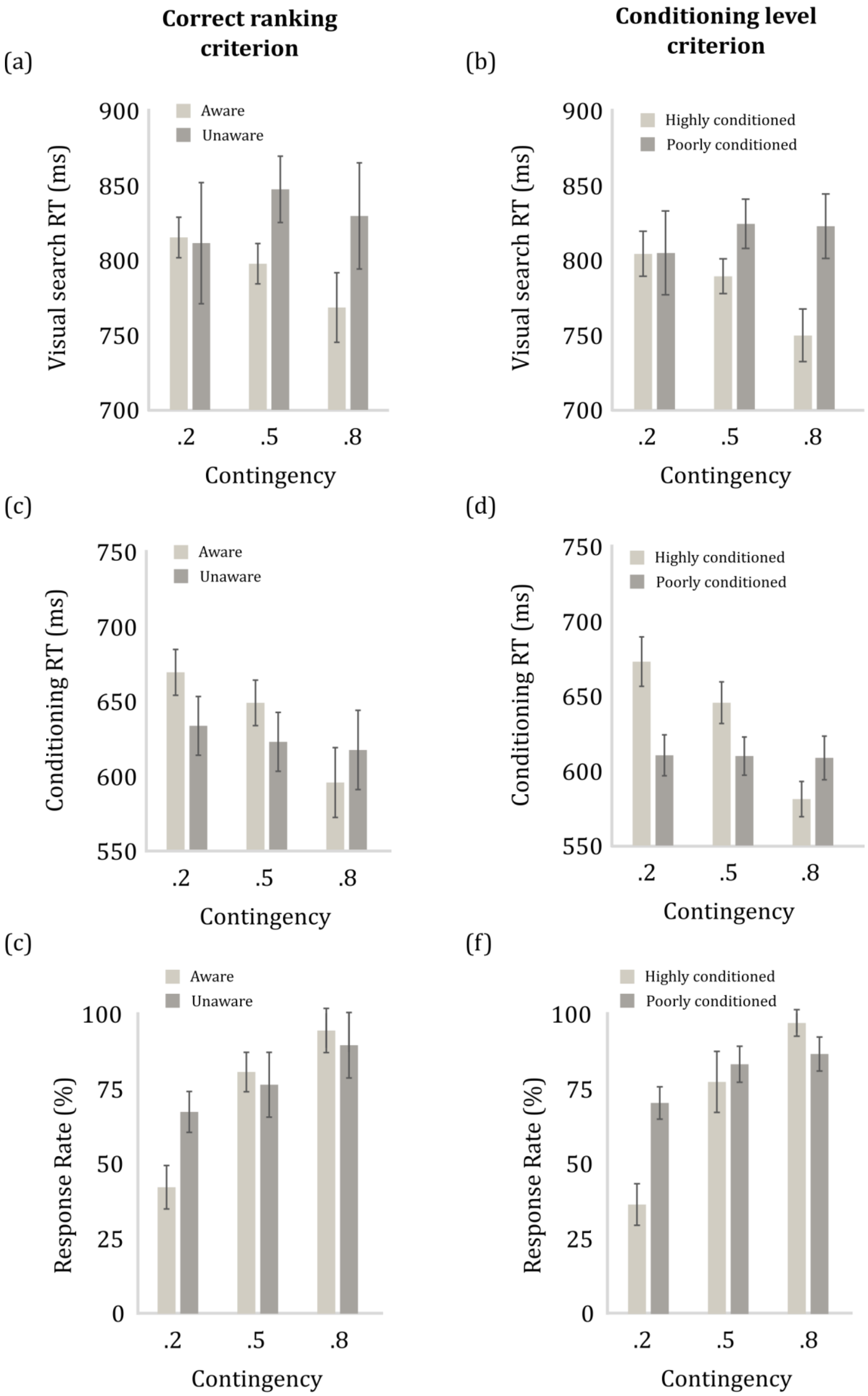
Correct ranking criterion
Conditioning level criterion
(a)
(b)
Visual search RT (ms)
900
850
800
750
700
Aware
Unaware
Highly conditioned
Poorly conditioned
.2
.5
.8
Contingency
(c)
(d)
Conditioning RT (ms)
750
700
650
600
550
(c)
(f)
Response Rate (%)
100
75
50
25
0

Figure 6. Graphical representation of the results of Experiment 1 as a function of division criteria.

(a) Visual search RTs in Experiment 1 across groups as defined by correct ranking criterion and cue-outcome contingencies. (b) Visual search RTs in Experiment 1 across groups as defined by conditioning level criterion and cue-outcome contingencies. (c) RTs during conditioning in Experiment 1 across groups as defined by correct ranking criterion and cue-outcome contingencies. (d) RTs during conditioning in Experiment 1 across groups as defined by conditioning level criterion and cue-outcome contingencies. (e) Response rates during conditioning in Experiment 1 across groups as defined by correct ranking criterion and cue-outcome contingencies. (f) Response rates during conditioning in Experiment 1 across groups as defined by conditioning level criterion and cue-outcome contingencies. Error bars represent the 95% confidence intervals for within-subjects designs (Cousineau, 2005).

Finally, I analyzed again the RTs in the visual search task considering also the between-factor Group. An ANOVA on RTs revealed a significant Contingency x Group interaction $F(2, 56) = 6.32$, $p = .003$, $\eta_p^2 = .184$. Post hoc analyses showed that the effect of Contingency was significant in the highly conditioned group $F(2, 36) = 11.41$, $p < .001$, $\eta_p^2 = .388$, but not in the poorly conditioned group ($p = .489$; Figure 6, panel b). Notably, the data that most contributed to the effect (highly conditioned group) strongly confirmed the "expectancy hypothesis". The linear fit was significant $F(1, 18) = 16.59$, $p = .001$, $\eta_p^2 = .430$, whereas the quadratic fit was not significant ($p = .196$).

DISCUSSION

The results from the visual search task indicate that expectancy is the major factor controlling the attentional salience of the reward cue when the reward-prediction error is not nil. According to my interpretation, such attentional bias would result from a change in the cues' attentional salience caused by the different levels of reward expectancy.

As already reported in the literature (Hogarth et al., 2008), participants that were highly inaccurate in rating the cue-reward contingencies showed no attentional bias during the test phase. Accordingly, I have found that only participants who ranked the cue-reward contingency in the right order (aware participants) showed evidence of capture in the visual search task. Moreover, additional evidence emerges with a deeper investigation of the level of conditioning that participants had developed. Indeed, highly and poorly conditioned participants were separated more finely by adopting a conditioning level criterion that took into account both the participant's response rate and the reported awareness of the cue-reward contingency. The goodness of the splitting criterion was confirmed by the fact that the two groups of participants (highly vs. poorly conditioned) showed also different conditioning RTs. As already documented by previous studies (Pool et al., 2014; Talmi et al., 2008), in the highly conditioned group RTs decreased as contingency increased, whereas no difference emerged in the poorly conditioned group. Although conditioning can take place even for subliminal cues (Knight, Nguyen, & Bandettini, 2003; Mastropasqua & Turatto, 2015; Pessiglione et al., 2008; but see Shanks, 2010), the significant correlation between the magnitude of capture elicited by the cue (Δ_{RT}) and the awareness of the cue-reward contingency ($\Delta_{AWARENESS}$) might indicate that the latter information (awareness) could be relevant for the development of an attentional bias toward the conditioned stimulus.

The attentional bias I have reported is in line with other studies suggesting that attention is captured by stimuli that formerly predicted a motivational outcome. Alternatively, however, because in Experiment 1 the three cues elicited different probabilities of instrumental responses during the conditioning phase, one might argue that the cues differed in terms of selection history (Awh et al., 2012), which in turns determined the attentional bias in the testing phase. If by “selection” we mean the act of attending the cue, then the different rate of responses given to each cue does not necessarily imply that the cues had a different selection history. Indeed, one may note that all cues needed to be strategically attended, as participants had to carefully decide how to distribute the limited number of responses available. Thus, from this perspective all cues had to be attended comparably.

However, if by “selection” we mean the instrumental action of responding to a certain cue (Chapman et al., 2014), then it can be argued that the different response rate associated to each cue was the major determinant of the subsequent attentional bias found in the visual search task.

To ascertain whether the selection history account could explain the results of Experiment 1, a second experiment was conducted in which the cues were equalized in terms of rate of responding during the conditioning phase, by requiring an instrumental response on each trial.

EXPERIMENT 2

METHODS

Participants

Twenty-two undergraduate students (M_{age} = 19.1 years, 17 females) took part in the experiment after providing informed consent. They were asked not to drink for

about 4 hours prior to the experimental session. They received €5 compensation for their participation.

Apparatus

As in Experiment 1.

Stimuli

As in Experiment 1, except that the three colored rings, which served as cues in the conditioning phase and as irrelevant stimuli in the visual search task, had no gaps along the circumference.

Procedure

As in Experiment 1, except that during the conditioning phase, on each trial, the participant's task was to either "accept" or "reject" the cue by pressing the "m" or the "x" key of the keyboard respectively. If participants decided to "accept" the cue, they gained the possibility of receiving the liquid reward, as a function of the cue-reward probability. However, whether or not they received the reward, as in Experiment 1, participants had a limited number of "accept" responses available. On the other hand, if participants decided to "reject" the cue, they had no chance of receiving the liquid reward and the number of available responses remained unvaried. In this way, not only the cues were equally attended, but they were also identical in terms of responses required, which implies that they had the same selection history.

RESULTS

All participants reported to be thirsty at the beginning of the experiment. Three participants were excluded from the analysis because their accuracy in the visual search task was less than 75%. The two criteria of division adopted in Experiment 1, namely the "correct ranking" and the "level of conditioning" criteria, have produced similar results. Therefore, in this and the following experiments I adopted the simplest correct ranking criterion. I then classified participants as "aware" and "unaware" applying the same correct ranking criterion of Experiment 1 (correct ranking). I performed a repeated measures ANOVA on visual search RTs for correct responses (overall accuracy in detecting target orientation was 89.8%) including all (n = 19) participants with Contingency (.2, .5, and .8) as a within-subject factor and Group (aware and unaware) as a between subject factor. Results showed a significant interaction between Contingency and Group $F(2, 34) = 8.24$, $p = .001$, $\eta_p^2 = .327$, and no significant main effects of Contingency and Group ($p = .248$ and $p = .292$ respectively). I therefore focused the analysis on the group of "aware" participants (n = 15). The accuracy in detecting target orientation for the remaining participants in the visual search task was 89.7% and outliers resulted in less than 2% of the correct trials. A one-way repeated measures ANOVA showed a significant main effect of Contingency (.2, .5, and .8), $F(2, 28) = 5.30$, $p = .011$, $\eta_p^2 = .275$. Data significantly fitted a linear trend, $F(1, 14) = 7.81$, $p = .014$, $\eta_p^2 = .358$, but not a quadratic trend ($p = .479$), thus favoring again the "expectancy hypothesis" (Figure 3 panel c). Pairwise comparisons (one-tailed t test) showed that RTs in the $p = .8$ condition were shorter than RTs in the $p = .2$ condition, $t(14) = 2.79$, $p = .007$, $d = 0.720$, although they did not differ with RTs in the $p = .5$ condition ($p = .142$).

I then analyzed the RTs during conditioning, separately for “accept” and “reject” responses. Outliers (<2%) were treated as described before. For “accept” responses, a one-way repeated measures ANOVA with the same factors as before revealed a main effect of Contingency $F(2, 28) = 11.13$, $p < .001$, $\eta_p^2 = .443$. Data significantly fitted a linear trend, $F(1, 14) = 21.65$, $p < .001$, $\eta_p^2 = .607$, indicating that during the conditioning phase participants were faster at deciding to accept the cue associated to the highest probability of reward. Analogously, for “reject” responses, the analysis revealed a main effect of Contingency $F(1.20, 16.80) = 6.40$, $p = .018$, $\eta_p^2 = .314$ (Greenhouse-Geisser corrected). Again, data significantly fitted a linear trend, $F(1, 14) = 7.72$, $p = .015$, $\eta_p^2 = .355$, but with an opposite direction, indicating that during the conditioning phase participants were faster at rejecting the cue associated to the lowest probability of reward.

Moreover, I analyzed the rate of responses of acceptance associated with the different colors. A one-way repeated measures ANOVA showed a significant main effect of Contingency (.2, .5, and .8), $F(2, 28) = 49.00$, $p < .001$, $\eta_p^2 = .778$. Data significantly fitted a linear trend, $F(1, 14) = 110.7$, $p < .001$, $\eta_p^2 = .888$, thus indicating that the rate of acceptance of a cue increased with its contingency, with the consequence that obviously the rate of refusal of a cue increased as its contingency decreased.

DISCUSSION

Experiment 2 was designed to explore whether the selection history hypothesis could account for the results of Experiment 1, where the three different cues were associated to different rates of responding. However, when the cues were made equal in terms of responses, namely in terms of their selection history, the attentional bias toward the best reward predictor was still present in the visual search task. By ruling out the selection history hypothesis, this result replicated the one emerged in Experiment 1 and gave support to the possibility that the attentional bias was due to the different reward expectancy associated with the cues during the conditioning phase.

However, because the $p = .8$ cue was accepted more often than the other cues, while the $p = .2$ cue was rejected more often than the other cues, one could argue that during conditioning this resulted in a tendency to develop an “approach” behavior toward the more “appetitive” $p = .8$ cue, and in a tendency to develop an “avoidance” behavior toward the less “appetitive” $p = .2$ cue. This putative approach vs. avoidance strategy would have reintroduced a difference in the selection history between the different reward cues, thus explaining the attentional bias found the visual search phase. However, because in Experiment 2 past selection differences were matched in both the attentional and the action domain, the potential influence of these tendencies must act at a conceptual level.

In order to exclude any possible influence of selection history on attentional modulation, even at a conceptual level, another experiment was performed in which the cues were never task relevant (i.e. they were never selected in any possible way), not even during the conditioning phase. This was achieved by adapting an omission contingency paradigm already developed by Le Pelley and colleagues (Failing et al., 2015; Le Pelley et al., 2015; Pearson et al., 2015).

EXPERIMENT 3

METHODS

Participants

Twenty-six undergraduate students (M_{age} = 23.3 years, 19 females) took part in the experiment after providing informed consent. They were asked not to drink for about 4 hours prior to the experimental session. They received €5 compensation for their participation.

Apparatus

As in Experiment 1, but with the addition of an eye-tracking system (Eyelink 1000 Tower Mount), with a sampling rate of 1000 Hz, end-to-end sample delay of $M <$ 1.8 ms, $SD < .6$ ms, and spatial resolution < .01° RMS.

Stimuli

Conditioning phase

The cue appeared as part of an array of six equally spaced (60°) elements placed on an imaginary circle (4° radius) centered on the screen. The cue and four elements of the array were outlined rings (2° in diameter, 0.25° thick). The remaining element of the array was an outlined diamond (2.4° in diagonal, 0.25° thick). The location of the elements in the array was randomly determined trial by trial. Depending on the cue-reward contingency, the cue could have one of three possible colors as in the previous experiments. The other elements of the array appeared in gray (4 cd/m^2). The background luminance was set at 13 cd/m^2. Reward delivery was accompanied by the on-screen simulation of a liquid dropping into a glass.

Visual Search

As in Experiment 2, except that during the visual search display no fixation cross was present.

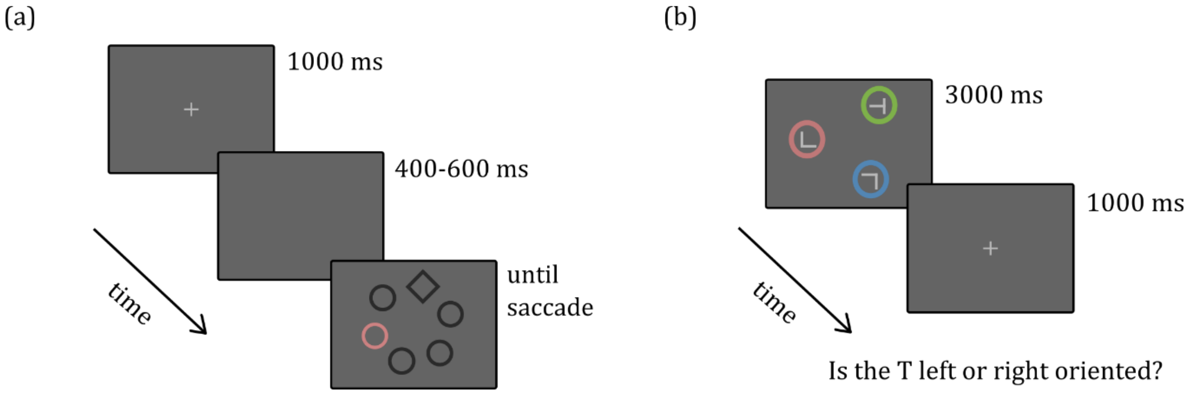

Figure 7. A schematic representation of the experimental procedure of Experiment 3.

(a) Conditioning task. (b) Visual search task.

Procedure

Conditioning

Each trial started with a central fixation cross presented for 1000 ms. Then the screen went blank for an interval of either 400 or 600 ms (randomly determined), after which the array of stimuli appeared. Participants' task was to make a saccade as fast and accurate as possible toward the diamond. A region of interest was defined around the target diamond and around the cue, and corresponded to the dimensions of the respective stimuli. Eye movements landing in these regions were controlled by means of the eye-tracking system. If participants made a saccade to the target, the reward was delivered according to the cue-associated probability, whereas no reward was delivered in case the saccade landed on the colored cue. In this way, an omission contingency procedure was implemented (see Figure 7 for details). Participants were not informed about the three cue-reward contingencies (.2, .5 or .8). For each participant, the reward probability associated with a given color was randomly determined. When delivered, the liquid reward dropped into a glass as in the previous experiments.

After completion of two conditioning blocks, in which a total number of 210 trials were equally divided between blocks and between the three cues, participants were asked to assess the cue-reward contingencies as in the previous experiments.

Visual search

As in Experiment 2, but with the following exceptions. First, a region of interest, controlled by the eye-tracker, was defined for each of the three letters, and consisted of the area covered by the ring in which the letter was embedded. Second, no fixation cross was present during the display of the three compound stimuli and participants were not instructed to keep their gaze on the center of the screen. Third, the time allowed for responding was set as 3 s, after which the response was considered as an error and the task continued with the next trial. Fourth, the compound stimuli were placed on an imaginary circle with 4° diameter centered on the screen.

RESULTS

All participants reported to be thirsty at the beginning of the experiment. I classified participants as “aware” and “unaware” applying the same “correct ranking” criterion of previous experiments. I performed a repeated measures ANOVA on visual search RTs for correct responses (overall accuracy in detecting target orientation was 98.2%) including all twenty-six participants with Contingency (.2, .5, and .8) as a within-subject factor and Group (aware and unaware) as a between subject factor. Results showed a significant interaction between Contingency and Group $F(2, 48) = 4.54$, $p = .016$, $\eta_p^2 = .159$, and no significant main effects of Contingency and Group ($p = .328$ and $p = .419$ respectively). I therefore focused the analysis on the group of “aware” participants ($n = 18$). The accuracy in detecting the target orientation for the remaining participants was 98.3%, and the outliers were less than 2% of the total RTs. A one-way repeated measures ANOVA on RTs in the visual search task showed a significant main effect of Contingency (.2, .5, and .8), $F(2, 34) = 5.88$, $p = .006$, $\eta_p^2 = .257$. Data significantly fitted a linear trend, $F(1, 17) = 13.48$, $p = .002$, $\eta_p^2 = .442$, but not a quadratic trend ($p = .714$), thus favoring again the “expectancy hypothesis” (Figure 8 panel a). Pairwise comparisons (one-tailed *t* test) showed that RTs in the $p = .8$ condition were significantly shorter than RTs in the $p = .5$ and $p = .2$ conditions, $t(17) = 1.84$, $p = .042$, $d = 0.434$, and $t(17) = 3.67$, $p = .001$, $d = 0.865$ respectively.

I also analyzed the first saccade directed toward a region of interest during the visual search task. In the 88% of the trials, this saccade was either the first or the second saccade from the onset of the visual search display. I calculated the percentage of the first saccades landing on the region of interest as a function of the former cue-reward probability. A one-way repeated measures ANOVA showed a significant main effect of

Contingency (.2, .5, .8), $F(2, 34) = 6.86$, $p = .003$, $\eta_p^2 = .288$. Data significantly fitted a linear trend, $F(1, 17) = 10.94$, $p = .004$, $\eta_p^2 = .392$, indicating that the percentage of the first saccades directed toward the cues was directly related to the previous cue-reward contingency (Figure 8 panel b).

Moreover, I analyzed the oculomotor capture triggered by the cue during the conditioning phase (i.e. omission trials). I calculated the percentage of saccades toward the cue for each of the three cue-reward probabilities. Because it seems reasonable to assume that the influence of the cues' value would emerge only after participants learned the cue-reward contingencies, I assessed how the percentages of saccades toward the cues varied as a function of training. To this aim, I divided the whole set of trials in seven consecutive bins (each bin comprising 10 trials per condition). Data were entered into a repeated measures ANOVA with Contingency (.2, .5, and .8) and Training (bin 1-7) as within-subjects factors. No significant main effect of Contingency ($p = .056$) and Training ($p = .059$), as well as their interaction ($p = .949$) emerged (see Figure 8 panel c).

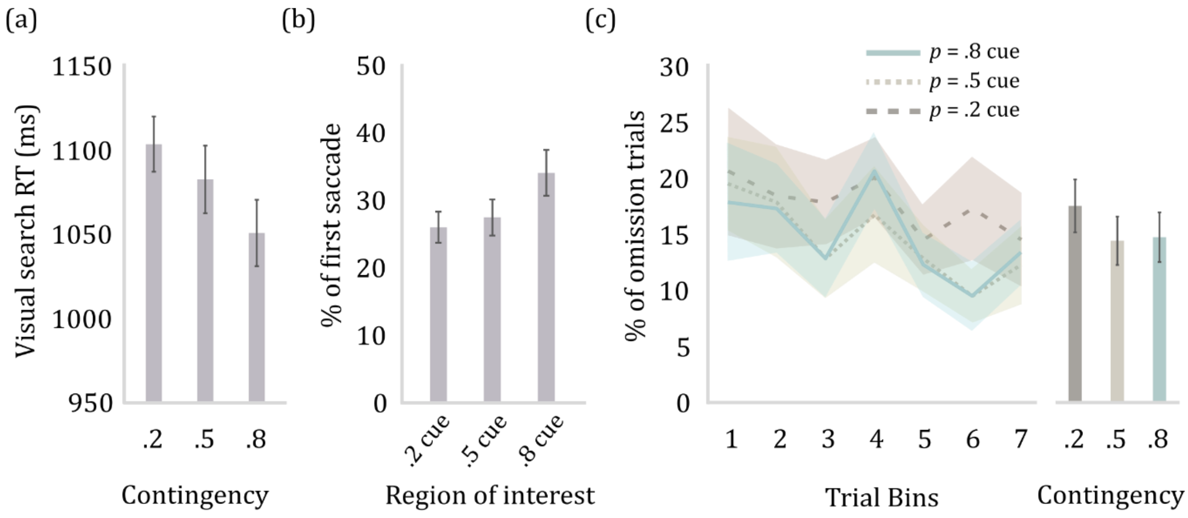

Figure 8. Graphical representation of the results of Experiment 3.

(a) Visual search RTs in Experiment 3 plotted as a function of the previous cue-reward contingencies. (b) Percentage of first saccade directed toward a cue during visual search as a function of the previous cue-reward contingencies. (c) Percentage of omission trials during the conditioning phase in Experiment 3 plotted as a function of the cue-reward contingencies and training (left panel), and as a function of contingency (right panel). Error bars represent 95% confidence intervals for within-subjects designs (Cousineau, 2005).

DISCUSSION

By using a hybrid procedure consisting of a conditioning phase in which the reward cues were task irrelevant, and a separated test phase in which the cues were devoid of any reward value, Experiment 3 provided further and more robust evidence in favor of the expectancy hypothesis. Not only were participants faster in detecting the target when it was encircled in the highest predictive cue, but they were also more prone to make their first saccade towards the same cue, thus confirming that reward stimuli affect human’s oculomotor behavior (Hickey & Van Zoest, 2012).

GENERAL DISCUSSION

The aim of the preset chapter was to investigate whether the attentional salience of a reward cue is more affected by reward expectancy or by reward uncertainty. Stemming from a long-lasting debate on this issue, and in light of the link between reward based associative learning and attention, the main question was whether an attention modulation by reward uncertainty could emerge in contexts in which uncertainty is not nil, namely when the cues are still associated with a reward-prediction error. With this goal in mind, the cue-reward contingency was manipulated while maintaining a degree of uncertainty for all levels of reward expectancy.

The RT-pattern that emerged in the visual search task of Experiments 1, 2 and 3, indicates that when the reward prediction error is not zero, expectancy is the major factor controlling the attentional salience of the reward cue, as proposed by Mackintosh (1975). This result is in line with previous studies showing that attention is preferentially captured by cues associated with the outcome most likely to occur (Anderson et al., 2011; Failing et al., 2015; Mine & Saiki, 2015; Theeuwes & Belopolsky, 2012). The results are also not inconsistent with previous studies showing that cues associated with the most uncertain outcome (p = .5) are more salient than cues predicting a reward that is certain (p = 1; Hogarth et al., 2008; M. J. F. Robinson et al., 2014, 2015), likely because in these studies the cue with the highest probability was not associated with a reward prediction error (also see, Sali et al., 2014).

Therefore, although a certain amount of reward uncertainty seems to be necessary for a cue to become an attentional attractor, the present results clearly indicate that reward expectancy weighs more than reward uncertainty in determining the attentional salience of the cue. However, both factors contribute to the salience of a reward cue, as suggested by a model of attention in associative learning recently proposed by Esber and Haselgrove (2011). Furthermore, this view is further supported by behavioral and neural evidence (Beesley et al., 2015). From the brain activity point of view, it has been shown that reward expectancy and uncertainty elicit different dopaminergic activities in the primates' ventral midbrain: the phasic response to conditioned stimuli increases monotonically with reward probability, while the sustained activity observed before the reward delivery is driven by uncertainty (Fiorillo, Tobler, & Schultz, 2003). Similarly, subcortical dopaminergic activity in humans correlates with both reward expectancy and uncertainty (Linnet et al., 2012; Preuschoff, Bossaerts, & Quartz, 2006). It can be argued that this differential encoding of reward variables could also signal the attentional system differently.

It is worth noting that during the conditioning phase of Experiments 1 and 2 the reward cue was presented in isolation, and was not embedded among other distractors. Therefore, it is unlikely that participants were reinforced to search for the reward cue among distractors, which undermines the possibility that the attentional bias emerged in the test phase could be either a conditioned visual search response learned before, as it may have happened in previous studies (e.g. Anderson et al., 2011), or a trained search response learned irrespective of the role of reward (Sha & Jiang, 2015). In Experiment 3, I sought to provide a stronger evidence for a value-dependent attentional modulation, and to this aim I implemented a hybrid procedure exploiting both the irrelevancy of the cue during the conditioning phase (Failing et al., 2015; Le Pelley et al., 2015; Pearson et al., 2015) and the absence of reward informational value in a separate test phase (Anderson & Halpern, 2017). The attentional bias I documented in the present chapter is likely to be the result of a Pavlovian mechanism that operates by shifting the reward properties from the reward to the cue, an idea originally proposed by Bindra (1978) and

Toates (1986), and that is central in the more recent theory of incentive salience (Berridge & Robinson, 2016).

Although Experiment 3 confirmed the results of Experiments 1 and 2 by adopting a different learning procedure, its conditioning phase did not fully replicate the results of experiments from which it took inspiration (Failing et al., 2015; Le Pelley et al., 2015; Pearson et al., 2015). Indeed, by implementing an omission contingency with three reward-uncertain cues, I failed to show that the most predictive cue elicited more counterproductive oculomotor capture. On the contrary, I found that participants tended to dwell erroneously more towards the less reward-associated cue. However, because of several procedural differences between the task adopted here and those of previous studies (Failing et al., 2015; Le Pelley et al., 2015; Pearson et al., 2015), a straightforward comparison is unwarranted. Still, the opposite tendency that I have reported here can have two important implications. On the one hand, if during conditioning participants erroneously had made more saccades toward the most valuable cue, then a selection history explanation could be invoked to interpret the attentional bias emerged in the visual search task. By contrast, participants tended to make more saccades towards the less valuable cue, which however did not affect the attentional effect emerged in the visual search task, a result that provides strong support for the expectancy hypothesis and that definitely rules out the selection history account. On the other hand, the oculomotor capture towards the less valuable cue is compelling and gives rise to additional questions about the relation, for example, between value-modulated oculomotor effects and the attentional strategies in uncertain contexts (exploration vs exploitation).

A concern might be raised regarding the appropriateness of the manipulation implemented here in light of a possible role of the expected value (EV), which is the product of outcome probability and outcome magnitude. One could argue that the EV should be matched across cues in order to disentangle between the uncertainty and the expectancy hypotheses. By contrast, I manipulated the cue-outcome uncertainty by varying only the probability of the outcome and not its magnitude, as this seems particularly appropriate to study how the cue becomes attentionally salient. One should note, indeed, that according to both the theory of Mackintosh (1975) and the theory of Pearce & Hall (1980), if the EV is kept constant across different cues (which means that reward magnitude is inversely related to its probability), a good predictor of a small outcome would be salient as much as an uncertain predictor of a large outcome, because the outcome reliability of the cue in the former case would be compensated by a greater outcome magnitude in the latter. Thus, the cues would result equally salient, and therefore it would not be possible to distinguish between the two theories. For this reason, in previous studies addressing the role of the two theories the variation in outcome probability was not accompanied by a change in the outcome magnitude, thus the EV was not maintained constant across the cues (Beesley et al., 2015; Fiorillo et al., 2003; Hogarth et al., 2008).

In conclusion, the results of Experiment 1, 2 and 3 are in agreement with the theory of attention formulated by Mackintosh (1975) and show that reward delivery leads to robust attentional learning (Chelazzi et al., 2013), so that attention is preferentially allocated to the relatively best reward predicting cues available. The results are also in line with the possibility that if a cue is consistently paired with an incentive stimulus, the cue acquires some motivational properties of the incentive stimulus (Toates, 1986), and consequently captures attention. Thus, I interpret the attentional bias as a result of the associative strength between cues and reward, and promoted by the conditioning phase. Moreover, in agreement with Robinson and

Berridge (2008) I acknowledge the possibility that the attentional bias might be also interpreted as signature of the incentive salience acquired by the cue during conditioning, supporting the idea that good reward-predicting stimuli can become attentional magnets that attract the organism's interest, even beyond the initial conditioning phase.

CHAPTER 3

INSTRUMENTAL PERFORMANCE: THE PIT EFFECT

In the preceding chapter, I investigated how neutral stimuli come to endow attentional properties when they are associated with motivationally significant outcomes. In particular, although a level of uncertainty in the relation between cues and outcome seems to trigger the attentional modulation, the major factor controlling the cue attentional capture is the outcome expectancy, or how reliable is the information provided by a cue about its motivational consequences.

THE PAVLOVIAN-INSTRUMENTAL TRANSFER EFFECT

Besides exerting an effect on the attentional system, conditioning and other learning mechanisms play a fundamental role in determining the organism consumption of food and other substances. Reward cues acquire also the power to enhance instrumental actions performed in order to obtain the associated outcome. Within this area of research, the motivational properties of the conditioned stimuli are made manifest by the Pavlovian-Instrumental transfer (PIT) effect, a phenomenon that provides a clear example of how reward cues can influence behavior. In the PIT, two separate associative learning processes interact - Pavlovian and Instrumental conditioning – resulting in the influence of Pavlovian CSs on instrumental actions. This effect can be valued employing a Pavlovian conditioning, an instrumental conditioning, and a test in which the two are combined. During the Pavlovian conditioning the agent is exposed to a contingency between a conditioned stimulus (CS or Pavlovian cue; e.g. a sound or a visual stimulus) and an outcome, whereas during the instrumental conditioning the outcome is associated with an action performed by the agent (instrumental action; e.g. lever pressing). Although the PIT has been traditionally and extensively studied in animals, it has recently been observed also in humans (for a review and a meta analysis see Cartoni, Balleine, & Baldassarre, 2016; Holmes, Marchand, & Coutureau, 2010).

INTERPRETATIONS OF THE PHENOMENON

The PIT effect has been initially attributed to a general motivating drive-like influence on the instrumental performance caused by the CS. It can be argued, indeed, that via a trained association the cue is capable to trigger an instrumental action.. However, this argument cannot account for the PIT effect because the CS and the instrumental actions are learned during separate trainings, and therefore the incentivizing effect of the CS on the instrumental action cannot be explained by an existing association between the CS and the rewarded action. Subsequently, it was observed that the CS exerts its influence selectively on the instrumental action associated with the same outcome, and not with an action associated to a different outcome (specific PIT). Thus, the motivation triggered by the CS must be considered outcome-specific. By these means, the CS would activate the outcome representation, which in turn promotes the instrumental action through an association learned during the instrumental conditioning phase (Balleine & Ostlund, 2007). However, Corbit, Janak, and Balleine, (2007) provided evidence that a third CS associated with an outcome that has not been used in instrumental training, can generally influence the instrumental responding trained with different outcomes (general PIT). These results are consistent with the argument that Pavlovian CSs generate a general excitatory state that can motivate and increase instrumental actions (Dickinson & Balleine, 2002). In agreement with this view, PIT has been interpreted as a measure of the CS motivational property or incentive salience (Berridge, 2001; Berridge & Robinson, 2003).

In this chapter, I will examine the PIT effect in human subjects. According with the incentive-sensitization theory, I aimed at testing that CSs not only influence the attention an organism deploys to them, but also affect the effort one is willing to spend in order to obtain an associated outcome.

I therefore tested human participants in a PIT paradigm in Experiment 4. Thirsty participants first learned to squeeze a rubber bulb to gain a liquid reward. Then, they underwent a Pavlovian conditioning in which three CSs were paired with different levels of liquid delivery, according to a predefined probabilistic schedule. Finally, participants were tested for PIT: they performed the instrumental action learned in the first phase in the presence of one of the three possible CSs. The guiding hypothesis was that the strength of the PIT effect would be proportional to the CS-US contingency: $p = .2$, $p = .5$ and $p = .8$. In other words, resembling the attentional results emerged in Chapter 2, the performance triggered by the CS should be greater for a CS that is a highly reliable predictor of the US (i.e., $p = .8$) as compared to a CS that predicted the US with a low probability (i.e., $p = .2$). Note that in a standard PIT paradigm the PIT effect emerges as an incremental rate of instrumental responding in the presence of the CS previously associated with the reward (e.g., $p = 1$ or .8) as compared to a baseline condition in which either no CS or a CS that was never paired with the reward is presented ($p = 0$). Since in the following experiment I used three CS with three different levels of contingency, a differential instrumental responding between the three CS in the PIT phase must be taken as evidence of the PIT effect. In other words, the rate of instrumental responding with the CS associated with the lowest contingency ($p = .2$) served as baseline for the PIT effect. Mean pressure, peak pressure and the number of grips acquired by means of the rubber bulb were taken as dependent measures of instrumental action.

Participants were free to choose their preferred liquid US (plain water or well-known sugary beverages). The importance of the choice will emerge in the following chapter. Here, I anticipate the assumption that plain water is not necessarily an intrinsic desirable stimulus, namely that its desirability is proportional to the organism's level of thirst. By contrast, sugary beverages can be examined in light of the addictive-like properties of sugar (Avena & Hoebel, 2003; Schulte, Avena, & Gearhardt, 2015; Stouffer et al., 2015).

The scope of the following experiment is twofold. First, to support the not so conspicuous existing evidence of the PIT effect in humans, also adding additional information by modulating the cue-outcome relation in terms of outcome predictability. Second, to create a reliable setting that could be adopted for a further manipulation described in the following chapter.

EXPERIMENT 4

METHODS

Participants

Thirty undergraduate students (M_{age} = 22.6 years, 18 females) took part in the experiment after providing informed consent. They were asked not to drink for about 4 hours prior to the experimental session. The experiment was carried out in accordance with the Declaration of Helsinki, and with the approval of the local research Ethics Committee (Comitato per la sperimentazione sull'essere umano dell'Università di Trento).

Apparatus

Participants were seated in a dimly illuminated room at a distance of 60 cm from the monitor (1920x1080 resolution, 100 Hz). The generation and presentation of the stimuli was controlled by using Matlab and Psychtoolbox-3 (Pelli, 1997), running on Windows 7. A rubber bulb was given to participant's non dominant hand. The rubber bulb was identical in shape, dimensions, material and physical resistance to a common bulb used for blood pressure measurements. The pressure generated by the squeeze of the bulb was read in Volts by means of a linear transformation applied by a gas pressure sensor (Vernier GPS-BTA). The output of the sensor (Volt) was acquired by a measure and control device (National Instruments myDAQ), sent to the computer and recorded by Matlab at 10-Hz sampling rate (see Figure 9Figure 9. Detail of the rubber bulb, gas pressure sensor and control device adopted in Experiment 4.). A liquid delivery apparatus was placed on the right side of the monitor and was triggered by the computer. Each delivery consisted of 2 ml of liquid dropping into a visible cup.

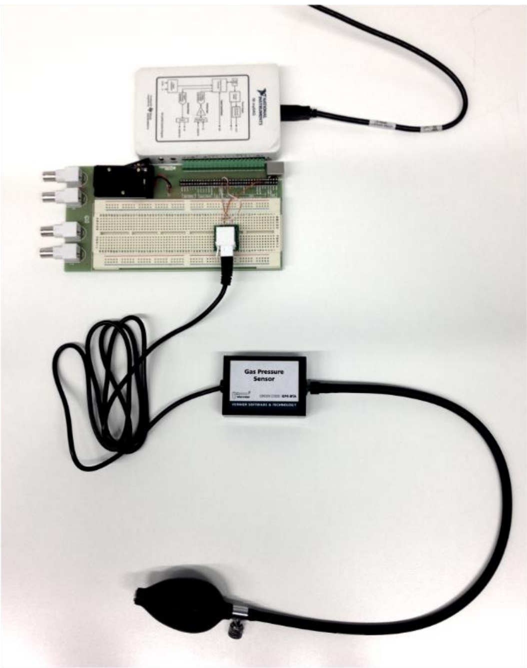

Figure 9. Detail of the rubber bulb, gas pressure sensor and control device adopted in Experiment 4.

Stimuli

First phase: instrumental conditioning

The drawing of a vertical mercury-like bar outlined in black was presented at the center of the screen. The overall dimension of the bar filled 75% of the total height of the screen and was 2° wide, with a 4° diameter ball at the bottom (see Figure 10). In addition, the bar was filled in dark yellow with a level that dynamically changed as a function of the pressure exerted by participants on the rubber bulb. The minimum pressure level reached the half of the bar, while the maximum pressure level filled the bar almost completely. Additionally, two mirrored black arrows pointing on the sides of the bar served as indicators of the minimal pressure required (see following procedure) and were positioned in height at the proper level. The arrows changed their color to dark yellow when the acquired pressure level exceeded it. The gray background luminance was set at 13 cd/m^2. Reward delivery was accompanied by the on-screen simulation of a liquid dropping into a glass.

Second phase: Pavlovian conditioning

Each CS was an outlined colored ring (2° in diameter, 0.25° thick). The CS could have one of three equiluminant (28 cd/m^2) colors: green, red or cyan, depending on the CS-US probability. The CS appeared in a random angular position on an imaginary circle with a radius of 5° from the center of the screen. Each CS was accompanied by an associated sound. The sounds were three sinusoidal waves with the frequency of 196, 329 or 784 Hz (corresponding to G3, E4 and G5 respectively) played at a comfortable amplitude. The gray background luminance was set at 13 cd/m^2. Reward delivery was accompanied by the on-screen simulation of a liquid dropping into a glass.

PIT

The mercury-like bar appeared at the same position as the first phase. In addition, one of the CSs appeared in a random angular position on an imaginary circle with a radius of 5° from the center of the screen, but it was never superimposed on the bar. Each CS was accompanied by its associated sound. The gray background luminance was set at 13 cd/m^2.

Procedure

The procedure adopted in the present study is similar to other procedures used in previous human PIT studies (e.g. Pool, Brosch, Delplanque, & Sander, 2015; Talmi et al., 2008), and was adapted from them. Participants' level of thirst was assessed verbally at the beginning of the experiment. Participants were also offered salty food to increase their level of thirst. They were asked to choose their preferred beverage (water or other well-known sugary drinks) that served as reward, and that would have been consumed later. Before starting the experiment, participants performed a few practice trials for the first phase only. The experiment was divided into three phases, and overall lasted about 45 min. The instrumental training was administered first, and then participants underwent a Pavlovian conditioning. The first phase was relatively short for two reasons: firstly, I wanted to minimize the possibility for instrumental response to become habitual, and secondly because a long instrumental training is detrimental when it precedes Pavlovian conditioning (Holmes et al., 2010). Lastly, participants were tested in a PIT procedure. Participants were allowed to drink the beverage they earned during the instrumental and Pavlovian conditioning phases only at the end of the experiment.

First phase: instrumental conditioning

Each trial started with a central fixation cross presented for 1000 ms. Then, the mercury-like bar appeared and remained on the screen for 10 s. The appearance of the bar was signaled by a brief "gong" sound. Participants were instructed that during the display of the mercury-like bar there were three secret time windows during which if the pressure level signaled by the bar was above the reference arrows outlined on the screen (see Figure 10, panel a), the liquid reward would have been delivered. In this way, participants were motivated in keeping the pressure level as high as possible by continuously squeezing the rubber bulb. Due to the anatomy of the bulb, after one squeeze the pressure increased and dropped very fast, irrespective of whether the bulb was released or remained squeezed. Therefore, in order to keep the level above the limit required, participants needed to squeeze the bulb vigorously and repeatedly. This instrumental action, which was performed with the non-dominant hand, required a significant effort. The three time windows were randomly selected on each trial across the whole 10 s period of stimulation with the restriction of being separated by at least 1500 ms. If the conditions were satisfied, the liquid was dropped into a visible glass by the apparatus and the stimulation appeared on the screen. So the reward gain for each trial could range from a maximum of three deliveries to a minimum of none. Therefore, despite depending on participants' effort, the instrumental reward schedule was probabilistic. Indeed, probabilistic schedule in this phase strengthens PIT (Cartoni, Moretta, Puglisi-allegra, Cabib, & Baldassarre, 2015). Due to the ongoing and increasing fatigue, each of the 20 trials was separated by a resting period that randomly ranged from 6 to 10 s, during which participants were invited to relax their forearm.

Second phase: Pavlovian conditioning

In this phase, participants were instructed to passively pay attention to the CSs on the screen, and that the reward was going to be delivered for free. Each trial started with a central fixation cross presented for 1000 ms. Then, one of the three CSs appeared accompanied by its associated sound for 3500 ms. A relatively long CS exposure was adopted to maximize the effect of Pavlovian conditioning (Holmes et al., 2010). Each CS had a fixed associated probability of signaling the reward delivery. The CS-US probabilities were .2, .5 or .8 and were unknown to participants. CSs associated color, sound and probability were randomized across participants. A probabilistic schedule was chosen to add some uncertainty to the task, in order to sustain participant's attention and to delay extinction during the last PIT phase (Haselgrove, Aydin, & Pearce, 2004). In cases of reward delivery, the apparatus dropped the liquid in a visible glass and a simulation of a filling glass appeared on the screen for 1000 ms. Conversely, an empty glass appeared on the screen for 1000 ms and no liquid was delivered (see Figure 10, panel b). A delay conditioning was used such that the presence of the CS overlapped with the delivery of the US. After an inter trial interval of 1500 ms, the next trial began. Across all 45 trials, the three CSs appeared an equal number of times and the order of presentation was randomized.

At the end of this phase, participants were asked to assess the CS-US contingencies on a 10-point scale, with 0 meaning that the reward "never" followed the CS, and 9 that it "always" did.

PIT

Participants performed the PIT task 10 minutes after the Pavlovian conditioning. Participants' task and instructions were the same as in the first phase, but they were also told that they would have been presented with other stimuli on the screen. Importantly, participants were aware that the only way of getting the reward was by squeezing the rubber bulb. The three CSs appeared an equal number of times across the total 45 trials of this task. This task was performed in extinction, so unbeknownst to participants no secret time windows existed during the stimulation period, and therefore no reward was delivered during this phase (see Figure 10, panel c). However, participants expected the delivery of reward in this phase too. Despite a partial extinction has been used in humans PIT tests, with potential reward delivery (Colagiuri & Lovibond, 2015; Pool et al., 2015; Talmi et al., 2008), the main reason for not adopting this strategy was to measure the PIT without any confound given by additional reward-association learning events that would be inevitable with a partial extinction procedure (but see Bouton, 2011).

After completion of the task, the amount of liquid that participant earned was converted in their preferred beverage and they were allowed to drink it.

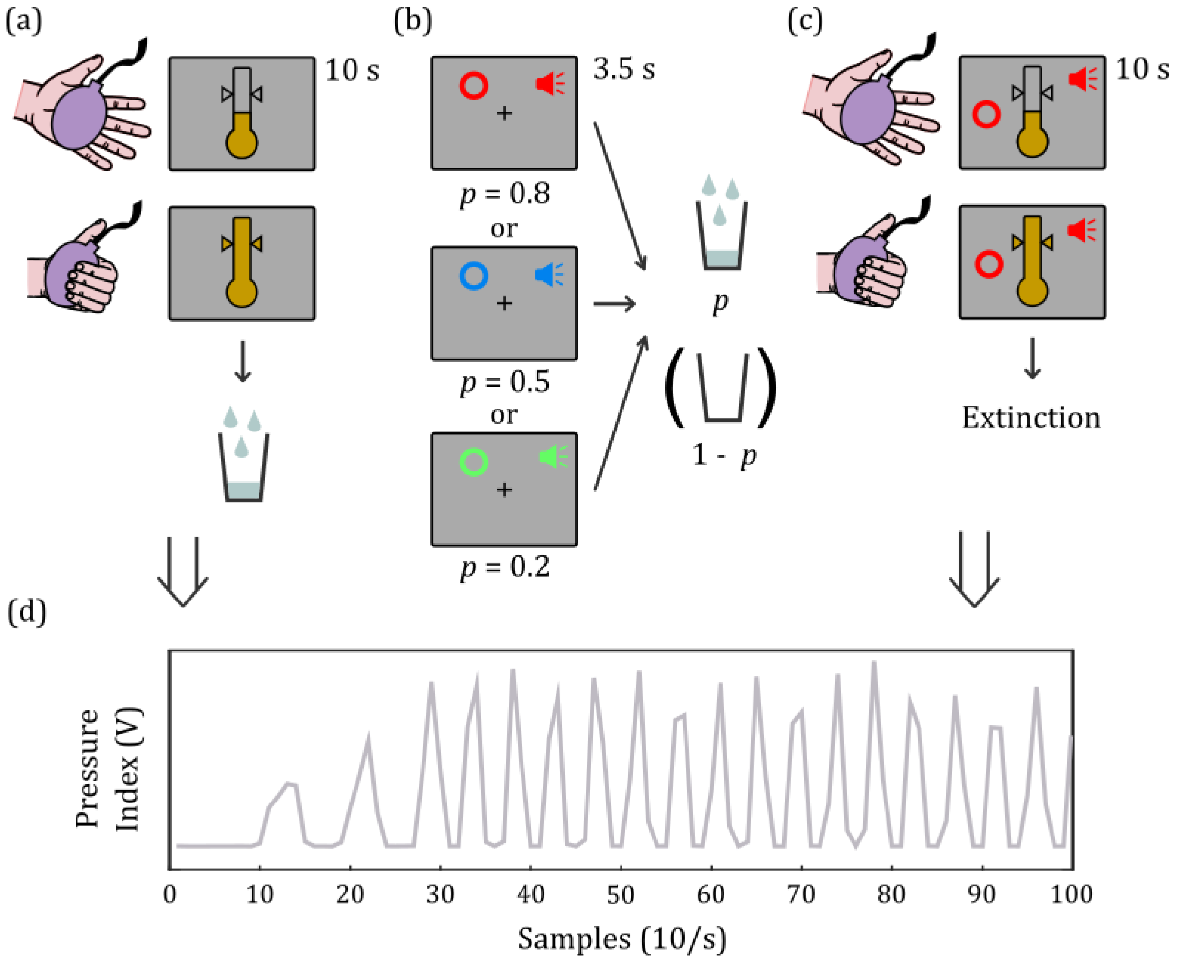

Figure 10. Schematic representation of the experimental procedure of Experiment 4.

(a) Phase one: instrumental conditioning; (b) Phase two: Pavlovian conditioning; (c) Phase three: PIT test (see Methods for details). (d) A graphical example of a trial output in the PIT test phase (and in the instrumental conditioning) showing the absolute pressure (expressed in Volts, vertical axis) sampled at 10 Hz during the stimulation period (100 samples for 10 s, horizontal axis).

RESULTS

All participants reported to be thirsty at the beginning of the experiment. Eight participants (26.7% of the sample) chose a sugary drink as US, while the rest (73.3%) chose plain water. The mean ratings of the CS-reward contingencies reported by participants on a 10-point scale were the followings: for $p = .2$, $M = 3.67$, $SD = 1.75$; for $p = .5$, $M = 5.23$, $SD = 1.65$; for $p = .8$, $M = 6.70$, $SD = 1.64$. The following analysis includes all participants.

Figure 10, panel d depicts an example of a trial outcome in the PIT test phase (and during instrumental conditioning). For each participant and for each trial, I extracted three variables of squeezing effort: mean pressure, peak pressure and number of grips. To detect a possible extinction-like trend across trials (i.e. the effort declined as the test unfolded), for each CS I divided the data into five temporally consecutive bins.

Mean pressure

First, I calculated the mean pressure by averaging all the samples within each trial. In case of a PIT effect, the mean pressure should increase as a function of the CS-US associated probability. Data were entered into a repeated measures ANOVA with Contingency (.2, .5 and .8) and Time (1 to 5 bins) as within-subjects factors, and Drink (water and sugary) as a between-subjects factor (when needed the degree of freedom were Greenhouse-Geisser corrected). The ANOVA showed a significant main effect of Contingency, $F(1.37, 38.23) = 6.36$, $p = .009$, $\eta_p^2 = .185$, a significant main effect of Time, $F(2.45, 68.58) = 3.96$, $p = .017$, $\eta_p^2 = .124$, but not a significant effect of Drink ($p = .743$) or any significant interaction (Contingency X Drink, $p = .188$; Time X Drink, $p = .187$; Contingency X Time, $p = .797$; Contingency X Time X Drink, $p = .749$; see Figure 11, panel a and d). Data significantly fitted a linear trend for both the Contingency factor, $F(1, 28) = 10.38$, $p = .003$, $\eta_p^2 = .270$, and the Time factor, $F(1, 28) = 9.04$, $p = .006$, $\eta_p^2 = .244$.

Peak pressure

I calculated the peak pressure (i.e. the most powerful squeeze) by extracting the highest value of the samples in each trial. Again, the peak pressure should increase with CS-US associated probability. As expected, a repeated measures ANOVA with the same factors as before showed a significant main effect of Contingency, $F(1.59, 44.58) = 5.17$, $p = .015$, $\eta_p^2 = .156$, a significant main effect of Time, $F(2.21, 61.77) = 4.92$, $p = .008$, $\eta_p^2 = .149$, but not a significant effect of Drink ($p = .646$) or any significant interaction (Contingency X Drink, $p = .352$; Time X Drink, $p = .265$; Contingency X Time, $p = .672$; Contingency X Time X Drink, $p = .878$; see Figure 11 ,panel b and e). Data significantly fitted a linear trend for both the Contingency factor, $F(1, 28) = 7.20$, $p = .012$, $\eta_p^2 = .205$, and the Time factor, $F(1, 28) = 8.47$, $p = .007$, $\eta_p^2 = .232$.

Number of grips

The number of grips (squeezes) was obtained by extracting the number of peaks on the samples (for example, the number of peaks in Figure 10, panel d is 19), which should increase as a function of the CS-US associated probability. Accordingly, a repeated measures ANOVA with the same factors as before showed a significant main effect of Contingency, $F(1.59, 44.63) = 3.82$, $p = .038$, $\eta_p^2 = .120$, but neither a significant main effect of Time ($p = .080$), nor a significant effect of Drink ($p = .308$), nor any other significant interaction (Contingency X Drink, $p = .730$; Time X Drink, $p = .437$; Contingency X Time, $p = .855$; Contingency X Time X Drink, $p = .965$; see Figure 11, panel c and f). For the Contingency factor, data significantly fitted a linear trend, $F(1, 28) = 7.83$, $p = .009$, $\eta_p^2 = .218$.

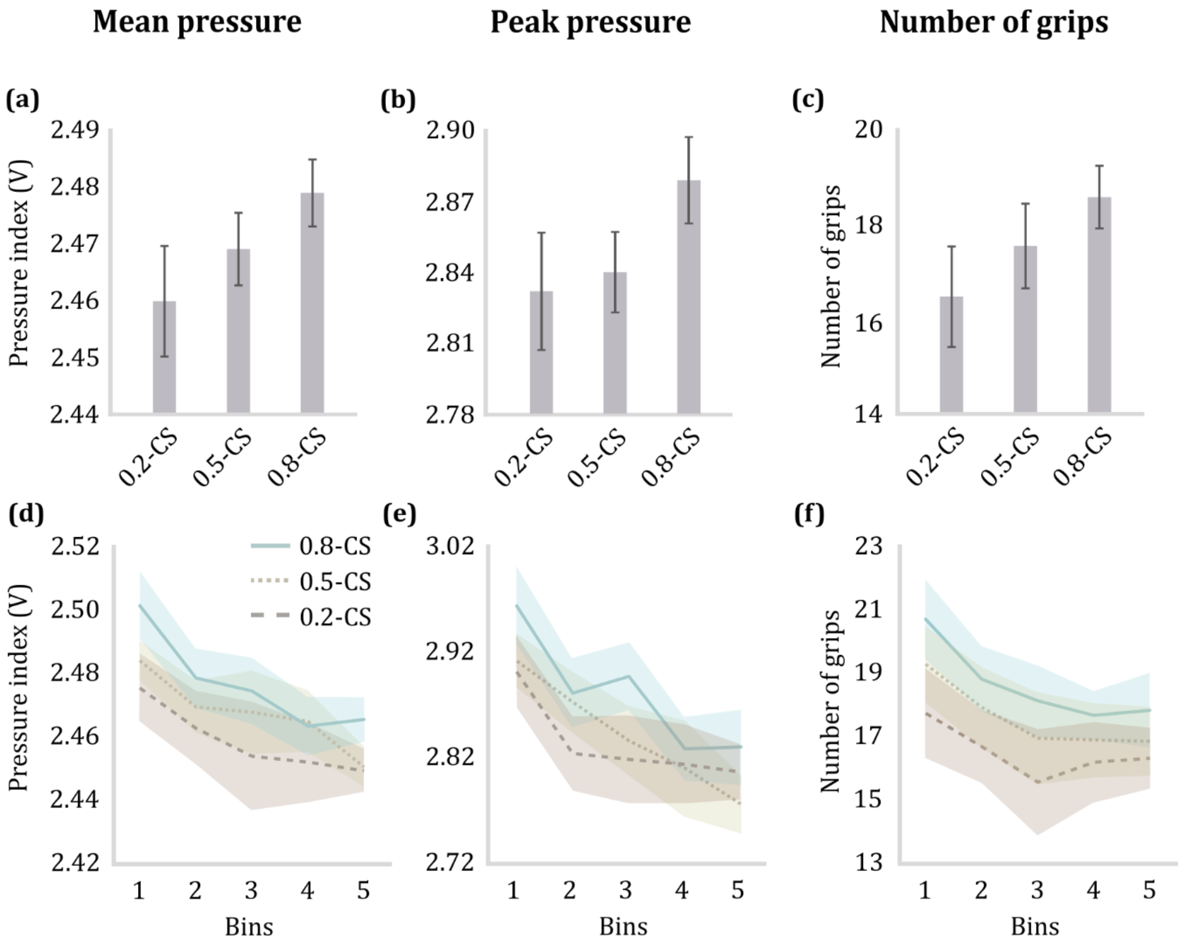

Figure 11. Graphical representation of the results of Experiment 4.

(a) Mean pressure of PIT test as a function of CS-associated probability. (b) Peak pressure of PIT test as a function of CS-associated probability. (c) Number of grips of PIT test as a function of CS-associated probability. (d) Mean pressure in PIT test as a function of CS-associated probability and time. (e) Peak pressure in PIT test as a function of CS-associated probability and time. (f) Number of grips in PIT test as a function of CS-associated probability and time. Error bars represent 95% confidence intervals for within-subjects designs (Cousineau, 2005).

DISCUSSION

Experiment 4 was successful in producing the PIT effect. The amount of effort (bulb squeezing) that participants made to obtain the liquid reward varied as a function of the CS contingency, as attested by the increments in all the three effort variables considered (mean and peak pressure, and the number of grips). That is, the high-probability (p = .8) CS triggered an increased effort as compared to the lower-probability CSs, which is an index of the PIT effect. These results are in line with previous literature on PIT in humans (Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008; Pool et al., 2015; Talmi et al., 2008) and add to existing evidence showing that Pavlovian CSs can acquire the motivational power to spur and invigorate an instrumental action for the associated outcome.

The CS-US contingency ratings indicate that, on average, participants learned the predictive value of the CSs during the Pavlovian conditioning, which then affected the subsequent PIT test. Given that the CSs were never trained in association with the instrumental squeezing of the rubber bulb, it is conceivable that the PIT effect emerged because CSs retrieved the US representation, which in turn enhanced the associated instrumental action.

Despite the addictive-like properties of sugar (Avena & Hoebel, 2003; Schulte et al., 2015; Stouffer et al., 2015) the drink factor had no apparent influence on the subsequent PIT effect. Indeed, participants chose both sugary drinks and plain water as rewards, but the instrumental invigorating effect given by the CS was not modulated by their choice.

Despite the overall general effort declined as time unfolded, thus following an extinction trend in the test phase, the non-significant interaction between Contingency and Time suggests that the CS exerted its influence on the instrumental action throughout the whole test phase.

The general picture that emerged from Experiment 4 was that the setting was well suited for measuring a reliable PIT effect. Therefore, in the next chapters I could rely on this paradigm to implement a further manipulation.

CHAPTER 4

THE *K* MANIPULATION ON THE ATTENTIONAL BIAS

THE ROLE OF PHYSIOLOGICAL STATES

It may sound trivial to argue that the state of need of an organism would affect the perceived properties of a related stimulus, at least in motivational terms. As a typical example, food would be attractive if an organism is hungry, but not attractive if it is not (Piech, Pastorino, & Zald, 2010; Tapper, Pothos, & Lawrence, 2010). We all know that a piece of our favorite cake seems irresistible and delicious when we are hungry, but might become sickly sweet and unattractive when we are fully sated. Indeed, it has been shown that substance related stimuli (e.g. smoking, alcohol, cocaine and heroin words or images) are attractive for regular substance users and addicts but not for non-users or light users (Field & Cox, 2008). The dynamic fluctuation of the motivational state relevant to a reward, such as states of appetite, drug-induced or stress states, might engage the cognitive system differently. An interesting issue, however, is if this mechanism operates also for reward associated cues, namely, whether the motivational properties of a reward-associated cue are affected by the physiological state relevant to the reward at the moment the cue is encountered.

In the context of the incentive-sensitization theory, the incentive salience attributed the CS is not a fixed property determined by its contingency with the reward, but rather the CS incentive salience varies with the physiological state of the organism. In other words, in order for the system to estimate the appropriate cue-related incentive salience, the information given by the cue at the moment of its encounter needs to be integrated by the physiological appetite state at that precise moment. This idea stems from the observation by Toates (1986), who argued that the hedonic value of incentive stimuli, like primary rewards, is modulated by drive states, a phenomenon previously called *alliesthesia* by Cabanac (1979).

This notion is at the core of the computational model of incentive salience proposed by Zhang and collaborators (Zhang, Berridge, Tindell, Smith, & Aldridge, 2009). The model combines the learned cue-reward (i.e. CS-US) association with the current physiological state (*K*) relevant to the reward associated with the cue. According to the model, a change (increment or decrement) of *K* corresponds to a variation of the CS incentive salience in the same direction. Alternatively, no variation in “wanting” happens if K remains constant. So for example if *K* is high when the CS-US learning relation is learned, and *K* remains high when the CS is re-encountered, the CS-triggered incentive salience will remain high. In other words, if K decreases or increases, the CS-triggered incentive salience changes accordingly.

In agreement with this view, previous studies have addressed how *K* modulates the motivational component of the cue incentive salience, by showing that a cue-triggered “wanting” can be disproportionally high if *K* is boosted by a sensitization of the mesolimbic system, by means of amphetamine injections in the Nucleolus Accumbens, or by means of an altered stress state (Pool et al., 2015; Smith, Berridge, & Aldridge, 2011; Wyvell & Berridge, 2001).

There are cases, however, that challenge the notion that the physiological state affects the incentive salience of the reward cue. Animal studies show, for example, that a CS can still trigger the pursuit of reward even when the reward is devalued (Holland, 2004; Wilson, Sherman, & Holman, 1981). Furthermore, the instrumental performance of rats can remain high when the outcome is not desirable anymore because of a shift from a hunger to a satiety state, a phenomenon known as *resistance to satiation* (Balleine, 1992).

One possible explanation for the failure of a shift of CS value as a consequence of reward devaluation might be attributed to the learning procedure adopted (Berridge, 2001). One may note, indeed, that the idea that the CS incentive salience varies with the physiological state is mainly questioned by studies that have used instrumental conditioning paradigms. Within this type of learning, the instrumental response is different from a Pavlovian related response. According to the original idea of Thorndike (1911), the mechanism involved in the stimulus-response-reinforcement (S-R) relies on the reinforcing properties of the reward that strengthens the S-R association, so that given a stimulus, a response is emitted. This learning mechanism does not require the agent to form a representation of a causal relation between its response and the outcome, or in other words to know the causal consequences of its action (Balleine & Dickinson, 1998). If an agent does not know the consequences of its action, it cannot adjust its behavior according to the relevance of the outcome or its motivational states. The seminal investigations of Dickinson, Balleine and colleagues, however, suggested that an instrumental response can be a goal-directed action when the S-R is not over trained (i.e. the response is not habitual), and requires the cognitive representation of both the outcome value and the action-outcome causal relation (Dickinson & Balleine, 1994). It might be then argued that an instrumental action is sustained more by a *cognitive* incentive salience mechanism based on the reward value, rather than by an implicit and visceral incentive salience ("wanting") triggered by the Pavlovian CS. In other words, the inability of reward devaluation to affect the instrumental action would not pertain to incentive salience or "wanting", but rather to a cognitive form of incentive. However, both incentive mechanisms are important for motivation, as they have similar and concurring effects on behavior, and their differentiation can be subtle (Berridge, 2001). For example, as described in Chapter 2, in a PIT paradigm the presence of an irrelevant CS previously paired with the reward can increase the instrumental responding for the same reward, a phenomenon that is usually interpreted as an incentive motivational state triggered by the CS (Berridge, 2012; Holland, 2004). The hypothesis concerning different learning mechanism appears to be, therefore, unsatisfying.

When a cue-triggered persistent "wanting" for a devalued reward is observed, it is legitimate to hypothesize that the cue has maintained a high level of incentive salience despite the reduced physiological activation state of the organism. This condition has been interpreted "as excessive enduring cue-triggered "wanting", which has detached from the US value" (Berridge, 2012 p1131). In other words, it is possible that once a CS has gained incentive properties from its association with an appetitive US, it could retain its incentive salience independently from changes in the US value. As acknowledged by Berridge, this possibility deserves further investigations, because "we need a better understanding of how detachments of CS motivation from US value can occur" (Berridge, 2012 p1131).

In light of this complex scenario, in the following experiments I sought to address, in humans, whether the physiological state can modulate the motivational component ("wanting") of the reward cue, as expressed by the corresponding attentional component (Experiment 5 & 6) and the performance related properties (Experiment 7), by means of a controlled reward devaluation procedure.

THE CASE OF ATTENTIONAL BIAS

Does the attentional grabbing power of a reward-predicting cue change as a function of the relevant physiological state? Recent studies seem to provide an initial affirmative answer to this question. For example, it has been reported that attention ceased to be captured by a chocolate odor cue once human participants had consumed chocolate at will (Pool et al., 2014). In other words, reward devaluation seems to diminish the corresponding CS attentional salience. Symmetrically, another animal study showed that a learned repulsion (i.e. a low incentive salience) for a CS that predicts an unpleasant salty taste (US) can immediately make the CS attractive if a new salt appetite is induced in rats (M. J. F. Robinson & Berridge, 2013; Tindell et al., 2009).

However, in the previous section I have discussed cases suggesting the possibility of a failure of a shift of a cue motivational salience following US devaluation, as predicted by the Zhang model. In these cases, the cue incentive salience might detach from the US value. In the context of attention, the cue attentional grabbing power might not be affected by the modulation of the primary organism's motivational states.

The next experiment aimed at testing whether the attentional salience of a reward-predicting cue changes as a function of the state of thirst. In Experiment 5, thirsty participants first underwent a conditioning phase through which visual cue gained differential incentive properties by being associated, with different contingencies, with the delivery of a liquid incentive. Importantly, the liquid was not consumed during this phase, but its accumulation was visible to participants and thus worked as a potent incentive. The procedure was identical to the one of Experiment 1 (Chapter 2). As a reminder, in Experiment 1 participants performed the test phase consisting in a visual search task carried out in extinction while still thirsty. Results showed that the best reward-predicting cue preferentially engaged attention, and therefore gained the greatest motivational value. Experiment 5 used the same paradigm, but crucially participants were allowed to drink between the conditioning and the test phase. In this way, as predicted by the Zhang model, the incentive salience of the cues should be diminished, because the physiological state of the organism was reduced before the cue was re-encountered in the test phase. It follows that no attentional bias should emerge in the visual search task. By contrast, if once established the incentive salience of the cue can be decoupled from the current drive state, I could expect the attentional capture to outlast reward devaluation. In other words, Experiment 5 was meant to be a stringent test for the Zhang model (Zhang et al., 2009).

Experiment 6 was administered as a control for the attribution of the attentional effect to the motivational properties of the US, and not to other possible mechanisms at work during the conditioning phase. In Experiment 6, the incentive property of the beverage was devalued from the outset, before participants underwent the conditioning phase. In this condition, none of the cues should gain incentive salience, because the liquid was devoid of any incentive properties. Under these circumstances, no attentional modulation was expected to emerge in the test phase.

EXPERIMENT 5

METHODS

Participants

Twenty undergraduate students (M_{age} = 21.2 years, 15 females) took part in the experiment after providing informed consent. They were asked not to drink for about 4 hours prior to the experimental session. They received €5 compensation for their participation. The experiment was carried out in accordance with the Declaration of Helsinki, and with the approval of the local research Ethics Committee (Comitato per la sperimentazione sull'essere umano dell'Università di Trento).

Apparatus

The same as in Experiment 1 (see Chapter 2).

Stimuli

The same as in Experiment 1.

Procedure

The procedure was the same as in Experiment 1, except that participants were allowed to drink ad libitum after the conditioning phase and before the visual search task (see Figure 12). Importantly, they drank the beverage they had chosen as reward during the conditioning phase, so that I specifically devalued the reward associated with the cue. Although they were not forced to, they were encouraged to drink to quench their thirst. To evaluate their level of thirst, participants completed a 3-item questionnaire on a 5-point Likert scale twice, the first time as soon as they arrived to the lab and before beginning the conditioning phase, and the second time soon after they drunk and before beginning the visual search task. The three items, taken from a previous study on water deprivation in humans (Rolls et al., 1980), were presented on the screen in this order:

1. How thirsty do you feel now? (*not at all – very thirsty*)
2. How pleasant would it be to drink something now? (*very unpleasant – very pleasant*)
3. How dry does your mouth feel now? (*very dry – not at all*)

Participants began the visual search task approximately 10 minutes later, an interval long enough to permit the assimilation of the fluid by the body, as reflected by both physiological and psychological measures (Rolls et al., 1980).

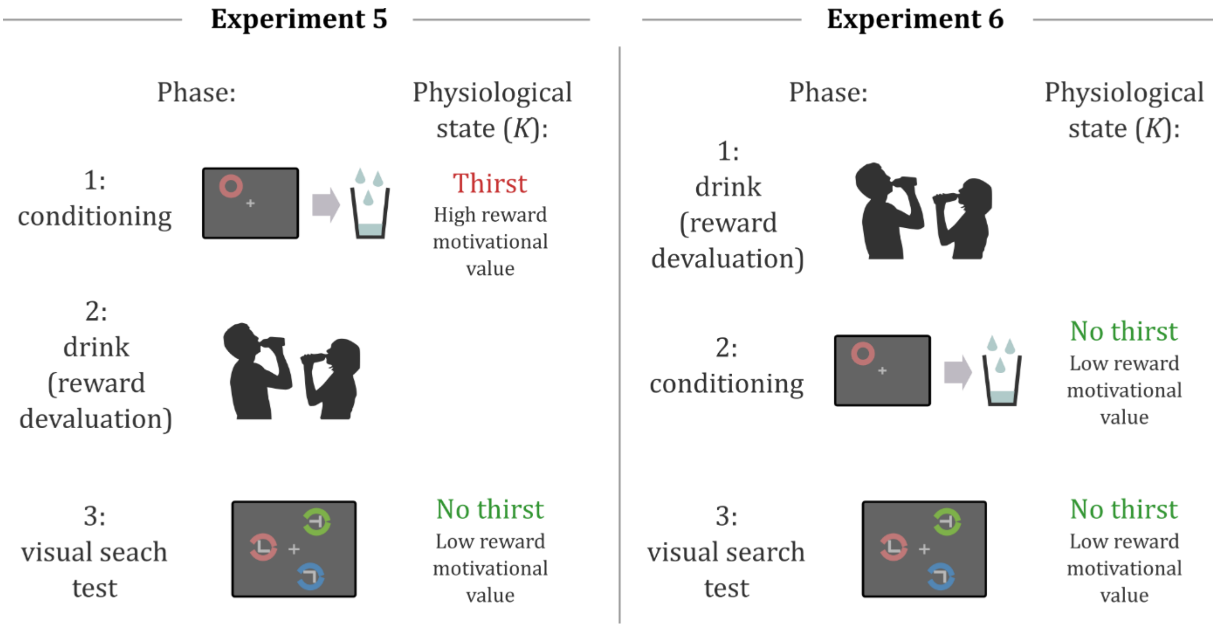

Figure 12. Phase diagram for Experiment 5 and 6 and physiological state relative to the beverage reward that corresponded to each phase.

See procedure for details.

RESULTS

All participants reported to be thirsty at the beginning of the experiment. Only two participants ranked the cue-reward contingency in the wrong order, and thus would be categorized as “unaware”. However, since the small group size, participants were not separated. Therefore, the following analysis includes all participants. First I analyzed the RTs for correct responses (88.2%) in the visual search task (outliers <2%). A one-way for repeated measures ANOVA showed with Contingency (.2, .5 and .8) as a within subjects factor showed a significant main effect of Contingency, $F(2, 38) = 7.19$, $p = .002$, $\eta_p^2 = .274$. Data significantly fitted a linear trend, $F(1, 19) = 15.21$, $p = .001$, $\eta_p^2 = .445$ (see Figure 13 panel a). Pairwise comparisons (one-tailed *t* test) showed that RTs in the *p* =

.8 condition were significantly shorter than RTs in the p = .5 and p = .2 conditions, $t(19)$ = 1.74, p = .048, d = 0.389, and $t(19)$ = 3.90, p < .001, d = 0.872, respectively.

I then analyzed the accuracy across cues in the visual search task. A one-way for repeated measures ANOVA on accuracy showed no significant effect of Contingency (p = .088).

Next, I analyzed how participants rated their level of thirst before the beginning of the conditioning phase and after they drank but before the beginning of the visual search task. A Wilcoxon signed-rank test indicated that post-task ranks were significantly lower than the pre-task ranks for all the three items (Z = 210, p < .001; Z = 190, p < .001; Z = 210, p < .001 respectively), a pattern of results showing that the devaluation procedure was successful.

A one-way for repeated measures ANOVA on the rate of instrumental responses associated with the different cue colors (i.e. reward probability) in the conditioning phase showed a significant main effect of Contingency, $F(2, 38) = 50.99$, $p < .001$, η_p^2 = .729. Data significantly fitted a linear trend, $F(1, 19) = 115.23$, $p < .001$, η_p^2 = .858.

I also analyzed the RTs for correct responses (97.4%) in the conditioning phase (outliers <2%). A one-way for repeated measures ANOVA again showed a significant main effect of Contingency, $F(2, 58) = 28.40$, $p < .001$, η_p^2 = .599. Data significantly fitted a linear trend, $F(1, 19) = 69.45$, $p < .001$, η_p^2 = .785 (see Figure 13 panel b). As in Experiment 1, the increment in response rate and the decrement in RTs as a function of reward probability was taken as reliable evidence that conditioning took place (Pool et al., 2014; Talmi et al., 2008).

Finally, the mean ratings of the cue-reward contingencies reported by participants on a 10-point scale were the followings: for $p = .2$, $M = 2.05$, $SD = 1.05$; for $p = .5$, $M = 4.55$, $SD = 1.39$; for $p = .8$, $M = 7.25$, $SD = 0.97$.

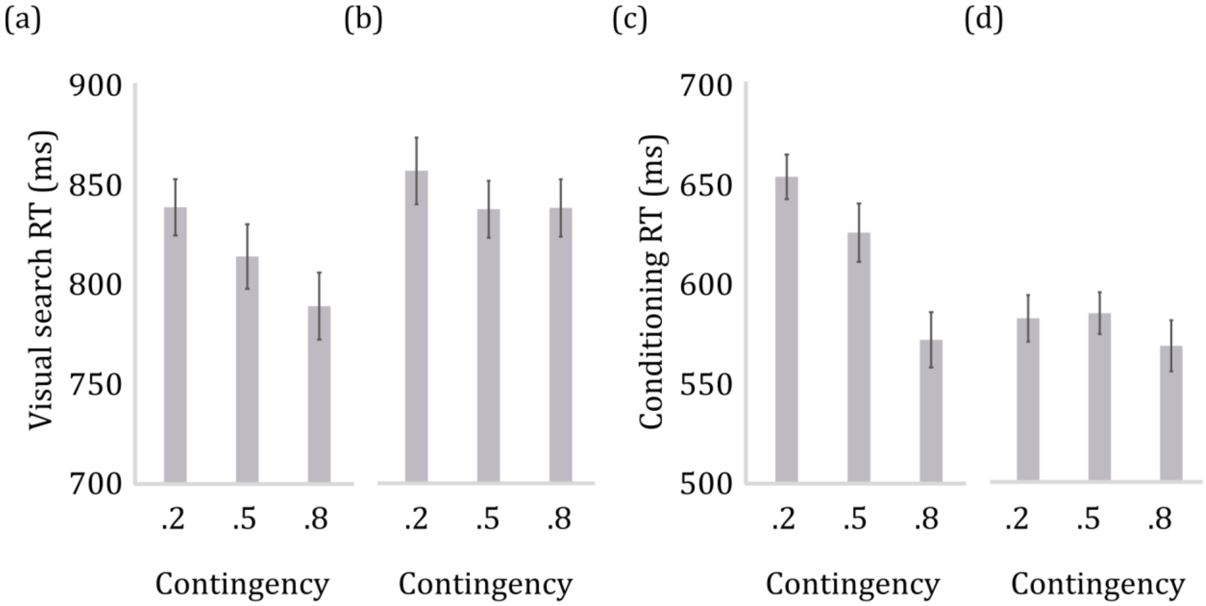

Figure 13. Graphical representation of the results of Experiment 5 and 6.

(a) Visual search RTs in Experiment 5 plotted as a function of cue-reward contingencies. (b) Visual search RTs in Experiment 6 plotted as a function of cue-reward contingencies. (c) Conditioning RTs in Experiment 5 plotted as a function of cue-reward contingencies. (d) Conditioning RTs in Experiment 6 plotted as a function of cue-reward contingencies. Error bars represent 95% confidence intervals for within-subjects designs (Cousineau, 2005).

DISCUSSION

The aim of Experiment 5 was to test the persistence of the cue attentional salience after the reward was devalued. Contrary to the expectation suggested by the Zhang model, the results showed that the best reward predictor (cue) retained its attentional salience despite the reward devaluation. This challenges the idea that the cue updates automatically its attentional salience when there is a shift in the participants' physiological state. By contrast, the cue retained some incentive properties (at least the attentional component) independently of the new motivational state of the organism. This result, while apparently at odds with the Zhang model, could be accounted for by the attentional value learning hypothesis, according to which the updated irrelevancy of the cue must be re-learned with an additional associative phase (Pearce & Bouton, 2001). This possibility is further examined in a following chapter.

Data from the conditioning phase were similar to those of Experiment 1: participants' motivation for the three cues was different, as revealed by the different response rates. In addition, the conditioning was successful as revealed by the difference in RTs during the conditioning phase.

As a final control, in the next experiment the reward was devalued before participants were submitted to the conditioning procedure. Under these conditions, no attentional bias was expected to emerge in the visual search task.

EXPERIMENT 6

METHODS

Participants

Twenty undergraduate students (M_{age} = 20.4 years, 15 females) took part in the experiment after providing informed consent. They were asked not to drink for about 4 hours prior to the experimental session. They received €5 compensation for their participation. The experiment was carried out in accordance with the Declaration of Helsinki, and with the approval of the local research Ethics Committee (Comitato per la sperimentazione sull'essere umano dell'Università di Trento).

Apparatus

As in the previous experiment.

Stimuli

As in the previous experiment.

Procedure

As in Experiment 1, but at the beginning of the experiment participants were allowed to drink ad libitum before the conditioning phase (see Figure 12). In this way, it seems reasonable to assume that the beverage seen during conditioning lost its incentive properties. Like in Experiment 5, participants completed the same three-item questionnaire twice, once before the beginning of the conditioning phase and once before the beginning of the visual search task.

RESULTS

All participants reported to be thirsty at the beginning of the experiment. I analyzed participants' ranking of the cue-reward contingency: participants were divided in "aware" (*n* = 8) and "unaware" (*n* = 12). It is worth reminding that participants began the conditioning phase after their thirst was quenched, so they were not motivated in maximizing the unrewarding outcome and this might explain the high proportion of unaware participants. However, it is not possible to exclude that aware participants, even if unmotivated, showed an attentional bias. Therefore, I first analyzed the RTs for correct responses (90%) in the visual search task (outliers <2%) by means of a repeated measures ANOVA including all (*n* = 20) participants with Contingency (.2, .5, and .8) as a within-subject factor and Group (aware and unaware) as a between subject factor. No significant effect of Contingency x Group interaction emerged (*p* = .920), as well as no main effect of Contingency (*p* = .276) or Group (*p* = .484), thus indicating that participant did not differentiate their RTs across the different cues (see Figure 13 panel c) and this behavior was not modulated by their cue-reward awareness as in Experiment 1. Therefore, the following analysis was administered on all participants.

I then analyzed the accuracy across cues in the visual search task. A one-way for repeated measures ANOVA on accuracy showed no significant effect of Contingency (*p* = .174).

I then analyzed how participants rated their level of thirst by comparing their responses in the first and the second test administration. A Wilcoxon signed-rank test indicated Items 2 and 3 did not change between the first and the second test (p = .312 and p = .152 respectively), whereas Item 1 was significantly higher in the second test (Z = 9.0, p = .017).

A one-way for repeated measures ANOVA on the response rate during the conditioning phase showed a significant main effect of Contingency, $F(1.24, 23.64)$ = 4.36, p = .040, η_p^2 = .187. Data significantly fitted a linear trend, $F(1, 19)$ = 5.64, p = .028, η_p^2 = .229.

Although the response rates varied as a function of the different cues, the difference in conditioning RTs (outliers <2%) was not significant (p = .198; see Figure 13 panel d), which suggests that actually in Experiment 6 no conditioning took place (Pool et al., 2014; Talmi et al., 2008).

Finally, the mean ratings of the cue-reward contingencies reported by participants on a 10-point scale were the followings: for p = .2, M = 3.15, SD = 2.03; for p = .5, M = 4.70, SD = 1.98; for p = .8, M = 5.35, SD = 2.60.

DISCUSSION

Experiment 6 served to control that the attentional bias emerged in Experiment 5 (and also in the experiments presented in Chapter 2) was due to the motivational properties of the liquid incentive during conditioning. To this aim, reward was devalued before participants began the experiment, as confirmed by the low rates of thirst given in the questionnaire before the conditioning phase. Under these conditions, and as predicted by the incentive-sensitization theory, there was no incentive salience expected to transfer from the beverage to the best predictive cue, and no bias of attention should have emerged in the visual search task. In agreement with this prediction, the visual search task revealed no RTs difference.

Although to a smaller extent, the response rate in the conditioning phase differed across the cues, as it occurred in Experiment 1 and 5. Because participants drank ad libitum before the conditioning phase, it is reasonable to assume that they were not particularly motivated to maximize the beverage gain, and therefore the different response rates were unexpected. A reasonable explanation is that once engaged in the task participants tried to play at their best in any case, irrespective of whether they were really "physiologically" interested in the liquid reward. However, the small difference in response rates alone cannot be taken as a reliable index of conditioning, because no RTs differences emerged across the different cue, as instead found in previous experiments (Pool et al., 2014; Talmi et al., 2008).

GENERAL DISCUSSION

The key result of Experiment 5 and 6 is that the attentional salience of a reward cue outlasted the devaluation of its associated reward, with reward here meaning unconditioned incentive (Bindra, 1978; Toates, 1986; Wise, 2004). As showed in Chapter 2, the best reward predictor during an initial conditioning phase performed while participants were thirsty, later triggered an attentional bias during a visual search task. Surprisingly, the attentional grabbing power of the strongest cue persisted with a comparable magnitude even when the incentive salience of the associated reward was devalued before the visual search task (Experiment 5). This evidence is consistent with the existing literature on value-based attentional learning (Chelazzi et al., 2013) and can be further explained by assuming that attention is preferentially deployed towards good reward predictors (Mackintosh, 1975). However, the fact that the incentive cue no longer captured attention when the salience of the incentive stimulus was devalued before the conditioning phase (Experiment 6) may suggest a possible role of motivational salience. Hence, the persistent attentional bias that emerged in Experiment 5 could be attributed to the incentive salience acquired by the cue during conditioning.

The fact that in Experiment 5 the most predictive cue captured attention despite reward devaluation is a result at odds with the Zhang model (also see Balleine, 1992; Dickinson & Balleine, 1994; Holland, 2004; Wilson et al., 1981). The model predicts that the incentive salience of the cue should be updated automatically after a shift in the primary drive state of the agent. In other words, if attentional bias is a hallmark of incentive salience, according to the Zhang model no attentional bias should have emerged in Experiment 5. However, the results were not in agreement with this prediction. Rather they suggest the possibility that, once established through conditioning, the incentive salience of the cue became independent from the motivational value of the US, which was weakened by changing the drive state (here thirst) of the organism.

The present findings are also not completely in line with the study by Pool et al. (2014). Both this study and Pool's study showed that incentive cues acquire attentional priority through their association with a primary reward, but contrary to the present findings Pool et al. (2014) found that the cue salience decreased after reward devaluation. The authors adopted a paradigm based on a spatial cueing task, in which two previously cues served as attentional cues. During the conditioning phase, one cue (CS+) was always paired with a chocolate odor, whereas the other cue (CS-) was always paired with odorless air. Then, in the spatial cueing task, target discrimination was faster at the position cued by the CS+ as compared to that cued by the CS-, thus showing that the CS+ summoned attention. However, this effect disappeared after participants ate chocolate until satiety. It is not obvious how to reconcile this result with that of Experiment 5, but one may note that in the paradigm adopted here participants performed a visual search task using a relatively crowded display, a paradigm perhaps a bit more challenging and sensitive than a simple spatial cueing task to detect evidence of attentional capture triggered by the cue incentive salience.

The persistence of the cue salience after reward devaluation is also puzzling in light of the results by M. J. F. Robinson and Berridge (2013) and Tindell et al. (2009). These studies showed that a repulsive cue paired with a salt state aversion became immediately attractive when a state of sodium depletion was chemically induced, thus making the salt an appetitive US. The transformation from repulsion to attraction took place without the animal being exposed anew to the cue-reward contingency, but rather it occurred just by virtue of the abrupt change in the motivational state of the organism with respect to the US, which suddenly became highly wanted. This result is rather interesting and raises a crucial question: if the initial motivational value of the cue is acquired during a consistent pairing with the US, how is it possible that its value can shift from aversive to appetitive without a new conditioning phase? The only possibility is that the change in the US motivational value is instantly passed to the cue via the association formerly established on the basis of the contingency between the two stimuli (i.e. a pure predictive learning process). However, if this were the case, here it should be expected the cue attentional salience to change immediately once the reward was devalued (Experiment 5). But this is not what it was found, which seems to suggest that while the cue motivational salience (i.e. "wanting") can be immediately updated as a function of the US value, once established the cue attentional salience can be at least partially independent from the US value, thus outlasting the US devaluation.

Finally, a remaining issue that deserves to be discussed is the nature of the attentional bias I have reported. In my view, the strongest cue acquired its attentional bias by virtue of its association with the reward, a process that may have also conferred the cue an increased incentive salience via Pavlovian conditioning (Berridge, Robinson, & Aldridge, 2009). However, because each cue was differently paired in terms of probability with the reward, the cue response probability varied accordingly during conditioning. Thus, participants were more likely to respond to the best predictive cue as compared to the other two cues. Yet, the fact that each cue elicited a response with a different probability raises the question of whether the attentional bias was in fact due to a different cue selection history (Awh et al., 2012). In addition to the evidence that emerged in Experiments 2 and 3 (reported in Chapter1), there are additional reasons why this is not the case. As already discussed, although each cue was associated with a different response probability, all cues were similarly attended in order to decide whether to respond or not. Still, one might argue that it is the rate of responding elicited by the cue that matters in terms of selection history (Chapman et al., 2014). However, if this were the case, I should have found an attentional bias also in Experiment 6, in which the response rates associated to each cue were statistically different. Since no attentional capture emerged in Experiment 6, as predicted by the incentive salience hypothesis, I can safely and more robustly dismiss the selection history account.

In conclusion, the studies presented in this chapter give support to the hypothesis according to which a cue can acquire attentional properties through its Pavlovian association with an unconditioned incentive (Bucker & Theeuwes, 2017). Crucially, the attractiveness of a reward cue can irrationally persist beyond the devaluation of the associated reward.

CHAPTER 5

THE *K* MANIPULATION ON THE PIT EFFECT

In the preceding chapter I examined whether the learned incentive properties of a reward cue change when the motivational value of the associated US is altered. Specifically, the concept of incentive salience was operationalized as one of its more prominent characteristics: an attentional bias. In this chapter, the aim is to further examine the *K* manipulation by looking at another component of incentive salience. That is, the performance enhancement properties of a reward-cue. The leading question of this chapter is whether a change in the value of a US may affect the associated CS-triggered effort as manifested by an instrumental action, measured in a PIT paradigm. In the context of the PIT studies, this remains an open question (Cartoni et al., 2016).

Among the possible solutions to the problem, a theoretical suggestion comes from the already mentioned incentive salience model outlined by Zhang and colleagues (Zhang et al., 2009). Given that the CS incentive properties vary with *K*, the model predicts that an upward shift of *K* would correspond to an increased CS-triggered *"wanting"*, while a downward shift of *K* would cause a decrease of the CS incentive salience. This prediction, however, is only partly confirmed by previous PIT studies modulating the US value, so that mixed evidence is present in the literature.

In agreement with the model, human participants engaged in a "stock market game" did not increase their effort to obtain a depreciated currency when shown a previously learned CS for the same currency, thus reporting a successful outcome devaluation effect (Allman, DeLeon, Cataldo, Holland, & Johnson, 2010; Eder & Dignath, 2016a). Likewise, when participants were exposed to a stressful experience, the PIT effect caused by a CS for a chocolate odor was amplified (Pool et al., 2015). However, successful devaluation procedures might have been effective on the PIT because of the specific paradigm used. Namely, a currency devaluation procedure in a "stock market game" could be interpreted as a cognitive rule as compared to a devaluation emerging from a motivational satiation procedure based on primary rewards (Cartoni et al., 2016). Another element to take into consideration when addressing the differential effects of the US devaluation on PIT is provided by the Eder and Dignath study (Eder & Dignath, 2016b). When the devaluation of a primary reward was achieved by a taste aversion procedure, its consequence on PIT was effective only if participants had to consume the US immediately after earning it.

A different scenario emerges from a number of studies on both humans and animals reporting that a CS retains its motivational control over instrumental responses (i.e. the PIT effect is unaffected) even if the corresponding US is devalued (Colagiuri & Lovibond, 2015; Colwill & Rescorla, 1990; Corbit et al., 2007; Hogarth & Chase, 2011; Holland, 2004; Watson, Wiers, Hommel, & De Wit, 2014). In particular, the enduring PIT effect despite reward devaluation has been interpreted as a persistent CS-triggered motivational response (Berridge, 2012). The fact that in some cases a persistent PIT effect was found despite reward devaluation may be partially explained by noticing that some studies have used rewards whose incentive value cannot be easily diminished by means of satiation or single-taste aversion procedures. So, for example, a highly palatable food (e.g. chocolate or candies) as well as drugs (e.g. tobacco) could retain, at some level, the ability to activate motivational states irrespective of the organism's satiation level. To put it differently, although a piece of cake is extremely motivationally salient when we are hungry, we all know that the same cake can still be desirable even after a full meal. In support of this possibility, a recent study reported that rats fail to exhibit devaluation effects in contexts paired with junk food as compared to contexts paired with less palatable regular chow (Kendig, Cheung, Raymond, & Corbit, 2016). In addition, although satiation was shown to be outcome-specific in some studies, it was not always *drive*-specific. So, for example, a previous study (Watson et al., 2014) showed that cues anticipating chocolate and popcorn increased the subsequent instrumental responding for the specific previously paired food (i.e. PIT), but satiation of one of the two foods failed to reduce the PIT effect. The apparent failure of reward devaluation can be explained by assuming that the food cue was effective because the food-specific satiation did not reduce the general hunger drive.

In light of this intricate scenario, the aim of the next experiment is to clarify the effects of changes in the US value on the corresponding CS incentive salience. With this goal in mind, human participants were tested in a PIT paradigm defined by two key features: first, by using a primary reward, and second the reward could be easily devalued, thus changing the corresponding incentive motivation. I have already presented Experiment 4 (Chapter 3), in which thirsty participants were tested for PIT: they performed the instrumental action learned in the instrumental conditioning in the presence of one of the three possible CSs. Results showed that the strength of the PIT effect was proportional to the CS-US contingency, so the performance triggered by the

CS was greater as the CS-US probability increased. It is worth reminding that participants were free to choose their preferred US (plain water or well-known sugary beverages). In this section, the US choice is particularly important considering the assumption that plain water is not necessarily an intrinsic desirable stimulus (like e.g. chocolate or pleasant drugs), namely that its desirability is simply proportional to the organism's level of thirst. By contrast, sugary beverages could be more resistant to devaluation by thirst quench because of the addictive-like properties of sugar (Avena & Hoebel, 2003; Schulte et al., 2015; Stouffer et al., 2015). In the next experiment, the procedure was identical to Experiment 4, except that participants' thirst was quenched (i.e., the US was devalued and *K* was lowered) after Pavlovian conditioning and before undergoing the PIT test. This critical manipulation allowed to measure whether the PIT effect survived reward devaluation. Mean pressure, peak pressure and the number of grips acquired by means of the rubber bulb were taken as dependent measures of instrumental action.

EXPERIMENT 7

METHODS

Participants

Thirty-one undergraduate students (M_{age} = 22.2 years, 21 females) took part in the experiment after providing informed consent. One participant was excluded from the analysis because, for religious reasons, he refused to quench his thirst. They were asked not to drink for about 4 hours prior to the experimental session. The experiment was carried out in accordance with the Declaration of Helsinki, and with the approval of the local research Ethics Committee (Comitato per la sperimentazione sull'essere umano dell'Università di Trento).

Apparatus

The same as in Experiment 4.

Stimuli

The same as in Experiment 4.

Procedure

As in Experiment 4, but after the Pavlovian conditioning and before the PIT test participants were allowed to drink the beverage of their choice ad libitum (see Figure 14). Although they were not forced to, they were encouraged to drink to quench their thirst. In this way, I implemented a sensory-specific devaluation of the US by immediate consumption and I manipulated the physiological factor *K* by lowering it. In order to assess whether the desired beverage seen during conditioning lost its incentive properties, participants completed a 3-item questionnaire as in Experiment 5. The scale was administered three times. The first time as soon as they arrived to the lab and before beginning the instrumental conditioning phase, the second time soon after they drunk but before beginning the PIT, and the third time at the end of the PIT test.

Participants began the PIT test approximately 10 minutes later, an interval long enough to permit the uptake of the fluid into the body, as reflected by both physiological and psychological measures (Rolls et al., 1980).

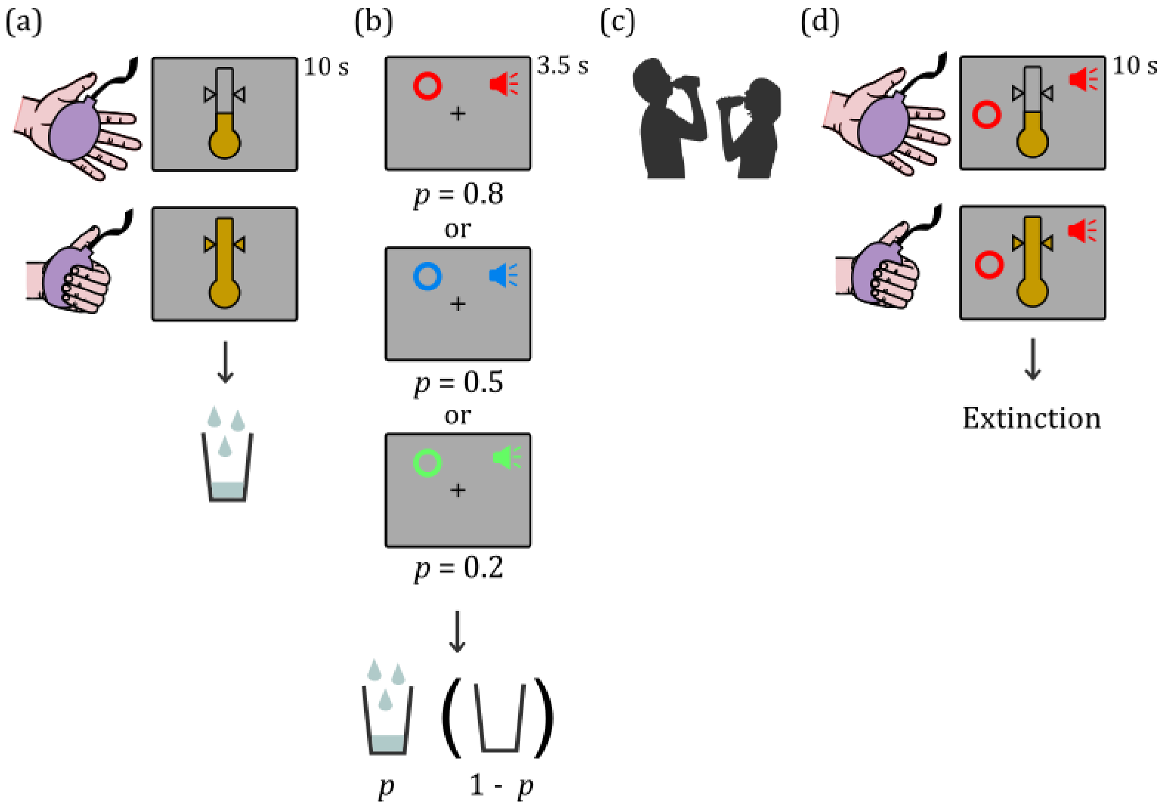

Figure 14. Schematic representation of the procedure of Experiment 7.

(a) Phase one: instrumental conditioning; (b) Phase two: Pavlovian conditioning; (c) Phase three: reward devaluation; (d) Phase four: PIT test (see Procedure for details).

RESULTS

Eight participants (26.7% of the sample) chose sugary a drink as US, while the rest (73.3%) chose plain water. The following analysis includes all participants. The mean ratings of the CS-reward contingencies reported by participants on a 10-point scale were the followings: for $p = .2$, $M = 3.52$, $SD = 2.06$; for $p = .5$, $M = 4.94$, $SD = 1.36$; for $p = .8$, $M = 6.97$, $SD = 1.47$.

Mean pressure

As in Experiment 4, I first calculated the mean pressure. If PIT effect endured reward devaluation, the mean pressure should increase as a function of the CS-US associated probability. A repeated measures ANOVA with Contingency (.2, .5 and .8) and Time (1 to 5 bins) as within-subjects factors, and Drink (water and sugary) as a between-subjects factor showed a significant main effect of Contingency, $F(2,56) = 5.28$, $p = .008$, $\eta_p^2 = .159$, a significant main effect of Time, $F(1.51, 42.37) = 5.45$, $p = .013$, $\eta_p^2 = .163$, but not a significant effect of Drink ($p = .227$) or any significant interaction (Contingency X Drink, $p = .626$; Time X Drink, $p = .611$; Contingency X Time, $p = .179$; Contingency X Time X Drink, $p = .569$; see Figure 15, panel a and d). Data significantly fitted a linear trend for both the Contingency factor, $F(1, 28) = 7.19$, $p = .012$, $\eta_p^2 = .204$, and the Time factor, $F(1, 28) = 6.57$, $p = .016$, $\eta_p^2 = .190$.

Peak pressure

Secondly, I calculated the peak pressure. The peak pressure should increase as a function of the CS-US associated probability if the PIT effect is still present. A repeated measures ANOVA with the same factors as before, however, showed that the main effect of Contingency did not reach significance ($p = .073$), while the main effect of Time was significant, $F(1.84, 51.46) = 9.72$, $p < .001$, $\eta_p^2 = .258$, but there was not a significant effect of Drink ($p = .335$) or any significant interaction (Contingency X Drink, $p = .716$; Time X Drink, $p = .719$; Contingency X Time, $p = .155$; Contingency X Time X Drink, $p = .067$; see Figure 15, panel b and e). Data for the Time factor fitted significantly a linear trend, $F(1, 28) = 13.05$, $p = .001$, $\eta_p^2 = .318$.

Number of grips

Lastly, I evaluated the number of grips. An enduring PIT effect would show that the number of grips increases as a function of the CS-US associated probability. A repeated measures ANOVA with the same factors as before showed a significant main effect of Contingency, $F(2, 56) = 5.23$, $p = .008$, $\eta_p^2 = .157$, a significant main effect of Time, $F(2.61, 73.10) = 4.32$, $p = .010$, $\eta_p^2 = .134$, but not a significant effect of Drink ($p = .833$) or any significant interaction (Contingency X Drink, $p = .623$; Time X Drink, $p = .793$; Contingency X Time, $p = .098$; Contingency X Time X Drink, $p = .167$; see Figure 15, panel c and f). Data significantly fitted a linear trend for both the Contingency factor, $F(1, 28) = 7.83$, $p = .009$, $\eta_p^2 = .218$, and the Time factor, $F(1, 28) = 5.82$, $p = .023$, $\eta_p^2 = .172$. The analyses have been Greenhouse-Geisser corrected when required.

Thirst ratings

I then analyzed how participants rated their level of thirst as soon as they arrived in the lab, after they drank but before beginning the PIT test, and at the end of the experiment. A Wilcoxon signed-rank test indicated that the ranks given after drinking ($M = 1.47$, $SD = 0.82$; $M = 1.73$, $SD = 1.08$; $M = 1.40$, $SD = 0.89$ respectively) were significantly lower than the initial ranks ($M = 4.17$, $SD = 0.70$; $M = 4.47$, $SD = 0.57$; M=3.93, SD=0.78 respectively) for all the three items ($Z = 463$, $p < .001$; $Z = 406$, $p < .001$; $Z = 462$, $p < .001$ respectively), a pattern of results showing that the devaluation procedure was successful. I also compared the ranks in the initial and the last survey. The same test indicated that for all the three items at the end of the experiment ranks were still significantly lower ($M = 2.00$, $SD = 1.02$; $M = 2.27$, $SD = 1.14$; $M = 1.83$, $SD = 0.99$ respectively) than those observed at the beginning ($Z = 404$, $p < .001$; $Z = 404$, $p < .001$; $Z = 460$, $p < .001$ respectively). Lastly, I compared ranks in the last survey with those in the second survey. The same analysis showed that, for all the three items, at the end of the experiment ranks were higher than those found after participants had drunk (Z = -3.23, p = .005; Z = -2.11, p = .038; Z = -3.24, p = .006 respectively).

Between-experiment comparison

Because the PIT was still present in Experiment 7, as attested by the significant modulation of the different CS-predictive power on the instrumental performance, it was worth investigating if after reward devaluation such CS modulation is at least reduced. Since Experiments 4 and 7 were administered following the same procedure except for the US devaluation, the above question can be investigated by means of a between-experiment comparison analysis.

Mean pressure

A repeated measures ANOVA with Contingency (.2, .5 and .8) and Time (1 to 5 bins) as within-subjects factors, and Group (Experiment 4 and 7) as a between-subjects factor showed no significant interaction between the three factors (p = .503), no significant interaction between Contingency X Group (p = .240) and no significant interaction between Time X Group (p = .679). The main effects of Contingency F(1.45, 84.11) = 7.90, p = .002, η_p^2 = .120, Time F(2.27, 131.65) = 13.67, p < .001, η_p^2 = .191, and Group F(1, 58) = 8.15, p = .006, η_p^2 = .123, were all significant. The fact that the overall mean pressure in Experiment 7 was lower than Experiment 4 can simply be the result of a group difference.

Peak pressure

The same ANOVA on the peak-pressure data showed no significant interaction between the three factors ($p = .862$), no significant interaction between Contingency X Group ($p = .609$) and no significant interaction between Time X Group ($p = .878$). The main effects of Contingency $F(1.61, 93.87) = 8.03$, $p = .001$, Time $F(2.39, 138.90) = 20.27$, $p < .001$, $\eta_p^2 = .259$, and Group $F(1, 58) = 3.26$, $p = .037$, $\eta_p^2 = .073$, were all significant. The fact that the overall peak pressure in Experiment 7 was lower than Experiment 4 can simply be the result of a group difference.

Number of grips

The same ANOVA on the number of grips showed no significant interaction between the three factors ($p = .944$), no significant interaction between Contingency X Group ($p = .620$) and no significant interaction between Time X Group ($p = .801$). The main effects of Contingency $F(1.76, 101.82) = 9.13$, $p < .001$, $\eta_p^2 = .136$, and Time $F(2.61, 151.49) = 9.19$, $p < .001$, $\eta_p^2 = .137$ were significant. The main effect of Group did not reach significance ($p = .069$).

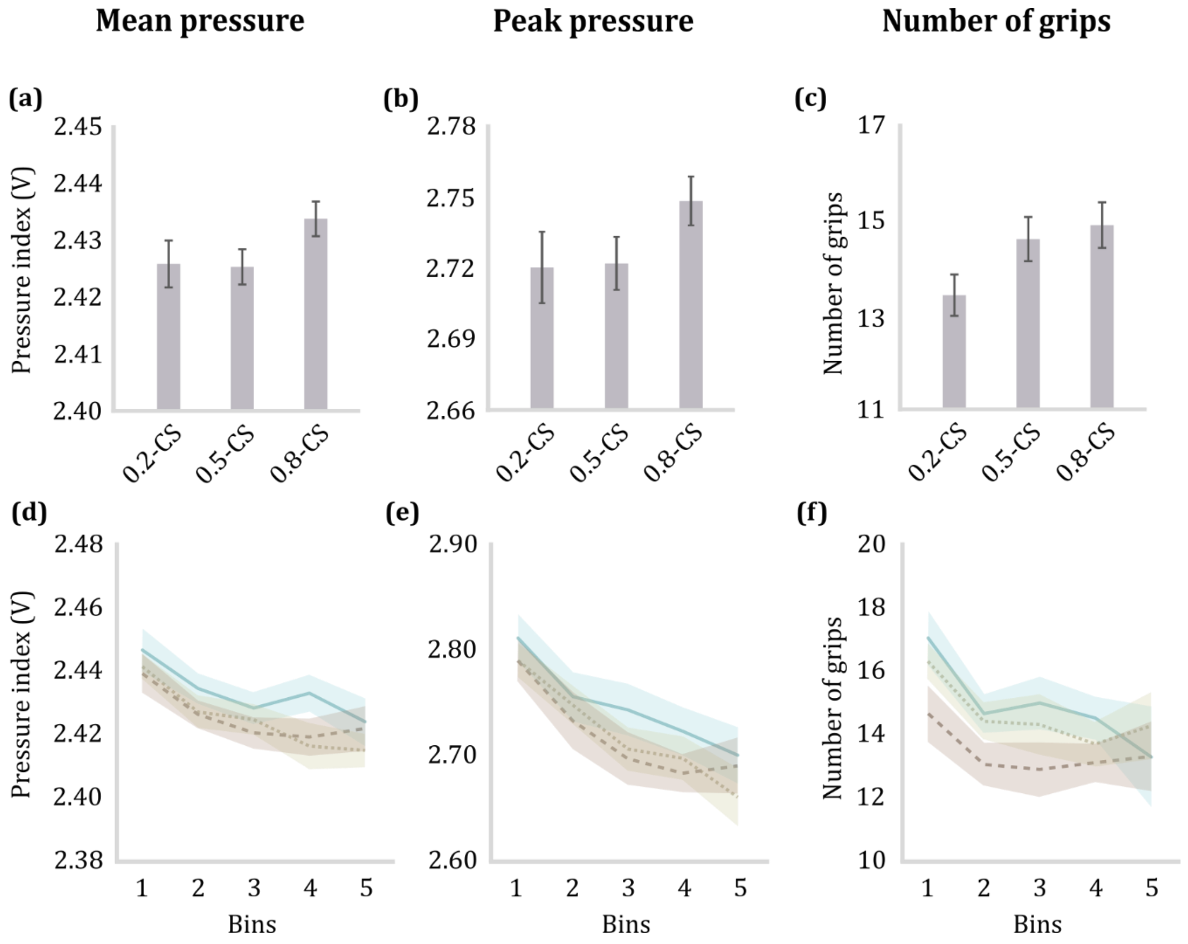

Figure 15. Graphical representation of the results of Experiment 7.

(a) Mean pressure of PIT test as a function of CS-associated probability. (b) Peak pressure of PIT test as a function of CS-associated probability. (c) Number of grips of PIT test as a function of CS-associated probability. (d) Mean pressure in PIT test as a function of CS-associated probability and time. (e) Peak pressure in PIT test as a function of CS-associated probability and time. (f) Number of grips in PIT test as a function of CS-associated probability and time. Error bars represent 95% confidence intervals for within-subjects designs (Cousineau, 2005).

DISCUSSION

Experiment 7 was designed to test the modulation of the PIT effect after reward devaluation. Two contrasting hypotheses were tested. According to the incentive salience model (Zhang et al., 2009), a decrease in the reward-driven physiological state should translate into a decreased motivational power of the associated CS. Conversely, another possibility, suggested by previous animal studies, was that the incentive properties of the Pavlovian CSs should remain unchanged even after a devaluation of the associated reward. The result of Experiment 7 clearly supports the latter hypothesis, showing that the mean pressure and the number of grips increased significantly with the US predictive probability associated to the CS shown during the test phase (although the peak pressure modulation was not significant).

That the US devaluation was effective is also suggested by the differences between pre- and post-ranks in the three-item thirst questionnaire reported by participants: all ranks were drastically reduced after participants drank to quench their thirst. Although at the end of the test phase ranks increased from those collected just after participants had drunk, they remained well below the initial ranks and far from signaling any thirst at all. However, this slight increase in ranks could signal that CSs might have stimulated the motivational properties of the associated US. Although I acknowledge that the three-item questionnaire might not appropriately reflect the constructs of wanting and liking in their explicit (or implicit) form (Pool, Sennwald, Delplanque, Brosch, & Sander, 2016), this idea deserves to be further investigated.

Participants, on average, were aware of the CS-US contingencies as attested by their ratings. It is therefore plausible that the CS retrieved the representation of the US, which, however, was no longer highly desirable because of the devaluation procedure. Nevertheless, the US-associated instrumental action was still enhanced by the presentation of the CS. The non-significant main effect of Drink indicates that this effect emerged independently of the type of drink chosen as US, and endured throughout the whole test phase, as suggested by the lack of interaction between Contingency and Time.

The between-experiment comparison suggests that the magnitude of the PIT was not different between the Experiment 4 and Experiment 7. Although the overall performance was lower in Experiment 7, as indicated by the main effect of the Group factor, the differential invigorating effect of the CSs was comparable across the two experiments, as suggested by the lack of any interaction with the Group factor.

GENERAL DISCUSSION

Does a change in the incentive value of a primary reward (US) alter the motivational properties of the associated CS as expressed by performance? To address this question I took advantage of the PIT effect.

The results of Experiment 4 provided a reliable setting to obtain a PIT measure. Indeed, the instrumental action performed to accumulate a beverage reward was enhanced by the presence of a consistent Pavlovian predictor of the beverage, thus corroborating the evidence of a human PIT effect. Moreover, while the general vigor of the instrumental action declined, the CS incentivizing power endured until the end of the task, a result consistent with the fact that the US maintained its incentive power since participants remained thirsty until the end of the experiment.

Interestingly, however, the results of Experiment 7 showed that the influence of the Pavlovian CS on the instrumental performance outlasted reward devaluation. In addition, such influence was not different between the two experiments as indicated by the between-experiment comparison, suggesting that US devaluation did not attenuate the PIT effect. Because the instrumental response was not controlled by the actual value of the outcome, the persistence of the PIT effect is, to some extent, surprising. Previous animal studies have already reported similar findings, but by using a standard palatable US (i.e. water), and by its direct and immediate consumption, here I showed that in humans the motivational power of a Pavlovian CS to modulate the instrumental performance can persist after reward devaluation. Although highly palatable sugary drinks are likely more desirable than plain water, the present results show that the endurance of PIT after US devaluation is unrelated to the palatability of the US used.

The PIT resistance to US devaluation could be due to a progressive shift of the action control from a response-outcome representation to a stimulus-response association (i.e. the action becomes a habit; Cartoni et al., 2016). To exclude this possibility I adopted a relatively short instrumental training, in which the risk of shift from an action to a habit was minimized. One should note, however, that despite instrumental over-trained actions are indeed less sensitive to US devaluation, the same actions become more sensitive to PIT (Holland, 2004), and therefore the CS motivational persistence I documented cannot be interpreted as due to a habit formation, also because the CS and the action that it invigorated were never trained together.

From a procedural perspective, it could be argued that the mercury-like bar appearing during both the instrumental conditioning phase and the PIT test phase, might have worked like a discriminative stimulus. To begin with, although I must acknowledge this is not a strong argument, an analogous procedure presenting a performance indicator both in the instrumental training and in the test phase has been used in previous studies (Pool et al., 2015; Talmi et al., 2008). Second, and most crucial, if the indicator had acted as a discriminative stimulus no differences in the rate of responding would have emerged as function of the Contingency, namely no PIT would have been observed.

According to the associative cybernetic model formulated by Balleine and Ostlund (Balleine & Ostlund, 2007) to explain the PIT effect, the CS activates the US representation, which in turn activates the action learned during instrumental conditioning. A straightforward prediction of the theory is that the PIT should be weakened when the representation of the US is no longer desirable, a condition that likely occurred in the test phase of Experiment 7. The unpredicted presence of the PIT effect in the same phase, therefore, suggests that the instrumental action was not motivated by the actual US sensory properties, but rather by the US sensory properties encoded previously during the conditioning phase. Another possibility, as suggested by the Konorskian view, is that the CS prediction and the US devaluation might affect different aspects of the US representation, and thus the CS can continue to exert its influence on the instrumental action by a motivational system activation (Dickinson & Balleine, 2002; Konorski, 1967).

In compliance with the incentive-sensitization theory (T. E. Robinson & Berridge, 2008), the results of Experiment 7 suggest a dissociation in the different measures of the reward components (Berridge & Robinson, 2003). Although participants explicitly reported neither to be thirsty nor to like receiving a drink, yet the presence of the CS increased the degree of instrumental effort participants were willing to make to obtain the devalued US. Specifically, the low ranks of the questionnaire items appear to be in contrast with the significant PIT effect, which has been interpreted as a measure of a more implicit *"wanting"* (Berridge & Robinson, 2003). Although the three-item questionnaire does not expressly adhere to the constructs of explicit wanting and liking as defined by the incentive-sensitization theory in its most recent formulation, it is worth noting that the questionnaire items could be considered at least an index of the participants' explicit perception of the US. As advised in a recent review on the topic

(Pool et al., 2016), participants provided the ranks right after reward consumption, a procedure that seems appropriate to measure the participants hedonic experience. However, I cannot exclude the possibility that the questionnaire may instead reflect a more complex *expected pleasantness* about the US, a construct that refers to both cognitive desires and related past liking experiences.

In this chapter I presented a study that adds to the existing evidence supporting the idea that a CS is not a mere predictor of the US, but rather is can become a powerful incentive, which can increase the effort the organism is willing to make in order to obtain the associated outcome. Here I showed that the motivational power of a CS can irrationally endure even after the associated outcome is no longer desirable, a result that is in line with previous findings on the reward cue attentional salience described in the previous chapter, and that can help explaining different addictive behaviors (M. J. F. Robinson, Robinson, & Berridge, 2014; T. E. Robinson & Berridge, 2008).

CHAPTER 6

THE INCENTIVE LEARNING HYPOTHESIS

In the previous chapters, I have discussed how reward-associated cues become capable of influencing certain aspects of cognitive processes like attention and the control of instrumental action. Furthermore, I have shown some examples of how such capability can exert its influence beyond the actual value of the associated reward independently of the reward-related physiological state. At odds with the prediction according to which the cognitive system should prioritize cues of motivationally significant outcomes (Mackintosh, 1975), the data I have reported suggest that in some cases the motivational properties of a reward cue does not follow the dynamic change of the reward value. This suggestion is in line with the hypothesis that the CS value can detach from the US value (Berridge, 2012), a possibility that might explain the apparent irrational behaviors previously reported in Experiment 5 and 7 and add to other existing literature reviewed before. In this chapter, I will investigate how to update a cue value when the reward value changes.

A DUAL PROCESS THEORY OF INSTRUMENTAL MOTIVATION

The mechanisms involved in the relation between learning processes and motivational systems have long been studied by Dickinson, Balleine and colleagues. The results of numerous investigations led the authors to formulate a dual process theory of instrumental motivation (Dickinson & Balleine, 1994), which aims at explaining the motivational control of an instrumental action. According to the theory, behavior is controlled by two separated and dissociable motivational processes (Balleine & Dickinson, 1998; Dickinson, Smith, & Mirenowicz, 2000). The first is the Pavlovian Motivational Process: CSs, discriminative stimuli or contexts, acquire motivational properties during action learning through a Pavlovian association with the outcome. Such stimuli endow motivational properties that depend directly on the current motivational value of the outcome. This process is also central in the incentive-sensitization theory by Berridge and Robinson (2016) introduced before, and predicts that the motivational power of the cues updates automatically and immediately after a shift in the outcome value (Tindell et al., 2009; Zhang et al., 2009). The second motivational process at play is the Incentive Learning Process, which is based on the knowledge of the action-outcome relation. The important difference of the Incentive Learning Process from the Pavlovian Motivational Process is that in order to appropriately update the outcome value following a shift in the motivational state, it is necessary to experience the outcome in the new state. This would explain why motivational shifts do not affect directly the value of the outcome of an instrumental action (Balleine, 1992; Dickinson & Balleine, 1994; Holland, 2004; Wilson et al., 1981). Rather, motivational shifts have such effect only once the instrumental action is associated *again* with the outcome in the shifted state (Balleine, 1992). In other words, the incentive value of an outcome in a particular motivational state *has to be learned*.

This process, called *incentive learning*, allows adapting the behavior according to the change of values in the environment. The necessity of an incentive learning process might sound bizarre when applied to daily life, because when we are satiated apparently we do not remain hungry for all the foods that were not in the meal we just ate. However, it is worth noting that re-experiencing the outcome in an altered state of motivation is rather common in a natural environment, a condition that could take place also in the laboratory if the tests were not conducted in extinction.

In the context of the previous findings reported in Experiment 5 and 7, a possible mechanism for re-modulating the incentive salience of reward cues is offered by the notion of incentive learning. Specifically, it might be possible that in order to attenuate the enduring and irrational effects generated by reward cues, one needs to re-associate the cues with the outcome in the new shifted motivational state, i.e. after the outcome devaluation.

INCENTIVE LEARNING IN PAVLOVIAN MECHANISMS

The appropriateness the Incentive Learning Process to interpret the persisting motivational effects of reward cues reported before might be questioned. Indeed, the process I have assumed to explain previous results is based on a Pavlovian mechanism, and the paradigms I have used, at least in the attentional domain, are not appropriated to investigate instrumental actions intended as being *goal-directed* (Dickinson & Balleine, 1994). For an instrumental action to be goal-directed, it is necessary to meet two criteria. First, the action-outcome contingency has to be represented, namely the agent needs to be aware of the consequences of its action. Second, the outcome has to be a goal for the agent. However, what I measured in the previous experiments is not suitable to respect the two above-mentioned criteria. First, in the attentional domain the capture effect can be considered automatic and not the result of a cognitive strategy. Second, the test was administered as an irrelevant task, so the outcome was not a goal in such a context. Nevertheless, the boundary between Pavlovian incentive salience and cognitive expectation is not clear (Berridge, 2001). For example, it has been reported that the incentive learning mechanism is not always necessary to update an agent's behavior toward the outcome (Rescorla, 1994; Shipley & Colwill, 1996). Moreover, the PIT experiment that I have reported together with previous similar evidence in the literature stands in contrast with the automaticity of value shift described in the Pavlovian Motivational Process (Berridge, 2012).

Despite the theoretical models of motivational modulation and learning processes, it has to be acknowledge that the predictions make by such models are challenged in a number of cases that might be sufficiently consistent to venture some new hypothesis. The driving idea in the following experiments is that the persisting incentive salience of a reward cue, as expressed in its capacity to still bias attention after reward devaluation, can be attenuated by incentive learning, namely when one re-experiences the association of that cue with the reward in the altered motivational state. In the following experiments, I operationalized the incentive learning as an additional session of conditioning with the same cue-reward relation, in a context of an altered motivational state in which the outcome has no value. Therefore, the next experiments were designed with this goal in mind: after thirsty participants underwent a conditioning phase, in which two cues signaled the reward with an associated high or low probability, they quenched their thirst (sensory specific reward devaluation). Then, participants were tested in an irrelevant visual search task in which target letters were embodied in the previous reward cues. According to the results of Experiment 5, participants should be faster in responding to the target when presented within the former best reward cue, thus replicating evidence in favor of the irrational attentional capture. After this phase, in Experiment 9 participants underwent a second and equal conditioning, in which the same cues with the same associated probabilities signaled an outcome, this time with a low motivational value. Then, participants were tested again for attentional capture in the same visual search task. If incentive learning has a role in attenuating the cue motivational effect, then no or less attentional bias should emerge. In the hypothetical scenario of a lack of attentional bias, the null result could also be explained by the fact that between the first and the second visual search test the attentional bias may have vanished. Therefore, to control for a possible effect of time, a preliminary Experiment 8 was administered. In Experiment 8 the experimental scheme was the same of Experiment 9, except that the second conditioning was omitted, but allowing the comparable amount of time to pass between the two tests (see Figure 16). Experiment 8 could provide also more information about the duration of the irrational attentional bias.

EXPERIMENT 8

METHODS

Participants

Twenty-three undergraduate students (M_{age} = 21.0 years, 19 females) took part in the experiment after providing informed consent. They were asked not to drink for

about 4 hours prior to the experimental session. They received €5 compensation for their participation.

Apparatus

As in Experiment 1.

Stimuli

Conditioning phase

As in Experiment 2, except that the cues were reduced to two, and assumed two of the same three equilluminant colors (red, green and cyan) in a balanced order across participants.

Visual Search

The compound-stimuli consisted of one L and one T (1.8° x 1.8°), which appeared randomly tilted to the left or to the right, each one inside a colored ring used as reward cue during the conditioning phase. The two compound stimuli were presented simultaneously and equally spaced (180°) on an imaginary circle (5° radius) centered on the screen. A fixation cross, inscribed in a circle with 0.5° diameter, appeared in the center of the screen.

Procedure

Similarly to Experiment 2, participants' level of thirst was assessed verbally at the beginning of the experiment and participants were offered salty food to increase their level of thirst. They were asked to select their preferred beverage from a variety (from water to well-known sugary drinks) as reward. The amount of liquid reward that dropped into the glass depended on their responses during the conditioning phase. Participants also performed a few practice trials using a gray cue with the 0.5 cue-reward contingency before the experimental session. The experiment was divided into five phases (see Figure 16), and overall lasted about 50 min.

Phase 1: Conditioning

As in Experiment 2, except that the cues were reduced to two, each one associated with a high (p = .8) or low (p = .2) probability of predicting the beverage reward upon acceptance. The total number of trials was 160, and the available “accept” responses were 80.

Phase 2: reward devaluation

Participants were allowed to drink ad libitum the beverage they had chosen as reward during the conditioning phase, so that I specifically devalued the reward associated with the cue. They were encouraged to drink to quench their thirst. To evaluate their level of thirst, participants completed the same 3-item questionnaire administered in the previous experiments.

Phase 3: first test

The same visual search administered in Experiment 2, except that the choice was made on two compound stimuli and the total amount of trials was 120, divided into 2 blocks of 60 trials. The target appeared within each colored ring in an equal number of trials.

Phase 4: waiting phase

In order to control for the effect of time in a delayed measure of attentional capture, participants waited 15 minutes before starting the second test. The amount of time was determined by a pilot test in which the time for conditioning was measured and averaged. Participants in this phase remained sit in front of the screen, which showed a countdown of the time that remained to be waited.

Phase 5: second test

The same visual search test of Phase 3 was administered for the second time.

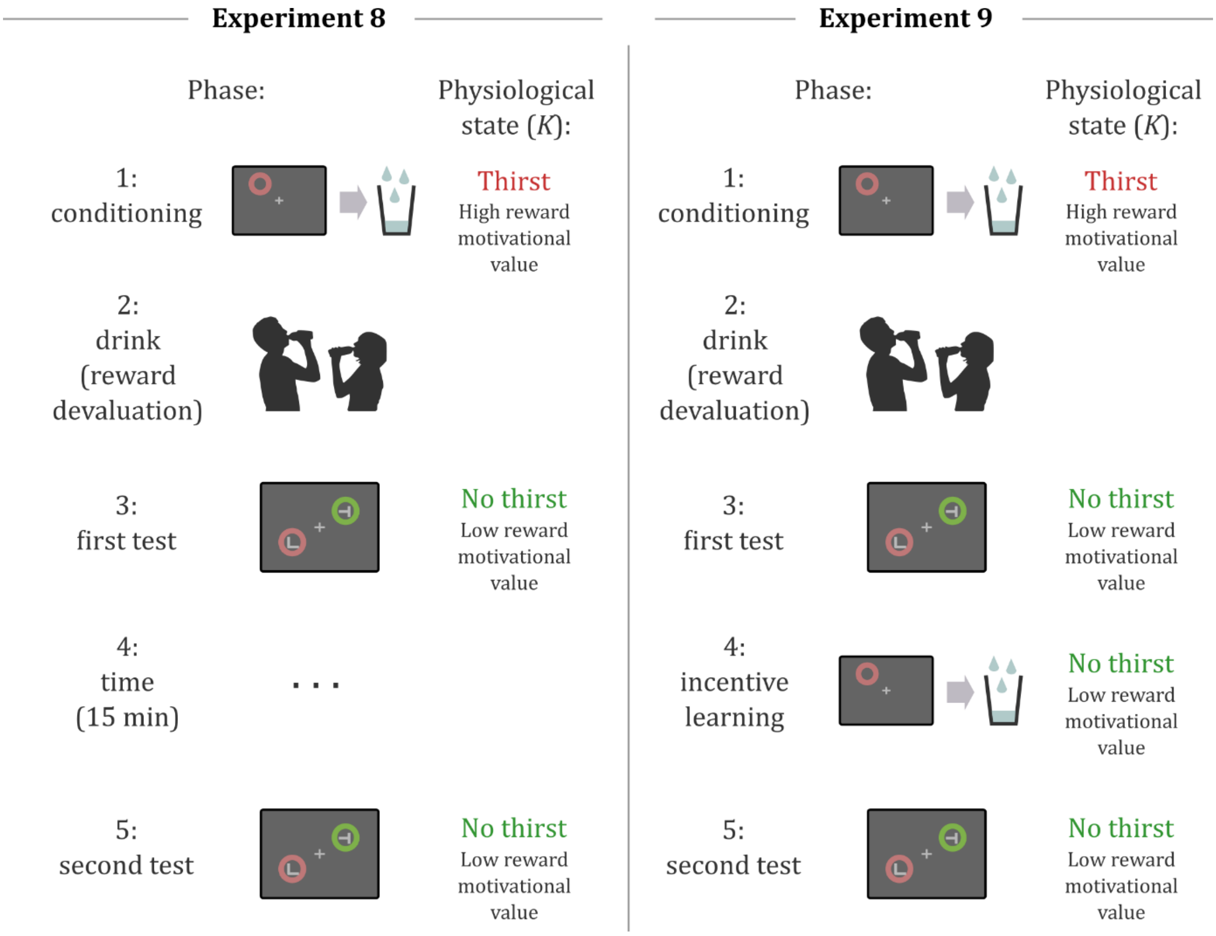

Figure 16. Phase diagram for Experiment 8 and 9 and physiological state relative to the beverage reward that corresponded to each phase.

See Procedure for details.

RESULTS

Phase 1: Conditioning

The analysis on RTs during the first conditioning were separated for “accept” and “reject” responses. For “accept” responses (outliers <2%), a paired *t* test showed that RTs in the p = .8 condition were significantly shorter than RTs in the p = .2 conditions, $t(22) = 5.58$, $p < .001$, $d = 1.164$, indicating that during the conditioning phase participants were faster at deciding to accept the cue associated to the highest probability of reward. For "reject" responses, the same analysis revealed that RTs in the p = .8 condition were significantly higher than RTs in the p = .2 conditions, $t(22) = -3.97$, $p < .001$, $d = -0.828$, indicating that during the conditioning phase participants were faster at deciding to reject the cue associated to the lowest probability of reward.

The analysis on the rate of responses of acceptance associated with the different cue showed that the response rate in the p = .8 condition was significantly higher than the response rate in the p = .2 conditions (paired t test), $t(22) = -9.06$, $p < .001$, $d = -1.888$, indicating that the rate of acceptance of a cue increased with its contingency (see Figure 17 panel c). Given that a binary response (accept or reject) was always required, that indicates that the rate of refusal of a cue increased as its contingency decreased.

The mean ratings of the cue-reward contingencies reported by participants on a 10-point scale were the followings: for p = .2, M = 2.78, SD = 2.07; for p = .8, M = 6.78, SD = 2.04. No participant ranked the cue-reward contingency in the wrong order.

Phase 2: reward devaluation

Here I report the analysis on how participants rated their level of thirst before the beginning of the conditioning phase and after they drank to quench their thirst (before the beginning of the first visual search test). A Wilcoxon signed-rank test indicated that post-task ranks were significantly lower than the pre-task ranks for all the three items (Z = 276, $p < .001$; Z = 253, $p < .001$; Z = 276, $p < .001$ respectively). These results indicate that the devaluation procedure was successful.

Phase 3: first test

A paired *t* test on RTs for correct responses (89.5%) in the first visual search test (outliers <2%) showed that RTs in the *p* = .8 condition were significantly shorter than RTs in the *p* = .2 conditions, *t*(22) = 3.33, *p* = .003, *d* = 0.694 (see Figure 17 panel a).

A paired *t* test on accuracy across cues in the visual search task showed that accuracy in the *p* = .8 condition was not significantly different from accuracy in the *p* = .2 conditions (*p* = .276).

Phase 5: second test

A paired *t* test on RTs for correct responses (93.0%) in the second visual search test (outliers <2%) showed that RTs in the *p* = .8 condition were significantly shorter than RTs in the *p* = .2 conditions, *t*(22) = 2.77, *p* = .011, *d* = 0.578 (see Figure 17 panel a).

A paired *t* test on accuracy across cues in the visual search task showed that accuracy did not differ depending on whether the target was encircled within the *p* = .8 or the *p* = .2 former cue (paired *t* test, *p* = .869).

First vs. second test comparison

In order to determine whether there was a difference between the results of the first and the second visual search test, a repeated measures ANOVA with Contingency (.2 vs. .8) and Test (first vs. second) as within subject factors was computed and showed a significant main effect of Contingency, $F(1, 22) = 21.03$, $p < .001$, $\eta_p^2 = .489$, a significant main effect of Test, $F(1, 22) = 22.54$, $p < .001$, $\eta_p^2 = .506$, but no significant interaction between Contingency and Test (*p* = .930), indicating that in the second test participants were generally faster in detecting the target (see Figure 17 panel a), but the effect of attentional bias was not reduced by time.

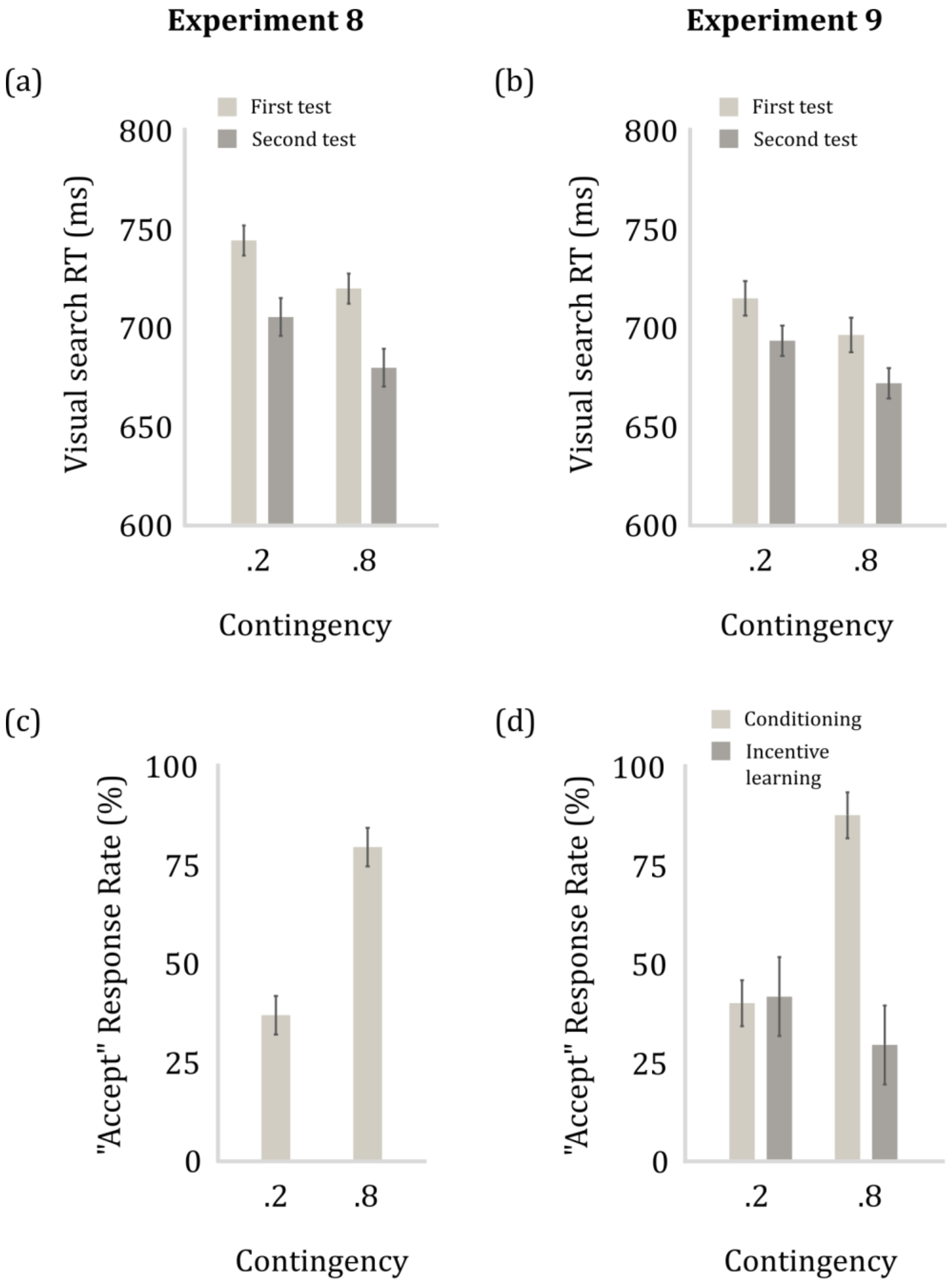

Figure 17. Graphical representation of the results of Experiment 8 and 9.

(a) Visual search RTs in Experiment 8 plotted as a function of cue-reward contingencies and test. (b) Visual search RTs in Experiment 9 plotted as a function of cue-reward contingencies and test. (c) "Accept" response rates in Experiment 8 plotted as a function of cue-reward contingencies. (d) "Accept" response rates in Experiment 9 plotted as a function of cue-reward contingencies and conditioning phases (the second conditioning is referred to incentive learning). Error bars represent 95% confidence intervals for within-subjects designs (Cousineau, 2005).

DISCUSSION

The results of the first visual search test successfully replicated the results reported in Experiment 5: the cues persisted in captivating participants' attention despite the low value of the formerly predicted reward (as indicated by the ranks of the questionnaire). In addition, results also showed that the same cues continued to capture attention even in a delayed test. The analysis revealed that the interval between the two tests was ineffective in reducing the attentional bias, as suggested by the lack of any interaction between the Contingency and Test factors. The main effect of Test can be interpreted as the effect of training: indeed, participants were generally faster in detecting the target in the second test as compared to the first.

The results of Experiment 8, therefore, can provide a reliable control for a further implementation of incentive learning in the experimental procedure, with the aim to disrupt or attenuate the persisting irrational attentional bias that reward-cues have shown to have gained.

EXPERIMENT 9

METHODS

Participants

Twenty-six undergraduate students (M_{age} = 24.2 years, 19 females) took part in the experiment after providing informed consent. They were asked not to drink for

about 4 hours prior to the experimental session. They received €5 compensation for their participation.

Apparatus

As in Experiment 1.

Stimuli

Conditioning phase

As in Experiment 8.

Visual Search

As in Experiment 8.

Procedure

As in Experiment 8, except for Phase 4, in which participants underwent a second conditioning for incentive learning (see Figure 16). In order to associate the reward cues to the devalued outcome in a condition of physiological shift, the same conditioning of Phase 1 was repeated.

RESULTS

Phase 1: Conditioning

For “accept” responses (outliers <2%), a paired *t* test showed that RTs in the p = .8 condition were significantly shorter than RTs in the p = .2 conditions, $t(24) = 2.46$, p = .021, d = 0.493, indicating that during the first conditioning phase participants were faster at deciding to accept the cue associated to the highest probability of reward. For “reject” responses, the same analysis revealed that RTs in the two conditions did not differ significantly (p = .134), indicating that during the first conditioning phase participants’ speed in rejecting the cues was comparable across the probability of reward.

The analysis on the rate of responses of acceptance associated with the different cue showed that the response rate in the p = .8 condition was significantly higher than the response rate in the p = .2 conditions (paired *t* test), $t(25) = -9.43$, $p < .001$, d = -1.849, indicating that the rate of acceptance of a cue increased with its contingency (see Figure 17 panel d). This indicates that the rate of refusal of a cue increased as its contingency decreased.

The mean ratings of the cue-reward contingencies reported by participants on a 10-point scale were the followings: for p = .2, M = 2.31, SD = 1.49; for p = .8, M = 7.38, SD = 0.85. No participant ranked the cue-reward contingency in the wrong order.

Phase 2: reward devaluation

A Wilcoxon signed-rank test indicated that post-task ranks were significantly lower than the pre-task ranks for all the three items (Z = 351, $p < .001$; Z = 300, $p < .001$;

$Z = 325$, $p < .001$ respectively). These results indicate that the devaluation procedure was successful.

Phase 3: first test

A paired *t* test on RTs for correct responses (88.7%) in the first visual search test (outliers <2%) showed that RTs in the $p = .8$ condition were significantly shorter than RTs in the $p = .2$ conditions, $t(25) = 2.17$, $p = .039$, $d = 0.426$ (see Figure 17 panel b).

A paired *t* test on accuracy across cues in the visual search task showed that accuracy in the $p = .8$ condition were significantly higher than accuracy in the $p = .2$ conditions, $t(25) = -2.22$, $p = .036$, $d = -0.435$.

Phase 4: incentive learning

The analysis scheme in this phase is the same as the on administered in phase 1. For "accept" responses (outliers <3%), a paired *t* test showed that RTs in the $p = .8$ condition were comparable to those in the $p = .2$ conditions ($p = .613$). Analogously, for "reject" responses the same analysis revealed that RTs in the two conditions did not differ significantly ($p = .727$), indicating that during incentive learning (i.e. the second conditioning phase) participants' speed in accepting and rejecting the cues was comparable across the probability of reward.

The rate of responses of acceptance did not differed between the two cues (paired *t* test, $p = .365$, see Figure 17 panel d), indicating that during incentive learning participants' response attitude in accepting and rejecting the cues was comparable across the probability of reward.

Phase 5: second test

A paired *t* test on RTs for correct responses (90.1%) in the first visual search test (outliers <2%) showed that RTs in the *p* = .8 condition were significantly shorter than RTs in the *p* = .2 conditions, *t*(25) = 2.87, *p* = .008, *d* = 0.564 (see Figure 17 panel b).

A paired *t* test on accuracy across cues in the visual search task showed that accuracy did not differ depending on whether the target was encircled within the *p* = .8 or the *p* = .2 former cue (paired *t* test, *p* = .313).

First vs. second conditioning comparison

As another index of motivation, it is interesting to analyze participants' behavior in the two different conditioning session. A repeated measures ANOVA on acceptance response rates with Contingency (.2 vs. .8) and Conditioning (first vs. second) as within subject factors showed a significant main effect of Contingency, *F*(1, 25) = 14.66, *p* < .001, η_p^2 = .370, a significant main effect of Conditioning, *F*(1, 25) = 43.85, *p* < .001, η_p^2 = .637, and a significant interaction between Contingency and Conditioning, *F*(1, 25) = 29.47, *p* < .001, η_p^2 = .541, indicating that participants acceptance attitude generally decreased, and was not different between the two cues in the second conditioning (see Figure 17 panel d).

First vs. second test comparison

A repeated measures ANOVA on visual search RTs with Contingency (.2 vs. .8) and Test (first vs. second) as within subject factors showed a significant main effect of Contingency, *F*(1, 25) = 7.72, *p* = .010, η_p^2 = .236, a significant main effect of Test, *F*(1, 25) = 7.85, *p* = .010, η_p^2 = .239, but no significant interaction between Contingency and Test (*p* = .674), indicating that the effect of attentional bias was not modulated or reduced by the procedure of incentive learning that was implemented in Phase 4, despite in the second test participants were generally faster in detecting the target (see Figure 17).

Between experiments comparison

Given that Experiment 8 and 9 were administered following the same procedure except for incentive learning, it is possible to compute an analysis between the two experiments. A repeated measures ANOVA with Contingency (.2 vs. .8) and Test (first vs. second) as within subject factors and Experiment (Exp. 8 vs. Exp. 9) as a between subject factor showed a significant main effect of Contingency, $F(1, 47) = 23.86$, $p < .001$, $\eta_p^2 = .337$, a significant main effect of Test, $F(1, 47) = 28.40$, $p < .001$, $\eta_p^2 = .337$, but no significant main effect of Experiment ($p = .329$) or any significant interaction (Contingency X Test, $p = .770$; Contingency X Experiment, $p = .587$; Test X Experiment, $p = .168$; Contingency X Test X Experiment, $p = .895$).

DISCUSSION

The results of Experiment 9 suggest that reward cues continue to capture attention even after participants were submitted to an incentive learning procedure. Indeed, the attentional bias emerged both in the first and in the second test and was neither reduced nor modulated by the incentive learning manipulation, as suggested by the between test comparison.

Because in this experiment each conditioning phase was administered in a different motivational state (Phase 1 and 4), it is worth commenting the difference between the two learning phases. The first conditioning in Phase 1 showed that participants were more likely to accept the best reward cue ($p = .8$) and were also faster in doing so, as compared to the less reliable reward predictor (*p* = .2). This behavior is in line with the idea that participants were strongly motivated in maximizing the beverage reward. However, the identical conditioning of Phase 4 (that was implemented as a chance for a new incentive learning) provided a very different scenario: participants generally reduced their responding attitude and importantly, they did not differentiate their attitude between the two cues (nor did their speed in responding was different). This behavior suggests that participants were not motivated in obtaining the reward anymore, a hypothesis in line with the results of the thirst questionnaire. It is therefore plausible that the incentive learning procedure was appropriate in the sense that the cues were paired with the outcome in a condition of a low physiological state (i.e. a low motivational state) relative to the same outcome. Notwithstanding its appropriateness, the new incentive learning was not able to override the effects of the original learning phase by means of which an attentional bias in favor of the best reward cue predictor was established.

GENERAL DISCUSSION

The most important result of Experiment 8 and 9 is that the attentional attraction towards a reward cue can resist the combined effects of reward devaluation, time and incentive learning. I have already discussed in the previous chapters other cases in which reward cues exert their behavioral influence despite reward devaluation. Moreover, that a reward cue can capture attention even after some time has passed (here at least 15 min) is something that has been documented also in previous works: for example, it has been shown that the attentional capture effect can endure for weeks or even months after conditioning (Anderson et al., 2011; Anderson & Yantis, 2013). It is worth noting, however, that Experiment 8 tested the lasting attentional effect in a context of reward devaluation, and thus provides new indications about the role of time in that context. However, the fact that incentive learning did not modulate the cue attentional-grabbing power is something that has never been reported. The results of Experiment 9 suggest that, surprisingly, incentive learning did not even reduce the effect.

If the attentional bias is considered as an indicator of incentive salience (Anderson et al., 2017; M. J. F. Robinson, Fischer, Ahuja, Lesser, & Maniates, 2016), the data I have reported in this chapter can be interpreted as an additional example in which "wanting" can operate independently from one's cognitive desire and liking. Indeed, here participants ranked the reward beverage as un-wanted and un-liked (although the validity of the questionnaire I have adopted in relation to the measures of wanting and liking can be questioned; see Chapter 4). Moreover, when the second conditioning is analyzed, it appears even more evident that participants were not interested in obtaining the beverage reward, because they deliberately changed their choice behavior towards the cues. In addition, even the speed of responses towards the cues during the second conditioning (both "accept" and "reject" responses) was comparable. Yet, the same cues were able to attract participants' attention as a function of their previous reward associative strength.

Another noteworthy element emerging from the second conditioning phase in Experiment 9 (i.e. the incentive learning manipulation) concerns the role of selection history in the attentional bias (Awh et al., 2012; Chapman et al., 2014). That is, the fact that the attentional bias I have reported is not due to a Pavlovian mechanisms that transfers motivational properties between the reward and the associated cue, but rather a consequence of a previous, repeated selection of one stimulus (i.e. the p = .8 cue) and the previous rejection of the other stimulus (i.e. the $p = .2$ cue). This alternative possibility was already investigated in Chapter 2, and the results tend to safely exclude alternative account. As another element of exclusion, in Experiment 9 the attentional bias emerged in the second test even if the cue that captured attention was not preferentially chosen over the other in the previous incentive learning conditioning phase (if anything, it tended to be chosen less; see Figure 17, panel d).

Finally, from the present experiments it is difficult to delineate the empirical boundary between the Pavlovian Motivational Process and the Incentive Learning Process. On one hand, the Pavlovian Motivational Process does not always seem to automatically affect the attentional bias. Indeed, the theoretical prediction of the Pavlovian Motivational Process (and the incentive salience model of Zhang et al., 2009) is that the attentional bias should immediately cease after reward devaluation. This prediction is at odds with the results of Experiment 5, 8 and 9. On the other hand, the role of the Incentive Learning Process in explaining the modulation of incentive salience can be questioned because such process involves instrumental goal-directed actions. To interpret the present results in light of the Incentive Learning Process, one must assume the attentional behavior towards a reward cue to be an instrumental action. Such assumption is arguably a stretch because the attentional capture is a rather automatic effect (i.e. the relation between the action and the outcome is not represented) and the outcome in the test phase was task-irrelevant (i.e. the outcome is not a *goal* for the agent). However, the appropriateness of the theoretical models has been challenged by a number of instances, including the phenomenon of the PIT in context in which reward is devalued (see Chapter 5). It is therefore plausible to allow a slight departure from the theoretical Incentive Learning Process in conceiving the hypothesis that incentive learning could be a factor in modulating the attentional capture generated by reward cues, when the attentional capture is interpreted as a sign of incentive salience. However, such hypothesis is not supported by the results of Experiment 9, which are at odds with the theoretical prediction of the Incentive Learning Process, which suggests that the attentional bias should vanish after one has the possibility to experience the reward in the altered motivational state.

The results presented in this chapter replicated the ones obtained in Experiment 5: the attentional bias emerged in both Experiment 8 and 9 even after reward devaluation. In addition, the results showed that the attentional bias outlasted both the passage of time and a new learning phase in which there was a chance of directly re-experience the association between the cues and their former valueless outcomes.

CHAPTER 7

FINAL CONSIDERATIONS

OVERVIEW

The investigation of reward cues' incentive salience from a behavioral perspective that I have reported in the present work delineates a quite intricate scenario.

Reward cues can acquire quite rapidly the behavioral features that characterize the incentive salience, such as the capacity to bias attention and to evoke a motivational state that invigorates or instigates instrumental actions. A brief conditioning session is sufficient to endow a reward cue with the capacity to act as an attentional magnet that attracts attention and the eyes beyond conditioning. Specifically, the attractivity of a reward cue is governed by how reliably it predicted the outcome during associative learning as compared to other uncertain predictors (Chapter 2). I have also reported additional evidence that a PIT effect can be found in humans, and that PIT does not seem to be modulated by different types of reward palatability (Chapter 3).

Surprisingly, such attributes of incentive salience seem to remain effective independently of outcome devaluation. Devaluing the reward by consummatory satiation does not abolish the capacity of a reward cue to capture attention (Chapter 4), nor does it modulate the capacity of a reward cue to invigorate an instrumental action in the PIT effect (Chapter 5). The persistent salience of the cue is "irrational" when the associated outcome is no longer valuable, or to put it in terms of reward utility, the pursuit of a reward cue is not justified when the decision utility is greater than the predicted utility (Berridge & Aldridge, 2008). Hence, a kind of "irrational" behavior may have occurred in the experiments reported here, where the cue maintained its incentive ability to capture participants' attention and to invigorate participants' actions despite the associated reward was devalued.

The persistence of incentive salience attributes after outcome devaluation is in line with Berridge's suggestion (Berridge, 2012), according to which a persistent CS motivational power could be interpreted as a case in which the CS value detaches from the US value. Reasonably, in line with the view according to which agents learn to attend to motivationally relevant stimuli and to ignore motivationally irrelevant stimuli (Mackintosh, 1975), the cue attentional salience should be adjusted according to the new outcome value with a new conditioning phase. In line with this suggestion, Dickinson and Balleine (Balleine, 1992; Dickinson & Balleine, 1994) have proposed the notion of incentive learning, namely the fact that for the current drive state to affect the instrumental action, the reward needs to be experienced in the same drive state. Although this opportunity seems to be necessary for updating the value of the action-outcome relation and to adapt the goal-directed performance accordingly (but see Rescorla, 1994; Shipley & Colwill, 1996), incentive learning seems not sufficient for abolishing the capacity of reward cues to capture attention once this has been established previously. Indeed, an "irrational" attentional bias towards a reward cue seems to endure for long periods and to resist new formed associations between the cue and the previous outcome when devalued (Chapter 6).

IMPLICATIONS

In the context of incentive salience, a pivotal question remains unanswered. How does the incentive salience change according to the value of the associated reward? Or, to put it more generally, does the incentive salience of a reward cue change after it has been acquired? In the attempt to broaden the context of the results reported in the present work, I deem that providing an answer to this question might be of crucial importance to understand of how learning and motivation interact in determining behavior, a behavior that could easily come to be irrepressibly maladaptive.

Drug addiction, for instance, is a circumstance in which a dissociation of the cue incentive salience from the outcome value is particularly evident. When in the appropriate *K* or physiological state, drug addicts can compulsively pursue and crave for drug cues even when the drug is neither pleasant nor cognitively wanted, a pathological condition well described by the incentive-sensitization theory of addiction (Berridge & Robinson, 1998, 2016, T. E. Robinson & Berridge, 1993, 2008). The social implications are quite impressive: a recent report claims that in the U.S.A. more than 1 person out of 20 has a substance use disorder and approximately 135,000 deaths every year are attributed to drug abuse (U.S. Department of Health and Human Services & Office of the Surgeon General, 2016).

Among other theories of addiction, such as the former major model of drive reduction theory or *allostasis* model of addiction, the incentive-sensitization theory of addiction encompasses more successfully the most recent empirical evidence (Berridge

& Robinson, 2016), although it is not yet acknowledged among health institutions (Badiani et al., 2017). A key aspect of this success is the notion that drugs of abuse (like cocaine, amphetamine, heroin, alcohol, nicotine, etc.) not only stimulate the dopamine mesolimbic system, but are also responsible for *sensitization*. Such dual effect is controversial in light of the drive reduction theory, and alludes back to the original experiments on rats' brain stimulation pioneered by Olds and Milner (1954). Drive reduction theory posits that reward assumption satisfies and reduces an organism' internal motivational drive, so the reward is pursued to reach the homeostasis of the system. However, it was striking to observe that drive and reward assumption might reflect the same state, rather than the opposite: indeed, the brain sites where stimulation incites behavior largely overlap with the sites where stimulation is rewarding (Berridge, 2001; Kringelbach & Berridge, 2016; Olds & Milner, 1954). In addition, stimulation of these brain sites is likely not accompanied by any hedonic experience (Berridge & Kringelbach, 2008; Johansen, 2005; Portenoy, Jarden, Sidtis, & Lipton, 1986). This have led to alternative explanations that are best reconciled in the most recent incentive-sensitization theory.

The mechanism of sensitization of the brain mesolimbic system holds a central role in the incentive-sensitization theory, and is likely a consequence of repeated drug assumption. Sensitization is physically expressed by an increased release of dopamine and by a modification of mesolimbic neurons. Functionally, a sensitized brain is hyper-reactive to the incentive motivational properties of drug cues (including contexts), and stimulates abnormally and compulsively the "wanting" for drugs, even in the absence of liking for the drug. Surprisingly, sensitization is triggered rather easily: to engage the mechanism is sufficient to assume low doses of drugs even in subjects with no history of drug usage (Boileau et al., 2006). Moreover, once developed sensitization is long lasting, and in some cases even permanent, and this is what makes drug use very dangerous.

Among rehab circles, there is a saying: “once addicted always addicted”. A recent report in the U.S.A. claims that “more than 60 percent of people treated for a substance use disorder experience relapse within the first year after they are discharged from treatment, and a person can remain at increased risk of relapse for many years” (U.S. Department of Health and Human Services & Office of the Surgeon General, 2016, pp. 2–2). However, there are multiple factors that discredit that hopeless saying. First of all, it has to be noted that most people who try drugs never develop an addiction (e.g. in the case of cocaine, long-term addicts are roughly 30%). Moreover, in addition to social and environmental factors, individual variability may play a key role in the development of addiction. Individual variability can be determined by genetic factors, gender, major stresses and neuropsychological traits that combined can affect the susceptibility of the mesolimbic sensitization (Berridge & Robinson, 2016; M. J. F. Robinson, Robinson, & Berridge, 2013). Individual variability is particularly evident in the laboratory controlled settings of animal studies (Flagel, Akil, & Robinson, 2009).

Interestingly, it has been proposed that everyone in normal life is, to some extent, affected by addiction-like mechanisms. Common desires that span from basic hungers to more complex feelings of love, guide various forms of cue-reward learning that share addictive-like mechanisms (Berridge, 2017; Berridge & Robinson, 2016; Pitchers et al., 2013). Although the magnitude of sensitization in addicts might rely on a different scaling, the idea of a common mechanisms and a shared brain substrate suggests that addiction may develop independently of the power of a substance (i.e. drugs). For example, overeating and binge-eating that characterize obesity can be considered as addiction for food (Davis & Carter, 2009; Gearhardt, Yokum, Stice, Corbin, & Brownell, 2011; Schulte et al., 2015). Even more, addiction may develop even if there is no consumption of chemical substances (Leeman & Potenza, 2013). Indeed, several forms of addiction unrelated to drugs have been described recently, with the similar characteristic of hyper-reactivity to related cues (Grant, Brewer, & Potenza, 2006; Olsen, 2011). For example, individuals with compulsive sexual behavior (CSB; a form of "behavioral" addiction) show greater engagement of limbic circuitry to sexual cues compared to healthy individuals (Voon et al., 2014). Gambling is another form of widely-recognized form of addiction: individuals with gambling disorder show an increased brain response in reward-related areas to gambling cues (Limbrick-Oldfield et al., 2017). Compulsive gambling, together with other compulsive behaviors, is also commonly developed in Parkinson's patients as an adverse effect that is likely caused by the sensitization of the neural response to non-drug rewards by dopaminergic medication which artificially elevates the dopamine response in the brain (O'Sullivan et al., 2011; Ray et al., 2012). Perhaps the most striking form of *drug-free* addiction is a recent addiction that has developed along with the diffusion of internet accessibility: the abundant and arousing contents of internet and related social media can determine a compulsive internet use that leads to dependence and other psychological distress (Brand, Young, & Laier, 2014; Love, Laier, Brand, Hatch, & Hajela, 2015). Internet addiction disorder (IAD) is alarmingly spreading facing a lack of dedicated research and the absence of any evidence-based treatment. In China, specific training camps have developed with the aim to dissuade adolescents from internet abuse, and media have reported the contingent death of at least one teenager (Cash, Rae, Steel, & Winkler, 2012; Weinstein & Lejoyeux, 2010).

If the mechanism that underlies addiction matches other more ordinary forms of motivated learning (Nestler, 2005; Olsen, 2011; Pitchers et al., 2013), and if the motivational properties of a reward cue are manifested in their ability to impair attention and to elicit motivational states that spur the pursue of reward and incite action (Berridge & Robinson, 2016), the behavioral effects of motivational learning reported in the present work can be linked to addiction, and can deepen our understanding of the basic mechanisms that can influence its development. On the basis of the present results suggesting an "irrational" persistence of behavioral impairments induced by reward cues encounter, unveiling the basic mechanisms in action could also help to shed light on how such behavioral impairments could be reduced or extinguished. This line of research is of particular interest, also considering the low reliability of the currently available treatments for addictive disorders (such as twelve-step programs, cognitive-behavioral therapy or mindfulness; Badiani et al., 2017; Berridge, 2017; U.S. Department of Health and Human Services (HHS) & Office of the Surgeon General, 2016), and might have pervasive social implications (Berridge, 2017).

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