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Selective attention to conditioned stimuli in human discrimination learning:

Untangling the effects of outcome prediction, valence, arousal and uncertainty

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Abstract

Selective attention is an amalgamation of processing systems geared to select different classes of information to optimise the agent's transaction with the environment. Emerging evidence suggests that three forms of selective attention are engaged by conditioned stimuli, depending upon the arousal, valence and uncertainty of the predicted outcome. To support this claim, we review a series of human discrimination learning procedures in which we recorded gaze position with an eye tracker. The results suggest that conditioned stimuli command efficient detection to the extent that they predict an arousing outcome (appetitive or aversive), which may be important for action selection. By contrast, attention is subsequently maintained on conditioned stimuli to the extent that they predict an appetitive outcome specifically, which may be important for affective state. Finally, attention is also maintained to conditioned stimuli that have an uncertain relationship with an outcome, irrespective of whether that outcome is aversive or neutral, which may be important for contingency learning. We describe these three systems as looking-for-action, looking-for-liking and looking-for-learning, respectively. The discussion focuses on how one might further isolate these three attentional systems and explore their differential role in action selection, affective state and learning. Finally, our studies are considered in the light of contemporary behavioural neuroscience to contribute to the translational neuropsychological theory of attention.

Introduction

Selective attention is an amalgamation of processing systems geared to select different classes of information to optimise the agent's transaction with the environment. Within selective attention, sub-systems can be distinguished that select different types of stimuli. The clearest example of this can be found in perceptual psychophysics, where it has been demonstrated that a variety of "low level" attributes of stimuli, such as colour, motion, orientation, size, etc. all drive selective attention (Wolfe and Horowitz, 2004) via at least partially segregated neural substrates (Knudsen, 2007, Yantis, 2008). The claim

made in this chapter is that the "higher level" attributes of stimuli acquired during associative learning are similarly selected for privileged processing within at least three distinct attentional systems, which appear to have partially segregated neural substrates.

Three forms of selective attention in associative learning

The idea that selective attention can be modulated by the predictive significance of stimuli has a long tradition in associative learning theory. The original theory put forward by Mackintosh (1975; see also Sutherland and Mackintosh, 1971) argued that animals attend preferentially to cues that are relatively good predictors of other events of biological importance (outcomes) such as food and water, and thereby learn more readily about relationships involving these cues. Therefore, through this attentional process the predictive history of a stimulus can inform new learning.

Subsequently, Pearce and Hall (1980) claimed that, rather than attending to reliable predictors, animals in fact attend most to stimuli that have been associated with uncertainty so that learning is directed to those stimuli for which the animal does not possess an adequate predictive mental model. According to this theory, the occurrence of an unpredicted outcome, or the absence of a predicted one, evokes a prediction error signal (surprise), which indicates that the animal does not have an adequate representation of the predictive structure of its environment and therefore needs to undertake further learning. Consequently, the animal should, in future, attend to cues that are associated with the prediction error signal in order that the animal might acquire veridical knowledge of the predictive significance of those stimuli, and so by degrees, acquire a veridical representation of the predictive structure of the environment. Once prediction is accurate, so that important outcomes can be anticipated and no error signal is evoked, there is no need to devote further learning resources to these stimuli, and attention to them declines.

The Mackintosh and Pearce-Hall theories therefore make opposing predictions concerning attention for conditioned stimuli. Mackintosh's theory suggests that attention will increase with the reliability of the predictive contingency between the stimulus and the outcome, whereas Pearce and Hall predict that attention will increase with the unreliability of the predictive contingency between the stimulus and the outcome. It is perhaps not surprising, given these opposing predictions, that much of the debate addressing these two theories has adopted an oppositional stance, where each camp has mustered evidence in favour of one or other position. However, a unified account was potentially embedded within Pearce and Hall's (1980) original formulation.

This unified account claims that there are two forms of attention in associative learning: one concerned with prediction and action, and one concerned with uncertainty and learning. More precisely, Pearce and Hall claimed that a reliable predictor commands an *"automatic"* form of attentional selection, which might today be variously labelled as fast, efficient, covert or pre-attentive, but which ultimately functions to detect predictive stimuli with maximum cognitive economy to enable rapid action selection. This automatic form of attentional selection increases with the strength of the predictive relationship between the stimulus and the outcome, and is principally involved in behavioural control. By contrast, unreliable predictive stimuli command a second form of *"controlled"* attentional selection, which may be operationalised as the maintenance of sensory focus upon the stimulus, or the holding of the stimulus in working memory (see Belopolsky and Theeuwes, 2009), which facilitates the formation of knowledge about the contingency between that stimulus and subsequent outcomes. This controlled form of attentional selection increases with the unreliability of the contingency between the stimulus and the outcome, and is principally involved in contingency learning. Our attentional data reviewed below tend to favour this sort of multiple systems account of selective attention in associative learning.

While the Mackintosh vs. Pearce-Hall debate raged in the arena of associative learning, a tangential discussion was developing elsewhere concerning the link between attention

and emotion (Vuilleumier, 2005, Vuilleumier et al., 2003). The disconnection between these two debates is unwarranted, however, because whenever cues have a predictive relationship with a biologically relevant outcome, they acquire affective value in their own right. Consequently, attention for predictive cues should not only vary in accordance with their associative strength and prediction error, but also, in accordance with the biological value of their associated outcome.

Research addressing the link between attention and emotion has focused to a large extent on the issue of whether attention is controlled by the arousing properties of a stimulus, or its valence. The arousal dimension is considered to range from neutral to arousing (i.e. a scale from 0–1), where both appetitive and aversive cues are arousing. By contrast, the valence dimension is thought to range from appetitive at one end to aversive at the other (i.e. a scale from -1 – 0 - 1), reflecting the hedonic or affective sign of the stimulus.

Research addressing the link between attention and emotion favours the view that the early form of attentional selection equating to Pearce and Hall's automatic process is commanded in accordance with the arousing qualities of stimuli, irrespective of their valence (Brosch et al., 2008, Engelmann and Pessoa, 2007, Lin and Nicolelis, 2008, Livesey et al., 2009, Vogt et al., 2008, Lewis et al., 2007; but see; Fox et al., 2001, Eastwood et al., 2001). Such early detection may accord with arousal, rather than valence, because it plays a critical role in the initiation of both approach and avoidance behaviour.

By contrast, following initial detection, the maintenance/avoidance of attention appears to respect the valence of the stimulus. For instance, cues associated with larger quantities of food command more attentional orienting in animals (Morris and Bouton, 2006), and increasing the incentive value of food (Mogg et al., 1998) and drugs of abuse (Field et al., 2004) by enforcing deprivation from these resources increases the maintenance of attention for cues associated with these resources. Finally, induction of

positive mood and individual differences in positive mood state are associated with enhanced attention to reward-related cues (Tamir and Robinson, 2007).

By contrast, aversive cues command attentional avoidance following initial detection, if they are sufficiently aversive (Pflugshaupt et al., 2005, Weierich et al., 2008). Such attentional avoidance of aversive cues is associated with individual differences in anxiety/negative mood and exposure to stress (Beevers and Carver, 2003, Calvo and Avero, 2005, Calvo and Eysenck, 2000, Frewen et al., 2008, Koster et al., 2005, Morrison and O'Connor, 2008), and is thought to play a role in regulating affective state (MacLeod et al., 2002).

To reconcile the fields of attention in associative learning and emotion, we propose the existence of three attentional systems, as summarised in Figure 1. The left column of Figure 1 outlines the prediction + arousal system, which equates to Pearce and Hall's automatic detection process. This framework proposes that preferential early detection of a stimulus is jointly determined by the associative strength of the stimulus (that is, the extent to which it predicts an outcome) and the arousal value of the predicted outcome (that is, the biological importance of the outcome irrespective of whether it is appetitive or aversive). Accordingly, the left column shows early detection increasing for stimuli to the extent that they predict an appetitive or aversive outcome, but not for stimuli that predict a neutral outcome. We think that such early detection is most important for action selection. By contrast, the prediction + valence system, outlined in the middle column of Figure 1, proposes that the subsequent maintenance or avoidance of attention to a stimulus is determined jointly by the associative strength of the stimulus and the appetitive/aversive valence of the outcome, which approximates the expected *utility* of the outcome [1] (see; Rangel et al., 2008). Accordingly, the middle

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[1] In the language of decision making, we claim that attentional maintenance/avoidance is determined by the utility of the outcome expectancy evoked by the CS, where utility is the sum of the biological value of the expected outcomes weighted by their probabilities (Rangel et al., 2008).

column shows attention being maintained to cues to the extent that they predict an appetitive outcome, avoiding cues to the extent that they predict an aversive outcome, and being unbiased for cues that predict a neutral outcome. This system may be most important for regulating affective state. Finally, the right column of Figure 1 outlines the uncertainty system, which equates to Pearce and Hall's controlled process. According to this framework, attention is also maintained to a stimulus to the extent that it conveys uncertainty about the probability of an outcome (prediction error), irrespective of whether the outcome is arousing (appetitive/aversive) or neutral. Accordingly, the right column shows attentional maintenance being maximal for cues with unreliable predictive relationships, compared to cues with reliable predictive or reliable non-predictive relationships, irrespective of whether the outcome is appetitive, aversive or neutral. We think this uncertainty system is most important for learning. Finally, we believe that these three attentional systems operate concurrently, such that experimental measurement of attentional selection to some extent conflates all three. The next section outlines human discrimination learning schedules undertaken in our lab, which have served to behaviourally isolate these three attentional systems, to some extent.
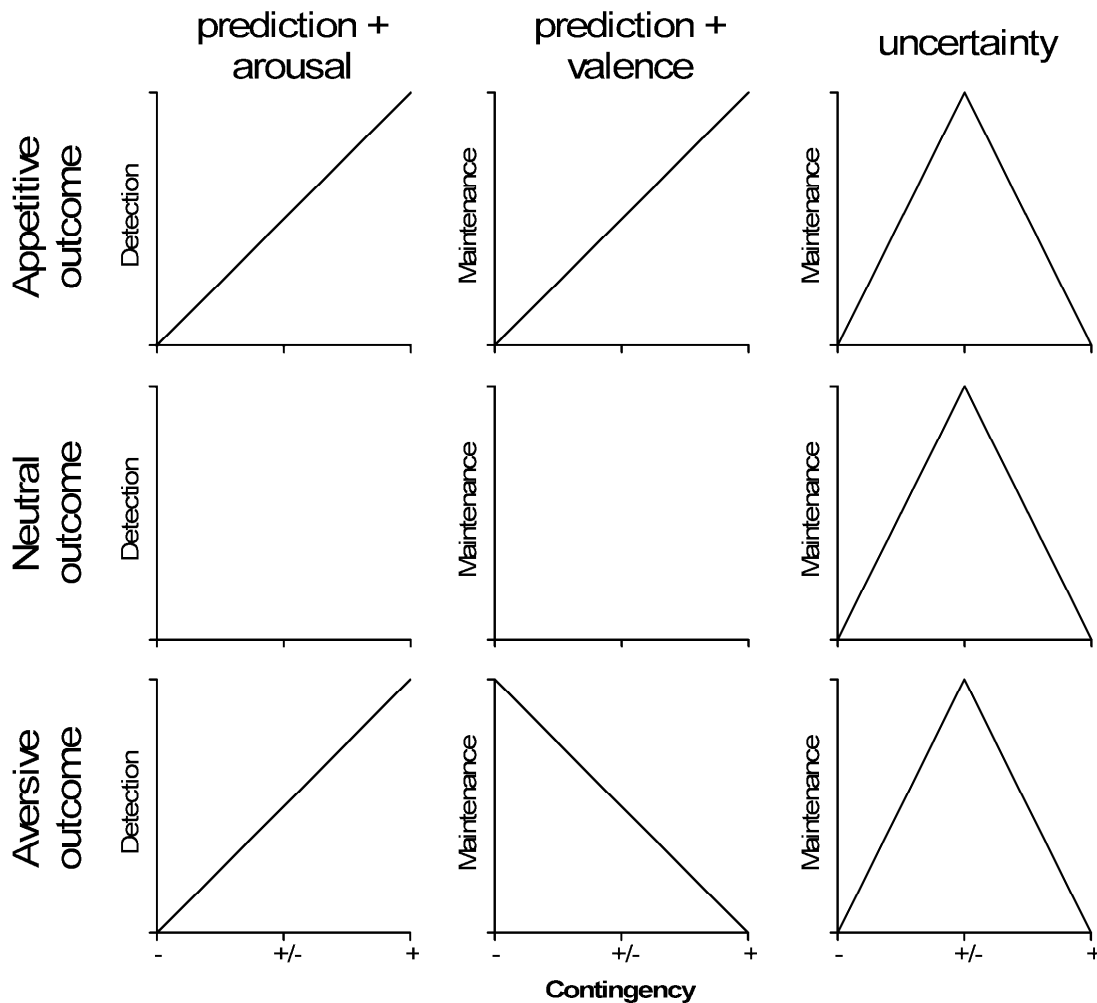
Figure 1: Descriptive predictions concerning the detection and maintenance of attention to conditioned stimuli after asymptotic learning. The nine stimuli outlined differ with respect to their contingency with an outcome (no contingency -, partial contingency +/-, and full positive contingency +), and the biological value of that outcome (appetitive, neutral, aversive). Three attentional systems are proposed, which jointly govern attention to conditioned stimuli. 1. The prediction + arousal system, outlined in the left column, quickly detects stimuli to the extent that they predict arousing outcomes, which may be important for action selection. 2. The prediction + valence system, outlined in the middle column, determines the subsequent maintenance/avoidance of attention to stimuli to the extent that they predict appetitive or aversive outcomes, respectively, which may be important for regulating affective state. 3. The uncertainty system also determines the maintenance of attention to stimuli, but in accordance with the uncertainty the stimulus conveys about future outcomes (irrespective of the outcomes' arousing properties). This form of attention may be important for contingency learning. The actual observed attentional selection of conditioned stimuli should conflate these three systems, making it difficult to untangle their relative contribution behaviourally. The studies presented in this chapter have assessed only some of these 9 conditions, but overall, this work supports the existence of these three attentional systems.

Looking-for-action versus looking-for-liking

Our program of research reviewed here was originally inspired by Robinson and Berridge's (1993) incentive salience theory of addiction. This theory proposes that stimuli that are associated with addictive drugs command excessive attention, which mediates the compulsive, under-controlled nature of drug seeking. In developing this account, Robinson and Berridge (1993) initially favoured a Pavlovian sign-tracking process (Bindra, 1978) through which drug stimuli control a strong approach response, but subsequently, their work has recognised that drug cues might also control drug seeking through the well-established motivational impact of reward-predicting stimuli on instrumental performance (Wyvell and Berridge, 2000, Wyvell and Berridge, 2001).

To test Robinson and Berridge's (1993) proposal in humans, we established an arbitrary stimulus as a signal for when a drug seeking response would be rewarded, so that we could measure the acquisition of an attentional bias for the stimulus and relate this attentional bias to the subjective expectancy of drug reward and the probability of performing the drug seeking response. According to Robinson and Berridge (1993), there should be a close mapping between these measures, consistent with the role of the attentional bias in behavioural control. However, the procedure can also address Mackintosh's and Pearce-Hall's theories of attention insomuch as Mackintosh, like Robinson and Berridge (1993), predicts that attention to the predictive stimulus should monotonically increase with training, whereas Pearce-Hall anticipates most attention during learning of the stimulus-outcome contingencies, when uncertainty is greatest.

The details of the discrimination procedure are outlined in Figure 2. To measure the selectivity of attention, we employed the relative validity schedule developed by Wagner and colleagues, AX+, BX-, which allows two stimuli to be presented concurrently during training, with one cue signalling the availability (A) or unavailability (B) of reward in that trial, and the concurrently presented stimulus (X) being redundant (less informative) with respect to the trial outcome, therefore constituting a contextual or background

stimulus (Wagner, 1969, Wagner et al., 1968). We simply added a second contextual cue (Y) to create the schedule AX+, AY+, BX-, BY-, to match the absolute number of times all stimuli were presented, allowing us to assess attention to the informative cues A and B relative to the common contextual cues, X and Y.

The pooled results from five replications of the procedure are presented in Figure 3 (Hogarth et al., 2006b, Hogarth et al., 2008b, Hogarth et al., 2007, Hogarth et al., 2009). The most striking aspect of these data was that conditioned effects across the different measures were selective to participants who became aware of the stimulus-outcome contingencies, and so only data from this group are included in Figure 3 (awareness was classified by the participants showing a significant difference in reward expectancies between A+ and B- trials in the final block of training). This finding is consistent with the view that human conditioning is mediated by outcome expectancy (Hogarth et al., 2007, Hogarth and Duka, 2006, Lovibond and Shanks, 2002) rather than by an associative architecture outside awareness (Lieberman et al., 1998a, Lieberman et al., 1998b, Perruchet, 1985, Perruchet et al., 2006). Moreover, visual inspection of the expectancy reports of individual participants revealed a sudden differentiation between A+ and B- trials, occurring at some point in training, suggestive of sudden rule based learning.

To determine what rules aware participants had learned, we showed them a picture of the four stimuli (see Figure 2) and asked them the question, "How did you decide when to press the space bar?". Some participants reported that they knew that stimulus A predicted a win and so pressed when they saw this stimulus, and that otherwise they knew that they would lose and so withheld pressing in this situation. Therefore, this group appeared to learn the identity and predictive significance of stimulus A, but not of the remaining three stimuli, and treated the absence of stimulus A as the S- condition. By contrast, other participants reporting that they knew that stimulus B predicted loss, and that they withheld responding when they saw this stimulus, and otherwise that they knew that they would win and so pressed in this situation. Therefore, this group

appeared to learn the identity of stimulus B, but not of the remaining three stimuli, and treated the absence of stimulus B as the S+ condition. Finally, some participants reported knowing that stimulus A predicted a win whereas stimulus B predicted a loss, and so pressed and withheld the response when they saw these two stimuli, respectively. Therefore, this group appeared to learn the identity of both stimulus A and B. We have grouped participants in Figure 3 on the basis of which of these three rules they reported, to examine their differential allocation of selective attention to the stimuli.

One may wonder what differentiates participants who learned these three types of rule. The first thing to note, in this regard, is the uneven number of participants in each group (Figure 3, which was significant by Chi square). The smallest number of participants, who learned A&B, might be expected on the grounds of cognitive economy – why should participants explore the alternative rule when the one they are using enables asymptotic discrimination performance? The learning of the A=win vs. B=lose rules, by contrast, might have been thought a matter of chance, depending upon which was detected first. However, the uneven split between these two groups instead suggests a preference for learning the A=win rule. This preference is perhaps due to the phrasing of the expectancy question "how likely are you to win ¼ of a cigarette" at point E in the trial sequence (see Figure 2), which effectively prompts acquisition of the A=win rule. However, it is also possible that differential learning of these two rules is founded upon a biological trait (Frank et al., 2004), but this remains to be verified.

Our concern here, however, is with the differential allocation of selective attention to stimuli depending upon which rule was learned. First of all, it should be noted that the three groups were indistinguishable with respect to the acquisition of differential reward expectancies and instrumental discrimination between A+ and B- trials. Yet the attentional performance of the three groups differed markedly. Analysis of the dwell time data shown in Figure 3 indicated that A-learners attended more to A than the contextual

cues X/Y(A), but not to B relative to X/Y(B). By contrast, B-learners attended more to B than X/Y(B), but not more to A than X/Y(A)[2]. Finally, A&B-learners showed the same pattern of attentional bias as A-learners, except their difference between A and X/Y(A) was smaller.

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[2] In fact, this contrast between A and X/Y(A) was significant in B-learners, but it was not replicated in two subsequent studies (see Figures 4 and 5) and so can be ignored as a false positive. In addition, in B-learners, the bias for B over X/Y(B) was significantly greater than the bias for A over X/Y(A), indicating that B-learners predominately showed an attentional bias for B.
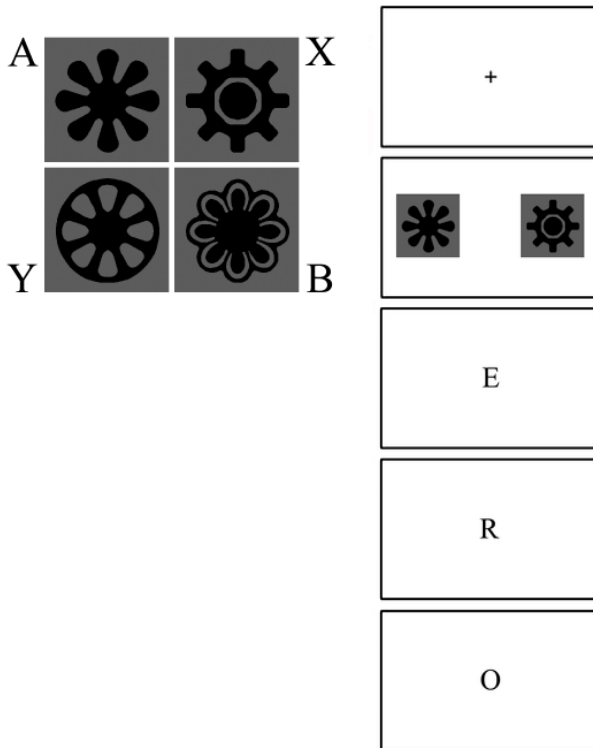
Figure 2: In discrimination training, a fixation cross was followed by a pair of stimuli for 3 seconds during which attention was measured with an eye tracker. Participants (smokers) then reported their expectancy (E) of the tobacco win outcome by pressing a number key from 1-10. Finally, participants could perform an instrumental tobacco seeking response (R - a space bar press), which yielded a tobacco win outcome (O – "you win ¼ of a cigarette") in AX+ and AY+ trials, or an equivalent tobacco lose outcome ("you lose ¼ of a cigarette") in BX- and BY- trials. Non responding produced no outcome. The schedule included four randomly intermixed trial types: AX+, AY+, BX-, BY-, which established stimulus A as a predictor of wins (S+), stimulus B as a predictor of equivalent losses (S-), and stimuli X and Y as redundant contextual cues that were common to both rewarded and unrewarded trials. To gain net reward, participants had to learn to perform the instrumental response more frequently in AX+ and AY+ trials (labelled A+ trials for short), than in BX- and BY- trials (labelled B- trials for short), so that wins outweighed losses. Analysis examined dwell time to the individual stimuli within the four trial types: stimulus A+, B- and the concurrently presented contextual stimuli X/Y in A trials (labelled X/Y(A)) and in B trials (labelled X/Y(B)). In addition, reward expectancy and percent trials with an instrumental response were compared across A+ trials and B- trials. The four stimuli shown were balanced in the role of A, B, X and Y.
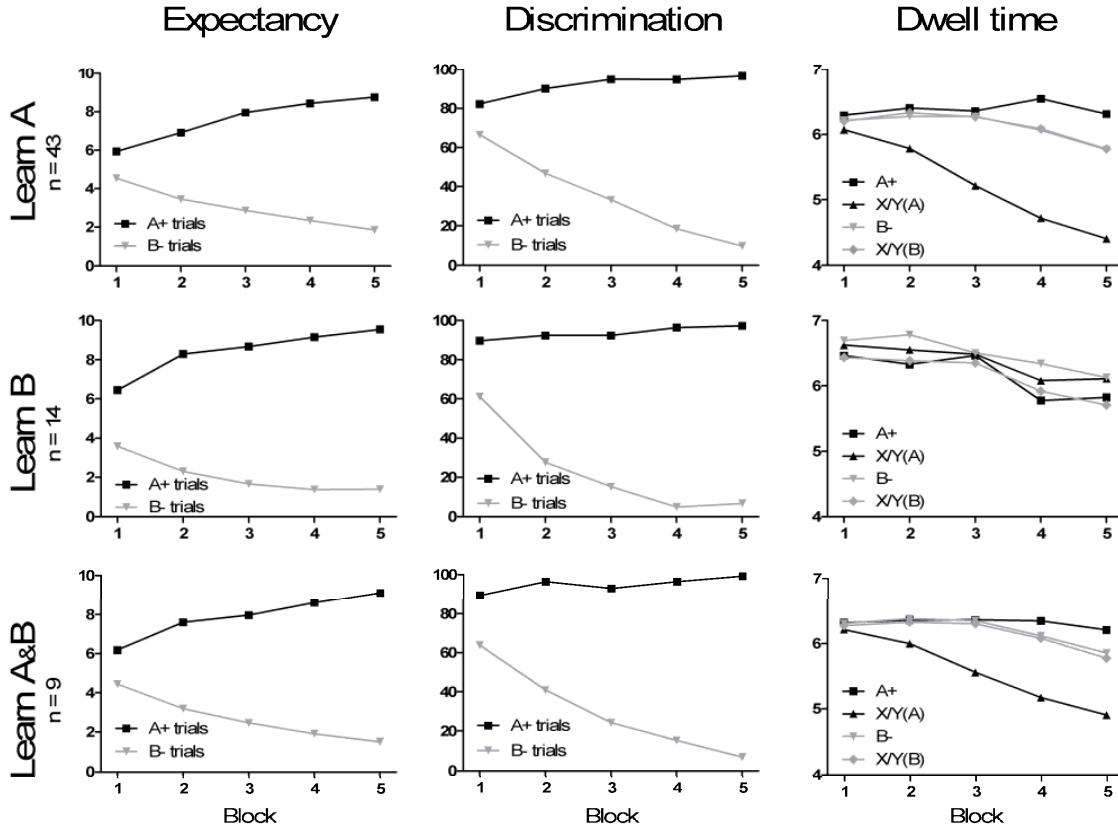
Figure 3. Left column: Reward expectancy (1-10 scale) on A+ trials (that is, AX+ and AY+ trials) and B- trials (that is, BX- and BY- trials). Middle column: Discrimination (% trials with an instrumental response) between A+ trials and B- trials. Right column: Dwell time (natural logmsec) to stimulus A and B as well as the concurrently presented contextual cues X/Y in A and B trials (labelled X/Y(A) and X/Y(B), respectively). Only contingency aware participants, indexed by a significant difference in reward expectancies between A+ and B- trials in block 5, are included. Moreover, aware participants were split according to whether post experimental questioning indicated that they had learned the A=win rule (top row), the B=lose rule (middle row), or both rules (bottom row). Attention, but not expectancy or instrumental discrimination, was influenced by which rule participants used.

Perhaps the most intriguing aspect of the attentional data in Figure 3, is A-learners' larger bias for A over X/Y(A) than B-learners' bias for B over X/Y(B), despite the fact that these two groups were ostensibly using A and B, respectively, to control their expectancy and instrumental choice equally. There are two differences in the information conveyed by stimulus A and B for these two groups. For A-learners, stimulus A signalled that the instrumental response should be performed to obtain reward, whereas for B-learners, stimulus B signalled that the instrumental response should be withheld to avoid equivalent loss. Thus, these cues have different connections to action initiation/withholding, and are associated with outcomes with different biological value, win/loss. The question, therefore, is whether the attentional biases seen in Figure 3 can be explained by looking-for-action, or, looking-for-liking.

Three observations challenge the simple link between attention and action. First, as we have noted, why was the preference for A in A-learners statistically significantly bigger than the bias for B in B-learners, when the two groups were ostensibly using these respective cues to control their performance equally? Second, why did A&B-learners show attentional selection of A but not B when they knew the relevance both cues had for behaviour? Finally, why did the preference for A in A-learners and A&B-learners increase with training, tracing the control by this stimulus over instrumental action, whereas the bias for B in B-learners remained relatively constant over blocks, failing to trace the control this stimulus exerted over instrumental action?

The alternative proposal is that attention was maintained to the extent that the stimuli had acquired reward value (i.e. in participants who were aware of the stimulus-reward contingency). This explains the large bias for A over X/Y(A) in A and A&B learners, compared to the small bias for B over X/Y(B) in B-learners (we'll leave aside other subtle differences in the data until later).

This idea that attention is commanded by the acquired reward value of cues, was substantiated by a subsequent modification to the design in which one key press was

rewarded with tobacco in AX+ and AY+ trials, whereas a second key press was rewarded with a financially equivalent amount of money in BX+ and BY+ trials (Hogarth et al., 2007, Experiment 2). Of the 11 aware participants (out of 16) in this study, five were A=tobacco-learners and six were B=money-learners (there were no A&B learners). The results are shown in Figure 4. A-learners attended to A over the context, but not B, whereas B-learners showed the converse attentional bias. This finding confirms that there is a strong relationship between predictive learning and selective attention. Most critically, however, B-learners showed a larger bias for B over X/Y(B) compared to B-learners in Figure 3, suggesting that this bias was enhanced as a result of B being associated with a rewarding outcome.
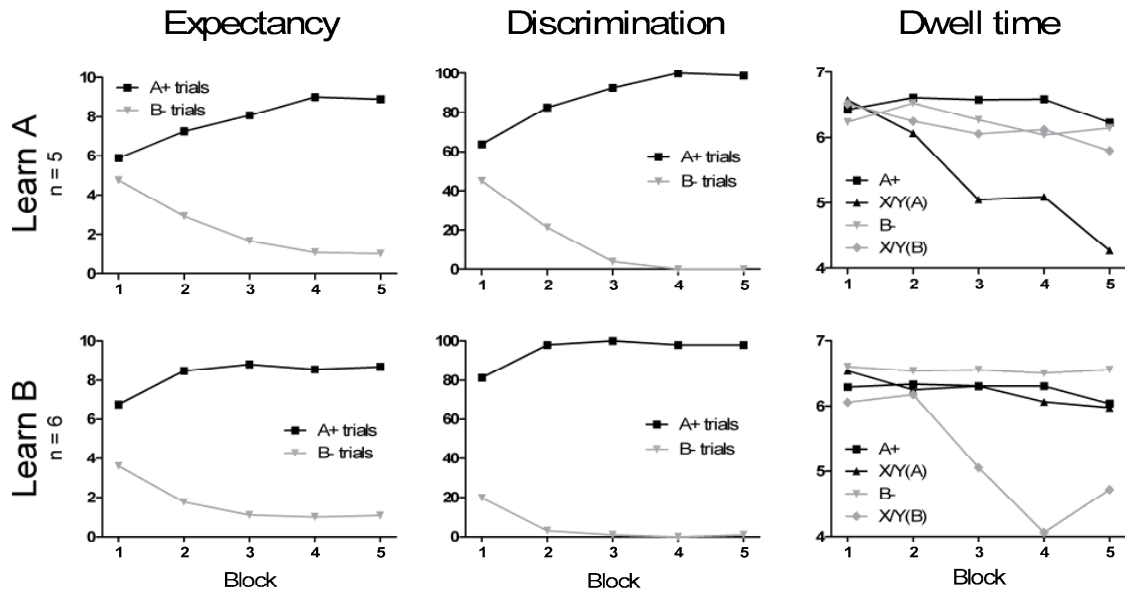
Figure 4: Outcome expectancy (1=money, 10=tobacco) and instrumental discrimination (% trials with a tobacco rather than a money response) in A→tobacco vs. B→money trials, plus, dwell time (natural logmsec) to stimulus A and B relative to the concurrently presented contextual cues X/Y. Aware participants were split by whether they learned the A=tobacco or B=money rule (no one learned both rules). Again, selective attention was dependent upon which rule was acquired.

If the attentional biases analysed so far reflect looking for liking, rather than looking for action, we should be able to dissociate this attentional bias from the control that stimuli exert over expectancy and instrumental performance. To test this proposal, we added a test phase to one of the replications included in Figure 3, which attempted to abolish the dwell time bias. To this end, we required participants to count visual targets that appeared amongst a rapidly alternating sequence of distracters in the centre of the screen, simultaneously during the 3-sec period of stimulus presentation, to force attention to remain in the centre rather than saccade to the peripheral location of the CSs (see; Hogarth et al., 2008b for details). Figure 5 shows the results from blocks of this test phase that did and did not include this secondary task (the measures are flat because they had reached asymptote by the final blocks of training). The first thing to note is that the pattern of bias seen in training continued in testing in the normal condition (without the secondary task). That is, A-learners showed a dwell time bias for A over X/Y(A), and no bias for B over X/Y(B), whereas B-learners showed the converse pattern – a bias for B over X/Y(B) and no bias for A over X/Y(A). Second, and most importantly, the inclusion of the secondary task was highly effective at abolishing attention to the peripherally located discriminative stimuli. In fact, examination of fixation count data (not shown) indicated that the discriminative stimuli were fixated in only 10% of secondary task trials. Nevertheless, despite this abolition of focal attention to stimuli, expectancy and instrumental discrimination remained fully intact in these trials. These data indicated that the dwell time biases to stimuli were unnecessary for stimuli to exert control over expectancy and instrumental performance. Indeed, these data indicate that covert detection of discriminative stimuli in the periphery of the visual field is sufficient for these stimuli to exert the same degree of control over expectancy and instrumental behaviour as when they command the maintenance of overt focal attention. Therefore, the overt maintenance of attention appears to be superfluous to behavioural control, whereas simple covert detection of stimuli appears to be sufficient for behavioural control (see; de Haan et al., 2008) for further information on the distinction between overt and covert attention).
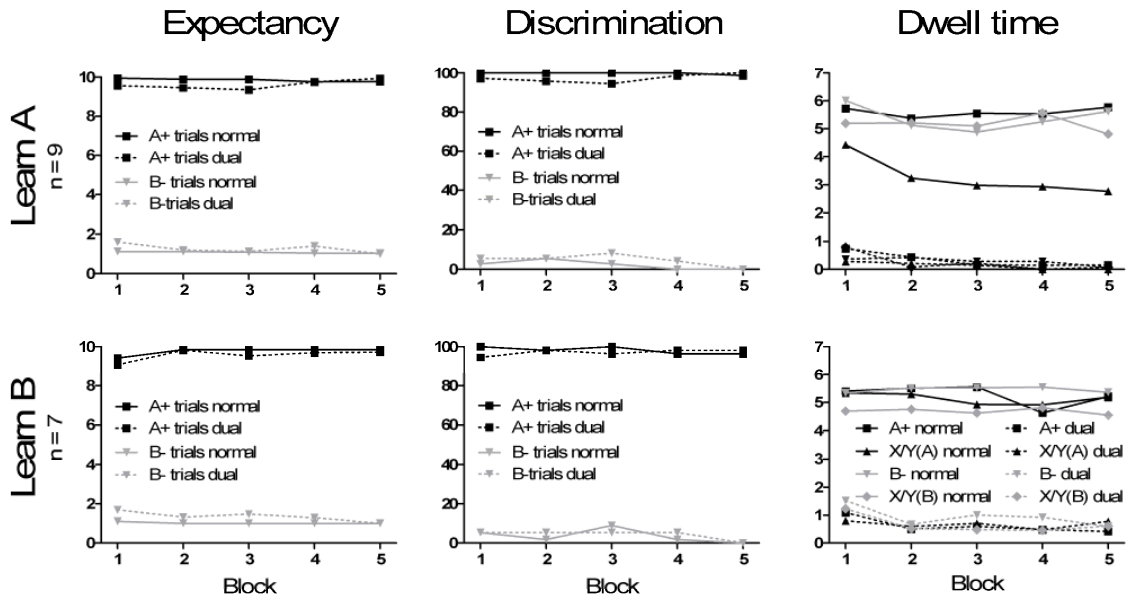
Figure 5: The dual task method. Reward expectancy (1-10 scale) and instrumental discrimination (% trials with an instrumental response) between A+ and B- trials, plus, dwell time (natural logmsec) to stimulus A and B relative to the concurrently presented contextual cues X/Y. Aware participants were split according to whether they learned the A=win or B=lose rule. The results show that introducing the secondary task abolished the attentional bias for stimulus A and B in A- and B-learners, respectively, without effecting the control these stimuli exerted over expectancy and instrumental discrimination. Thus, these attentional biases were superfluous to behavioural control.

In a follow up study, we explored whether the 3-seconds of "dead time" during which stimuli were presented, and no action could be undertaken (see Figure 2), allowed the superfluous attentional biases controlled by reward value to be expressed (Hogarth et al., 2009). The inspiration for this study came from Premack and Collier (1966), who allowed participants to control the duration of stimulus presentation by holding down a key – known as an observing response in the operant literature (Wyckoff, 1952) – in a discrimination procedure not dissimilar to our own. Their critical finding was that observing times for stimuli paired with reward declined with training, which would be expected if attention was deployed efficiently to control instrumental behaviour, rather then increased, as might be expected if attention was controlled by the acquired reward value of cues.

The implication of Premack and Collier's (1966) finding was that the opportunity for immediate action caused participants to dispense with the overt maintenance of attention to reward cues, and instead, to employ a more economic form of stimulus detection, sufficient for expectancy and instrumental choice, but no more. To test this idea, we ran second a group alongside one of the replications included in Figure 3, but rather than present stimuli for a fixed 3-sec period, this group could control stimulus duration by holding down a key using a method akin to Premack and Collier (1966).

The results from the observing response group are shown in Figure 6 and indicate that A-learners and B-learners acquired no dwell time bias for stimulus A and B, respectively, in contrast to when stimulus presentation was fixed (Figure 3). Nevertheless, the control exerted by these cues over expectancy and instrumental discrimination performance was equivalent regardless of whether or not the dwell time bias was expressed, again confirming that these dwell time biases played no role in expectancy or behavioural control.
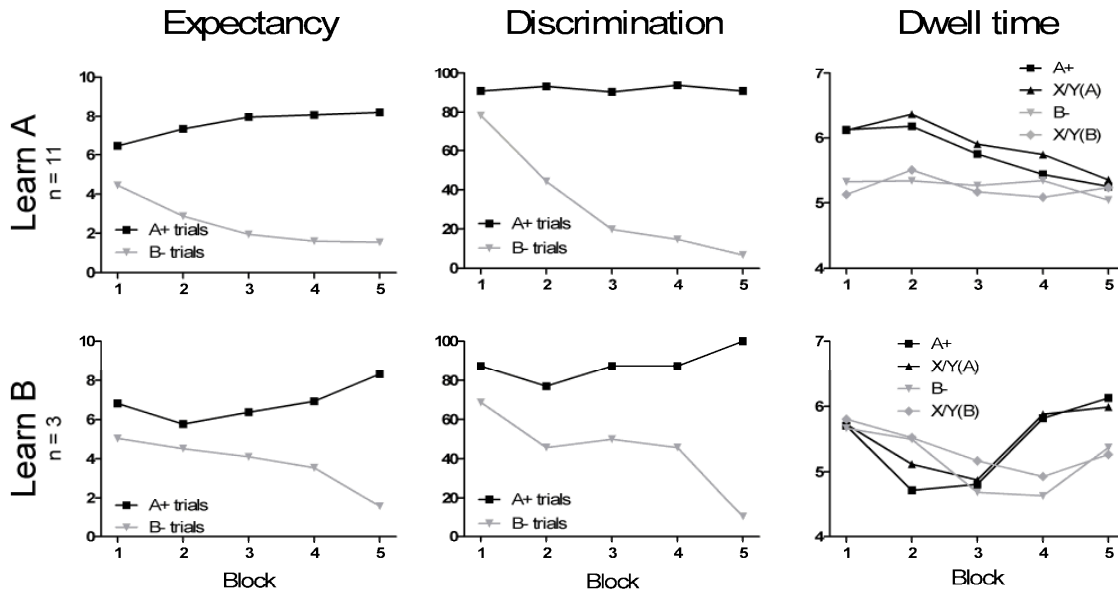
Figure 6: The observing response method. Reward expectancy (1-10 scale) and instrumental discrimination (% trials with an instrumental response) between A+ and B- trials, plus, dwell time (natural logmsec) to stimulus A and B relative to the concurrently presented contextual cues X/Y. Aware participants are split according to whether they learned the A=win or B=lose rule. The results show that providing control over stimulus duration abolished the attentional bias for stimulus A and B in A- and B-learners, respectively, yet stimulus control of expectancy and instrumental performance remained unaffected.

Summary- Untangling arousal and valence

The foregoing data support Figure 1 in suggesting that the detection and maintenance of attention to conditioned stimuli are determined by the arousal and valence of the predicted outcome, respectively. With respect to the early detection of the CSs, our data clearly indicate that efficient detection, but not attentional maintenance, plays a role in the behavioural control exerted by these stimuli. In fact, in Hogarth et al., (2008b) stimuli A and B were able to control expectancy and instrumental choice without being foveated on 90% of trials, indicating that parafoveal detection of these stimuli was sufficient for them to exert behavioural control. We might claim that such parafoveal detection was equal for the appetitive stimulus A and the aversive stimulus B, as predicted by the left column of Figure 1, from the fact that these cues controlled expectancy and instrumental choice equally in A- and B-learners. This conclusion fits with recent data showing that early detection of cues respects the arousal of those cues rather than their valence (Brosch et al., 2008, Vogt et al., 2008). However, the specific claim that early detection is enhanced for CSs that predict an arousing outcome is at present indirect because we currently have no way of measuring the enhancement of detection with the eye tracker[3].

The maintenance of attention to CSs, by contrast, was evidently determined by the valence of the predicted outcome, as anticipated by the middle column of Figure 1. The

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[3] One might think that the latency of the first fixation to stimulus A and B might be faster than for the contextual cues X/Y, reflecting the enhancement of early detection of cues associated with arousing outcomes. Unfortunately, however, we have found that first fixation latency was not reliably different between these cues. This measure may have been insensitive because the location of the predictive and contextual cues was randomised across trials. In the future, we may seek to measure the enhancement of early detection directly by fixing the location of stimuli, or by including alternative measures such as signal detection (Engelmann and Pessoa 2007), EEG (Brosch et al. 2008), attentional blink (Livesey et al. 2009) or spatial cueing effects (Vogt et al 2008). It remains to be seen how these alternative measures might be integrated into the conditioning procedure.

key finding supporting this claim was that dwell time biases were greater for the appetitive stimulus A in A-learners than for the aversive stimulus B in B-learners, despite the fact that the two cues were equally relevant for behaviour control in the two groups. These data suggest that the dwell time bias was enhanced by the prediction of the win outcome in stimulus A, compared to the prediction of the lose outcome in stimulus B. Thus, the valence of the predicted outcome appeared to determine the maintenance of attention to the CS (note that this conclusion relies on the assumption that the win and the lose outcome were equally subjectively arousing). The second key finding was that the dwell time bias for stimulus A was unnecessary for this stimulus to control expectancy and instrumental choice, consistent with the claim that this bias is linked to affective appraisal rather than behaviour control. It is important to note that although the dwell time bias for B was reduced compared to A, there was no evidence of attentional avoidance of B. Presumably, the lose outcome was not sufficiently aversive to drive avoidance, but this remains to be clarified.

The interplay of these two systems may explain the total pattern of results shown in Figure 3. According to this account, A-learners efficiently detected stimulus A to control instrumental choice, and subsequently, maintained gaze on stimulus A because of its acquired appetitive value (enabled because attention is not demanded elsewhere). These two forms of selection added together, creating a large dwell time bias for stimulus A relative to X/Y(A). By contrast, we propose that A&B-learners had a less specific search image for stimulus A because they also used B, or the absence of A or B, as the critical information to control instrumental choice (Plaisted and Mackintosh, 1995). Consequently, this weaker detection of A summed with the maintained bias for A, driven by the reward association, to yield a smaller overall dwell time bias for A over X/Y(A) compared to A-learners. Finally, we suggest that B-learners detected stimulus B to control instrumental choice, but did not maintain attention to this stimulus because it had no reward association. Instead, the initial detection carried over to generate a small dwell time bias compared to X/Y(B) because attention did not disengage to meet other

demands (Posner et al., 1980) and the aversive properties of the cue were insufficient to drive clear attentional avoidance.

Looking-for-learning

The foregoing analysis claims that a CS paired with an aversive outcome should not command a substantive dwell time bias. However, this proposal is, at first sight, contradicted by one of our published studies (Hogarth et al., 2006a). In this study, the AX+, AY+, BX-, BY- design was used (outlined in Figure 2), but instead of reward, stimulus A signalled that a 97 dB aversive, startling white noise outcome would occur subsequently with 100% probability, and that an instrumental avoidance response would cancel this outcome with a 50% probability (to ensure that an A-noise contingency would be in force even if participants performed the avoidance response in every trial). By contrast, stimulus B signalled the absence of the aversive noise, and stimuli X/Y were contextual cues as before. This early method did not include the within-trial expectancy question, and consequently, a substantially smaller proportion of the sample became aware of the stimulus-outcome contingencies (5 out of 16), as indexed by post-experimental questioning, which also suggested that all five aware participants were A&B learners. The important finding shown in Figure 7, was that these aware participants acquired a substantive dwell time bias for stimulus A over X/Y(A), but not for B over X/Y(B). At first sight, these data suggest that the aversive S+ acquired a maintained attentional bias, contradicting our claim that this bias should be selective to appetitive cues.
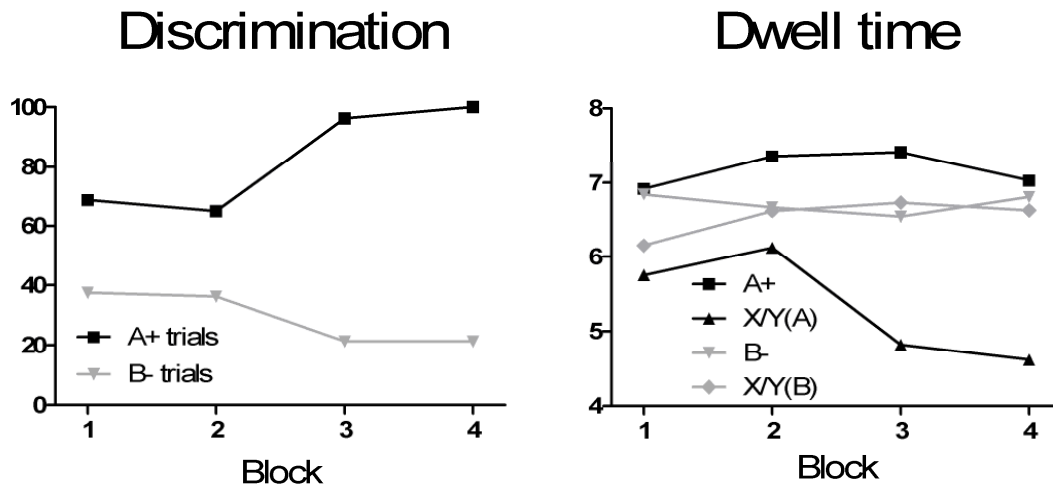
Discrimination

Dwell time

Figure 7: Aversive conditioning study. Avoidance response discrimination (% trials with the avoidance response) between A+ and B- trials, plus, dwell time (natural logmsec) to stimulus A and B relative to the concurrently presented contextual cues X/Y. The five contingency aware participants included were all A&B-learners.

An alternative explanation of Figure 7, is that dwell time bias for stimulus A was not driven by the prediction of an arousing outcome, but by the uncertainty engaged by the this stimulus as a result of its partial contingency with the noise outcome and/or effectiveness of the avoidance response. To test this claim, we ran a modified design based upon Figure 2, inspired by Kaye and Pearce (1984), in which the stimulus pairs AX+, BX+/- and CX-, were followed by the aversive noise outcome with a probability of 100%, 50% and 0%, respectively (Hogarth et al., 2008a). There was no instrumental avoidance response, so participants' only task in the procedure was to accurately report the Pavlovian contingencies in the within-trials expectancy question, "how likely is the loud noise", on a 1-10 scale. The top row of Figure 8 shows the expectancy reports of the 11 aware participants (out of 16) who showed a significant difference in their expectancy reports in the final block of training, in the direction of A>B>C, and most importantly, the dwell times for the four stimuli: A, B, C versus the concurrently presented contextual stimulus X.

The key finding was that the unreliable predictor stimulus B commanded a greater dwell time bias relative to the contextual cue X(B), than did A vs. X(A) and C vs. X(C). Thus, the stimulus that was associated with the greatest predictive uncertainty commanded the greatest dwell time bias. Moreover, although A and C commanded greater dwell than the contextual cue X, these biases were of equivalent magnitude, indicating that the reliable aversive predictor stimulus A commanded no greater bias than the non-predictor stimulus C. This finding confirms our claim that the prediction of an aversive outcome does not enhance the dwell time bias, in contrast to our earlier finding that the prediction of an appetitive outcome does. The reason why stimulus A and C commanded a greater dwell time than stimulus X may simply have been because X was presented in every trial, meaning that stimuli A and C had greater novelty and lower frequency than X. The implication of these findings is that the bias for stimulus A in Figure 6 was determined by the predictive uncertainty associated with this stimulus rather than the prediction of an arousing (aversive) outcome.

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The bottom row of Figure 8 shows a replication of the design in which we replaced the aversive startling noise outcome with a neutral 50 dB tone, to determine whether the loss of dwell time bias for A (compared to B) was driven by attentional avoidance. The important finding was that the original effects seen in the top row were replicated with the neutral outcome, confirming that the attentional effects were determined by the differential uncertainty associated with each stimulus, rather than any affective value acquired through association with the aversive outcome.
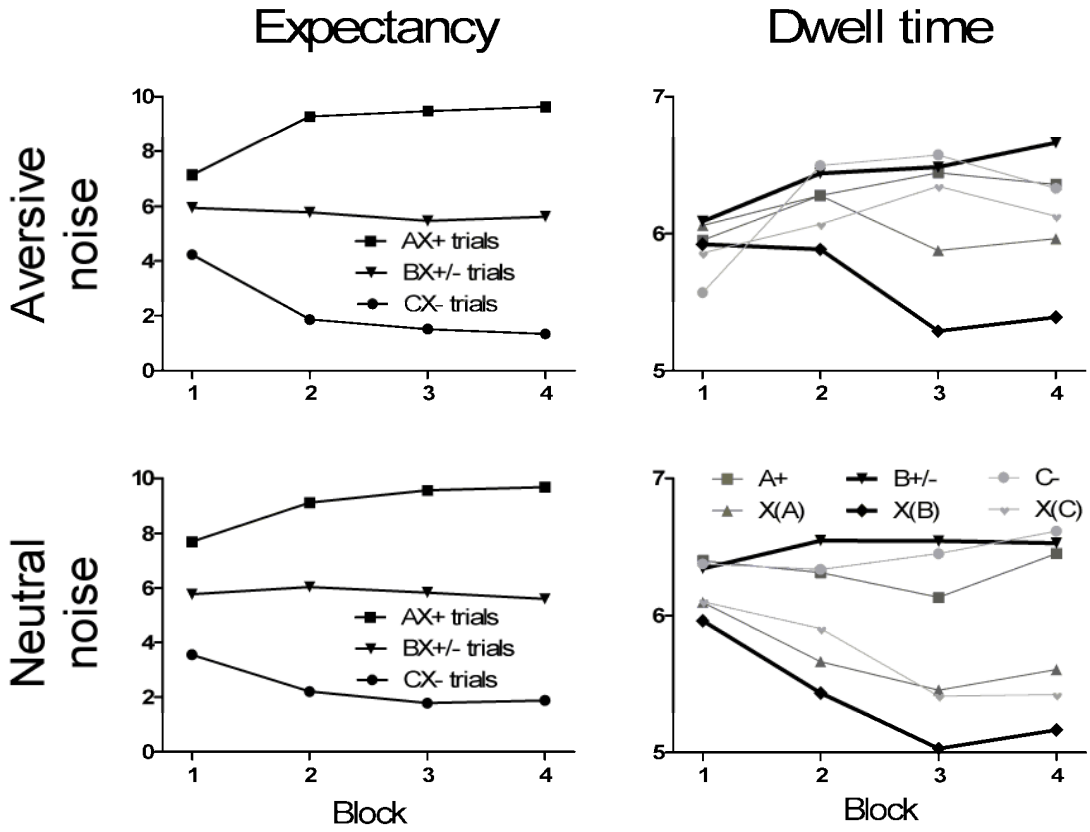
Figure 8: Two studies exploring the maintenance of attention to stimuli with differential relationships to an aversive (top row) and neutral noise outcome (bottom row). Noise expectancy ratings (1-10 scale) and dwell times (natural logmsec) to a full, partial and non-predictor stimulus A, B and C, respectively, relative to a concurrently presented contextual cue X. The key result was that the dwell time bias was greatest for the partial predictor stimulus B which was associated with the greatest uncertainty, with both the aversive and neutral outcome.

Summary - Untangling arousal, valence and uncertainty

Our data suggest that conditioned stimuli command the three forms of attentional selection (see Figure 1). Conditioned stimuli appear to command efficient detection to the extent that they are associated with an arousing outcome (irrespective of valence), and command the maintenance of overt attention to the extent that they are associated with an appetitive outcome. In addition to this, conditioned stimuli also appear to command the maintenance of overt attention to the extent that they convey uncertainty about the probability of an outcome, irrespective of whether the outcome is aversive or neutral. We propose that these three forms of attentional selection play a role in action selection, affective state and learning, respectively.

There are several ways one might develop this work to further isolate the three attentional systems. First, further contrasts are needed of the nine conditions outlined in Figure 1. One gap in our analysis, for example, is that we have not assessed uncertainty effects for CSs paired with an appetitive outcome. Second, there is need to discover a measure of attention that is sensitive to the enhancement of early detection as distinct from the maintenance of attention measured by dwell time. For this purpose, we have hinted at signal detection (Engelmann and Pessoa, 2007), EEG (Brosch et al., 2008), attentional blink (Livesey et al., 2009) or spatial cueing (Vogt et al., 2008), but the incorporation of these measures into the current procedures remains to be explored. Third, a broader range of aversive outcomes might be tested, to determine the conditions under which attentional avoidance is generated. Forth, closer analysis is required of the time course of stimulus viewing, to identify the point at which looking-for-action is superseded by looking-for-liking or looking-for-learning. Finally, direct contrasts might be made of discriminative instrumental versus Pavlovian procedures, which are otherwise yoked for cue-outcome frequency (see; Rescorla, 1994), to assess attentional performance when instrumental action is and is not possible. The ultimate objective of this program of work would be to isolate and dissociate the three attentional

systems for application to brain imaging to contribute to a neuropsychological model of attention.

Once the appropriate parameters are established to isolate the three attentional systems, one could more clearly reassess their proposed differential role in action selection, affective state and learning. For instance, one might assess whether enhanced detection for arousing cues predicts differential behavioural control exerted by these stimuli in tests of cue competition (De Houwer and Beckers, 2002, Kruschke et al., 2005). Further, one might test whether dwell time to appetitive cues, or avoidance of aversive cues is modulated by mood induction, individual affective state (Beevers and Carver, 2003, Tamir and Robinson, 2007), or post-conditioning revaluation/devaluation of the incentive value of the outcome (Holland and Straub, 1979, Hutcheson et al., 2001), to explore the link between attentional maintenance and affect. Finally, one might examine whether dwell time associated with uncertainty predicts the associability of stimuli in tests of learning (Wilson et al., 1992, Holland and Gallagher, 2006), although this work would have to reconcile apparent contradictory evidence that learning is sometimes superior for reliable predictors (see; Le Pelley, 2004, Le Pelley and McLaren, 2003). In all, this work should clarify the role of the three attentional systems in action, affect and learning.

The neural basis of attention in associative learning

One final issue concerns the neural substrates of the three attentional systems. Perhaps the most informative work addressing this issue has come from the animal behavioural neuroscience lab of Peter Holland, and this topic is discussed extensively in a separate chapter. Our aim is not to compete with this chapter, but rather, to highlight a small set of exemplary studies which appear to have isolated one of the three attentional systems in a way reminiscent of our human studies. Our purpose in highlighting the relationship between these human and animal studies is to hint at what shape a translational

program of research might take to contribute to a neuropsychological theory of attention in associative learning.

Holland and colleagues recently identified a form of CS orienting that plays no role in the control that CS exert over instrumental behaviour (Groshek et al., 2005, McDannald et al., 2004), reminiscent of the studies outlined in Figures 5 and 6, where abolition of the dwell time bias to the CS had no impact on CS control of expectancy and instrumental performance. In these animal studies, rats learned that a 10-sec external light or noise CS was followed immediately by the availability of food in a feeding tray. In parallel with our results, rats developed an attentional bias for the conditioned stimuli, indexed by a higher frequency of orientation of the eyes or ears towards that stimulus in the early portion of its presentation, while learning to approach the food tray in response to the CS in anticipation of food delivery, in the latter portion of its presentation. The fact that attentional orientation was not necessary for reward seeking by the rats was demonstrated by deactivation of the central nucleus of the amygdala, which abolished the attentional bias for the CS, but left intact the ability of the CS to elicit food seeking. El-Amamy and Holland (2007) recently confirmed this dissociation between the attentional bias and instrumental performance in a Pavlovian to instrumental transfer design.

These data have a striking similarity to our own (Figures 3, 5 and 6), in that the bias for the CS and its control of reward seeking emerged in parallel across conditioning, yet the abolition of the attentional bias had no impact on CS control of behaviour. The question, therefore, is what caused a form of attentional bias to develop that played no functional role in behaviour? We believe that this bias reflected the looking-for-liking system, which was recruited by the prediction of the reward outcome evoked by the CS, and enabled by the fact that the CS was presented for a 10-sec period of dead time during which instrumental responding was ineffective (the implication being, that if the CS and food availability were simultaneous, as in Figure 6, the looking-for-action system – efficient detection – would have been unmasked in mediating instrumental responding). If this

assertion is true, then by implication, the central nucleus of the amygdala is one component of the neural circuit underlying the looking-for-liking system.

Another recent experiment from Holland's lab (Maddux et al., 2007) dissociated the substrates underlying the looking-for-action and looking-for-learning systems. In this study, performance of the five choice serial reaction time task was used to index the role of attention in guiding behavioural choice, whereas the ability of surprise (prediction error) to enhance learning was used to index the role of attention in facilitating contingency learning. This study found that lesions of the cholinergic projection from the substantiate innominata/nucleus basalis magnocellularis (SI/nBM) to the medial prefrontal cortex interfered with the role of attention in guiding behavioural choice but not in the enhancement of learning. By contrast, lesions to the cholinergic projection to the posterior parietal cortex had the converse effect - interfering with the role of attention in learning but not in behavioural control. Finally, lesions of the central nucleus of the amygdala, which is linked to the SI/nBM, interfered with both forms of attention. Collectively, therefore, the foregoing studies from Holland's lab support the notion that although the circuits underlying looking for action, liking and learning are commonly routed through the central nucleus of the amygdala, they diverge thereafter to separate cortical projections through the SI/nBM.

Our human procedures could in the future contribute to a neuropsychological theory of attention in associative learning by first optimising the parameters needed to behaviourally isolate the three attentional systems, as described earlier, and then transferring these methods into an MRI scanner, to help elucidate the full extent of the circuits underlying each attentional system (see; Armony and Dolan, 2002). The animal work could then pinpoint these neuroanatomical substrates beyond the resolution of the scanner.

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