

Motivation and Visual Attention in Adolescents and
Adults

by

Daniel Barry Dodgson

A thesis submitted to the University of Birmingham for the degree of

DOCTOR OF PHILOSOPHY

School of Psychology

College of Life and Environmental Sciences

University of Birmingham

June 2018

UNIVERSITY OF
BIRMINGHAM

University of Birmingham Research Archive

e-theses repository

This unpublished thesis/dissertation is copyright of the author and/or third parties. The intellectual property rights of the author or third parties in respect of this work are as defined by The Copyright Designs and Patents Act 1988 or as modified by any successor legislation.

Any use made of information contained in this thesis/dissertation must be in accordance with that legislation and must be properly acknowledged. Further distribution or reproduction in any format is prohibited without the permission of the copyright holder.

Abstract

This thesis explores how the motivation to process a visual stimulus influences attentional control. A core aim was to develop and test a motivation-based as opposed to a perception-based explanation for reward association effects on visual selective attention. To do so, in a series of 12 experiments, stimuli were first imbued with a value, reinforced with monetary wins and losses. Then, these same value-associated stimuli were used as distractors in spatial attention paradigms, including flanker and visual search tasks, incentive cues in a simple detection task, or targets in an ensemble perceptual judgment task. Of primary interest were measures of attentional capture by value-laden opposed to neutral stimuli. Taking a developmental approach, in a subset of the experiments value-driven biases in late adolescents compared to adults were also examined while simultaneous electroencephalography was recorded. Collectively, the results from these experiments suggest that the effects of motivational salience are inconsistent with perception-based accounts but can be encompassed in a motivation-based framework that suggests value-associated stimuli compete to alter current goals. This motivation-based model is grounded in the cognitive control literature and posits a competition among potential goals driven by the costs versus benefits of cognitive engagement with stimuli.

Acknowledgements

First, I would like to thank Professor Jane Raymond for all the support and motivation she has offered to me throughout my Ph.D study. Her advice has been invaluable. Thanks also to Professor Stephen Wood for his assistance at the start of the process.

I would also like to thank all current and former members of the Visual Experience Lab. I am especially appreciative to Aleksandra Pastuszak, Andrew Clouter, Jess Kerlin, Risa Sawaki, Sara Asseconi, and Professor Kimron Shapiro for offering their insight, helpful advice and support during my time in Birmingham. I am also thankful to Danielle Mathieson who assisted with the data collection for Chapters 2 and 5.

Finally, thank you to my parents, Janet and Barry Dodgson, and partner, Natalie Eaves, for always believing in me, and for all of the love and support over the years.

Table of Contents

Chapter 1. General Introduction	1
Chapter 2. Value-based Modulation of Visual Attention Depends on Competition Among Motivational States	46
Abstract	47
General Methods.....	55
Experiment 1	63
Method	63
Results and Discussion	64
Experiment 2	70
Method	71
Results and Discussion	71
Experiment 3	73
Method	74
Results and Discussion	74
Experiment 4	76
Method	78
Results and Discussion	80
Experiment 5	84
Method	85
Results and Discussion	86
General Discussion	88
Chapter 3. Motivational Competition in Adolescents	98
Abstract	99
Method	106
Results	110
Discussion	116
Chapter 4. Motivationally Driven Attentional Capture	120
Abstract	121
Experiment 1	124
Method	127
Results and Discussion	132
Experiment 2	136
Method	137
Results and Discussion	139
General Discussion	142
Chapter 5. Adolescent Incentive Cue-related Signal Suppression: An EEG Study.....	145
Abstract	146
Experiment 1	152
Method	152
Results	160
Experiment 2	168
Method	168
Results	169
General Discussion	170

Chapter 6. Can Value-associated Stimuli Influence Ensemble Perception?	178
Abstract	179
Experiment 1	184
Method	184
Results and Discussion	189
Experiment 2	191
Method	192
Results and Discussion	193
General Discussion	194
Chapter 7. General Discussion	197
Chapter 8. List of References	209

List of Figures

Figure 1.1. Example trial from the training task and the test task used to demonstrate value-driven attentional capture by Anderson et al. (2011). Taken from Anderson et al. (2011).	12
Figure 1.2. Representation of the Selection History account of attentional bias. Taken from Awh et al. (2012).....	16
Figure 1.3. Example trial sequence from an arrow flanker task. Adapted from Seer et al. (2017).....	27
Figure 1.4. Classic conflict adaptation result. Taken from Egner, Ely, & Grinband (2010).	29
Figure 2.1. Predicted super-distraction effects for flanker task performance after congruent versus incongruent trials using a processing priority framework based on perceptual or motivation-based competition.	52
Figure 2.2. A. Example trial during the Learning Task. B. Example of two successive trials in the Flanker Task.....	60
Figure 2.3. Group mean CE_{Con} and CE_{Incon} plotted separately for each current trial flanker value or brightness condition in Experiment 1 (A) and Experiment 2 (B), respectively. .	67
Figure 2.4. Group mean super-distraction effect for each current trial flanker value/brightness condition. A. Experiments 1 – 3. B. Experiments 4 (WM and No-load) and 5.	69
Figure 2.5. Group mean CE_{Con} and CE_{Incon} for each current trial flanker value in Experiment 3.	76
Figure 2.6. Group mean CE_{Con} and CE_{Incon} plotted separately for each current trial flanker value in the WM load (A) and the No-load (B) conditions in Experiment 4.....	83
Figure 2.7. Group mean CE_{Con} and CE_{Incon} plotted separately for each current trial flanker brightness in Experiment 5.	87
Figure 3.1. Example of a value-learning task trial (A), and a Flanker task trial sequence (B).	110
Figure 3.2. Congruency effects (incongruent – congruent) following a congruent and an incongruent trial for adolescents (A) and adults (B).	114
Figure 3.3. Super-distraction effects (Value - No-value) following a congruent and an incongruent trial for adolescents (solid line) and adults (dashed line).	115
Figure 4.1. A. Example trial during the Value-learning task. B. Example of a 2-trial sequence during the Test task in Experiment 1 in the colour working memory condition. C. Example of a 2-trial sequence during the Test task in the shape working memory condition.	132
Figure 4.2. Mean value driven attentional capture effect (VDAC), calculated as High-value – No-value distractor conditions, for both the colour and the shape working memory (WM) conditions.	134
Figure 4.3. Mean value driven attentional capture effect (VDAC) when the distractor on the previous trial was associated with no-value and high-value.	140
Figure 5.1. Schematic of a value-learning task trial (A), and a letter-target detection task trial (B). In the value-learning task.....	156
Figure 5.2. Response time congruency effects for reward and no-reward trials across all age-groups.	163
Figure 5.3. ERPs elicited by the incentive cues.	165

Figure 5.4. TFR results during the pre-stimulus period prior to the incentive array during the Letter detection task.	167
Figure 6.1. Left) The value-learning task trial structure in both Experiment 1 and 2. Right) The extinction task structure in Experiment 2..	188
Figure 6.2. Percent increases in the judgments of average circle size from the actual average size depending on the high value-biasing condition in the Extinction task. A) Experiment 1. B) Experiment 2.	190

List of Tables

Table 2.1. Definitions used in the flanker task.....	51
Table 2.2. Participants' Demographic Information and Mean Questionnaire Scores from all Experiments (standard error in parenthesis).....	57
Table 2.3. Mean Proportion of Optimal Choices as a Function of Block during the Value-Learning Task for Experiments 1, 2, and 3.	64
Table 2.4. Mean RT as a Function of the Trial Type for All Experiments.	65
Table 3.1. Mean percent optimal choices (standard error in parenthesis) as a function of block during the value-learning task.	111
Table 3.2. Mean RT (with standard error in parenthesis) as a function of trial type.	112
Table 4.1. Mean reaction times in milliseconds (with standard error in parenthesis) on the Value-Learning task in Experiment 1 (depending on Day) and in Experiment 2.	133
Table 4.2. Mean reaction times in milliseconds (with standard error in parenthesis) for each value distractor across both working memory (WM) conditions.	134
Table 4.3. Mean reaction times in milliseconds (with standard error in parenthesis) for each value distractor when preceded by No-value and High-value distractor trials.	139
Table 5.1. Mean accuracy (standard error in parenthesis) for each age-group, decision stage and reward condition in the Value-learning Task.	160
Table 5.2. Mean RT (ms) and accuracy (standard error in parenthesis) for each age-group, congruency, and reward condition in the Letter-Target Detection Task.....	161
Table 6.1. Mean RTs (ms) and percent increase in the estimates of circle size in the value-learning task for low-value and high-value circles in Experiment 1 and 2.....	189

Publications, Presentations, and Contributions

From my doctoral study at the University of Birmingham, the following articles and conference proceedings are in preparation, submitted, or accepted for publication and/or presentation at conferences. In all cases and for each chapter of this thesis, the second author (Professor Jane E. Raymond) advised on study design, data analysis and editorial guidance during the writing process. Danielle Mathieson also assisted with the data collection for Chapters 2 and 5 of this thesis.

Papers submitted for publication from this doctoral research

1. **Dodgson, D.B.** & Raymond, J.E. Value-based modulations of visual attention depends on competition among motivational states. *Journal of Experimental Psychology: General*. Submitted June 2017. (Chapter 2).
2. **Dodgson, D.B.** & Raymond, J.E. Value-Associations Bias Ensemble Perception. *Attention, Perception & Psychophysics*. Submitted November 2018. (Chapter 6).

Papers in preparation for submission from this doctoral research

1. **Dodgson, D.B.** & Raymond, J.E. Motivational competition in adolescents. (Chapter 3).
2. **Dodgson, D.B.** & Raymond, J.E. Adolescent incentive cue-related signal suppression: An EEG study. (Chapter 5).

Abstracts from this doctoral research

1. **Dodgson, D.B.** & Raymond, J.E. (in press). Motivational trade-offs drive attention capture. *Journal of Vision*. Poster presented at the 18th annual Vision Sciences Society meeting 2018. (Chapter 4).
2. **Dodgson, D.B.** & Raymond, J.E. (2017). Value-associated stimuli bias ensemble size estimates. *Journal of Vision, 17*, 1298. doi: 10.1167/17.10.1298. Poster presented at the 17th annual Vision Sciences Society meeting 2017. (Chapter 6).
3. **Dodgson, D.B.** & Raymond, J.E. (2016). Value-associated stimuli can modulate cognitive control settings. *Journal of Vision, 16*, 90. doi: 10.1167/16.12.90. Poster presented at the 16th annual Vision Sciences Society meeting 2016. (Chapter 2).
4. **Dodgson, D.B.** & Raymond, J.E. (2015b). Value associations enhance preparatory top-down attentional control and attentional suppression. *Perception, 44*, 107. Poster presented at the 38th European Conference on Visual Perception 2015.
5. **Dodgson, D.B.** & Raymond, J.E. (2015a). Attention immaturity in late adolescence: Conflict adaptation with value associated stimuli. *Journal of Vision, 15*, 1060. doi: 10.1167/15.12.1060. Poster presented at the 15th annual Vision Sciences Society meeting 2015. (Chapter 3).

Chapter 1. General Introduction

***“Intra due cibi, distanti e moventi d’un modo, prima si morria di fame, che liber’ omo
l’un recasse ai denti;”***

*“Before a man bit into one of two foods equally removed and tempting, he would die
of hunger if his choice were free.” Translated from Dante (1320), Paradiso IV.*

Overview

Visual stimulation from the environment is noisy and vast. Thus, processing the entire scene would exceed the known capacity of cognitive resources available for information processing. Therefore, perceptual decision-making must, often implicitly, prioritize stimuli for attentional selection. Two types of visual stimuli are known to be prioritized for selection. The first type consists of stimuli that are relevant to current goals (top-down). The second branch of stimuli may be irrelevant to goals but are physically salient (bottom-up). However, this classic view of attentional selection in visual information processing is inadequate.

Stimuli with learned value-associations also need to be prioritized because processing them may be beneficial, i.e., in obtaining a positive outcome or avoiding a negative outcome. There is now abundant evidence that value-associated stimuli do indeed bias perceptual decision-making. For example, value-associated stimuli are prioritized when attention is temporally constrained (Raymond & O’Brien, 2009) and when they are presented as irrelevant distractors in a spatial attention task (Anderson, Laurent, & Yantis, 2011). Thus, these stimuli are often neither relevant to current goals nor physically salient yet garner perceptual selection. As a result, this third class of stimuli are currently neglected in classic accounts of perceptual selection and must be incorporated into theories of perceptual decision-making.

One line of research suggests that value-associated stimuli directly influence the orienting of attention, interacting with top-down and bottom-up factors (Awh, Belopolsky, & Theeuwes, 2012; Chelazzi et al., 2014; Failing & Theeuwes, 2017). These ideas are discussed in more detail below, but briefly, these accounts suggest that because stimuli have previously been selected and performance was then rewarded, value-associated stimuli garner an attentional priority. Thus, in this view they compete at a perceptual level with goal relevant and physically salient stimuli for selection. A second view is based around the idea of motivated cognition (Botvinick & Braver, 2015; Braver et al., 2014; Kool, Shenhav, & Botvinick, 2017; Shenhav et al., 2017; Shenhav, Botvinick, & Cohen, 2013). This theory suggests that competition between stimulus- and task-initiated motivational states (goals) determines how cognitive resources are utilized. The motivational competition is determined by internal computations of the expected costs-benefits of each motivational state to the observer. For example, an empty coffee cup visible while reading might motivate a trip to the kitchen, disrupting the reading task, whereas the content of the text itself might motivate reading. To maintain focus on the immediate reading goal, the reader must either suppress perceptual processing of the task-irrelevant object (empty cup) or suppress the irrelevant motivational state it instantiates (“I want more”). In the case of value-associated stimuli, it is not clear whether they influence perceptual processing or motivated cognition. However, to date the literature has favoured the former notion, largely ignoring the possibility that regulation of motivational states may be involved.

The objective of this thesis was to investigate the role of motivational competition in understanding the effects of value-associated stimuli on cognition in typical adults and during adolescence. To do so, I conducted a series of experiments in which participants first engaged

in a value-learning task, whereby participants learned to associate novel stimuli (or colours) with a motivational meaning (positive, neutral, or negative). Then, participants performed either a task requiring spatial selective attention or a task requiring sustained cognitive control. In both types of task, the costs and benefits of attending to value-associated stimuli were manipulated.

This thesis is presented in seven chapters. Chapter 1 provides a review of the attentional control and motivated cognition literatures, linking each perspective to value-driven effects on cognition. Chapter 1 also offers a review of how the motivated cognition perspective may apply to adolescents' *hypersensitivity* to rewards. Chapter 2 directly contrasts the differing prediction that can be made from perceptual competition and motivational competition accounts of value-driven distraction in a cognitive control paradigm requiring shifts between cognitive control strategies (flanker task). Chapter 3 investigates how adolescents differ from adults in the computation of costs and benefits when deciding how to initiate strategic control in the flanker task. Next, Chapter 4 investigates the role of increasing the cognitive costs of attending to value-associated distractors in a classic value-driven attentional capture paradigm (e.g., Anderson et al., 2011). Chapter 5 examines differences between how adolescents and adults engage in motivational competition in a cueing paradigm with concurrent electroencephalography (EEG). In Chapter 6, the role of value-associated stimuli in a novel ensemble coding paradigm is examined. Finally, a general discussion of the motivational competition account of cognition is provided in Chapter 7.

Perceptual Competition and Representational Strength

From noisy visual scenes, information pertinent to current cognitive goals must be attended, and distracting information needs to be ignored. Visual selective attention is the mechanism by which important information is processed. Classically, visual attention has been considered as a 'spotlight' that is cast over the visual field (Posner, 1980). Anything within the focus of attention is preferentially processed compared to objects in the periphery of attention. In overt shifts of attention, the focus of attention converges on items presented to the fovea. However, attention can also act independently of eye-movements in the form of covert shifts (Eriksen & St. James, 1986; Posner, 1980). In addition to being considered spatially, visual attention can also be directed in an object-based manner. This latter form of attention is guided by stimulus features that discriminate items.

Conventionally, two distinct biases are thought to control attentional selection; top-down and bottom-up control. Attentional templates (Duncan & Humphreys, 1989) form the basis of top-down (or goal-directed) control of visual attention. In essence, templates are descriptions of potentially relevant stimulus features related to task requirements that should be attended (Desimone & Duncan, 1995), alongside templates of potentially distracting information that should be ignored. Attentional sets are not restricted to visual biases and can also encompass typical motoric responses to stimuli (Corbetta & Shulman, 2002). By virtue of the predictive nature of top-down attentional control, it is not an independent venture and is reliant on a coordinated effort involving multiple brain systems, including between long-term memory of similar prior experiences, learning, working memory (for the maintenance of templates and goals), selective attention (to implement these templates), and motor control

(to initiate responses). Cognitive control is the process by which this coordinated effort is governed.

However, the rigidity of cognitive control is not absolute. If cognitive control always proceeded strictly in a goal-driven manner until completion of the current goal, cues signalling, for example, danger would be missed. Therefore, attentional control can also be stimulus-driven (bottom-up), independent of top-down attentional control (Theeuwes, 1992). Stimuli that stand out relative to the surroundings capture attention and gain access to higher-level processing. Such physical salience is usually characterized by low-level features that are primarily processed early in the visual processing stream, such as luminance, contrast, colour, shape, depth, and velocity and direction of motion (Itti & Koch, 2000). The speed with which bottom-up attentional control captures covert and overt attention suggests that it is automatic; the mere presence of a physically salient event will capture attention (Theeuwes, 1992).

Therefore, when viewing a typical visual scene object selection must be competitive. Each item in the rich visual environment must compete to reach awareness, and stimuli with task-relevance or physical salience are most likely to win this competition (Desimone & Duncan, 1995). Using functional magnetic resonance imaging (fMRI) in humans, this competition has been demonstrated right throughout the visual cortex from as early as V1 (Beck & Kastner, 2009; Desimone & Duncan, 1995). Studies in non-human primates have shown that bottom-up competition is resolved in a stimulus-driven manner. For example, when two stimuli are presented within the same receptive field, neural activity in the receptive field matches that when only the most salient stimulus is present. This demonstrates that bottom-up competition in the visual cortex is biased in favour of the most salient

stimulus, and the second stimulus is inhibited (Reynolds & Desimone, 2003). Similar to the influence of bottom-up salience, top-down mechanisms have also been shown to bias competitive interactions within receptive fields (Beck & Kastner, 2009; Bichot, Rossi, & Desimone, 2010; Luck, Chelazzi, Hillyard, & Desimone, 1997). This neurophysiological evidence shows the role of both top-down and bottom-up mechanisms in biasing object selection at both the psychological and neural levels (Connor, Egeth, & Yantis, 2004; Ogawa & Komatsu, 2004).

Many psychological and computational models of attentional control posit that competitive interactions determine the distribution of attention across a topographical saliency/priority map. The map consists of stimulus representations, which comprise the perceptual attributes that form objects and that separate objects from others according to Gestalt principles. Stimulus representations also code the spatial location of the objects (Egeth & Yantis, 1997). Such representations are sometimes referred to as object files because they are formed of stimulus specific information (Kahneman, Treisman, & Gibbs, 1992). Within the priority map the strength of each representation is determined, at least initially, by stimulus-driven factors, including physical salience (Itti & Koch, 2000; Theeuwes, 1992). Some models posit that the maps adjust as the visual information progresses through the visual hierarchy and new information is added to the representations (Ptak, 2012; Serences & Yantis, 2006). Others suggest that different feature maps are created depending on the distinct stimulus features in the scene, and then these individual maps are combined into a global map, although this final step is not necessary in all models (Fecteau & Munoz, 2006; Treisman, 1982; Treisman & Gelade, 1980; Wolfe, 1994). Regardless, the item with the greatest physical salience garners the greatest representational peak and thus attention is grabbed by that

item. In other priority mapping models, the map's topography is also modulated by top-down mechanisms. As in biased competition, top-down attentional control can boost the strength of task-relevant stimulus representations (Desimone & Duncan, 1995; Fecteau & Munoz, 2006; Ptak, 2012; Yantis & Jonides, 1990). Similar ideas have also been suggested that do not make explicit references to a topographical map, but suggest that the sum of coordinated activity of neurons through the different levels of the visual system each representing the same object, or coherence fields, determine attention (Serences & Yantis, 2006). Coherence field theories potentially offer more explanatory power when discussing temporal attention because priority maps are somewhat limited to spatial attention. Importantly, though, in both types of model attention is given to items in the environment that are represented most strongly in visual pathways, whether they create peaks on topographical maps or recruit the greatest neuronal coherence.

The relative influence of top-down and bottom-up mechanisms on the eventual topography of the priority map is a matter of debate. Many researchers hold the belief that physical salience captures attention regardless of top-down attentional sets. In essence, a singleton will attract attention irrespective of an observer's goal, with the caveat that the singleton must fall within an expected spatial location (Itti & Koch, 2000; Theeuwes, 1991, 1992). Theeuwes (1992) demonstrated that when observers search for a unique shape always presented in the same colour amongst homogeneously shaped distractors, the presence of a colour singleton distractor slows response time (RT) compared to trials without a singleton distractor. Theeuwes (1992) explained this effect suggesting that despite the exact attentional set being known and colour being task-irrelevant, top-down control had no influence and the physically salient distractor still captured attention. Others, though, have shown that top-

down attentional sets can effectively modulate the impact of physically salient distractors (Folk & Remington, 1998; Folk, Remington, & Johnston, 1992). Specifically, a singleton distractor, presented simultaneously with the target, is more likely to capture attention when it is defined by a feature shared with the target as was the case in Theeuwes (1992), than when it does not (Folk et al., 1992).

In addition to the behavioural evidence, electrophysiological data also offers an important perspective on the interplay between bottom-up and top-down attentional control in the modulation of priority maps. Event related potentials (ERPs) are the evoked activity found in EEG recordings in response to the presentation of stimuli or during the pre-stimulus preparation epoch when responses are planned. Two particularly relevant components of the ERP when discussing attentional deployment are the N2pc and the distractor positivity (Pd). The N2pc has an established history as an index of attentional allocation (Luck, 2005). Typically, it is observed around 200 ms after stimulus onset as a negative going deflection of the ERP at contralateral compared to ipsilateral scalp sites relative to the visual field where the attended stimulus is located. Conversely, the Pd component is thought to be a marker of attentional suppression (Hickey, Di Lollo, & McDonald, 2009). It is typically observed later than the N2pc as relatively more positive voltage in contralateral versus ipsilateral scalp sites relative to the stimulus of interest. Both components are strongest at parietal-occipital scalp sites. Studies using these components to investigate the role of top-down and bottom-up attentional control in selection have found limited evidence for pure bottom-up attentional capture completely independent of top-down mechanisms (Ansorge, Kiss, Worschech, & Eimer, 2011; Eimer & Kiss, 2008). For example, Eimer and Kiss (2008) found that the N2pc to a salient visual singleton was only present when it matched the task relevant feature of the

task, consistent with the earlier behavioural findings of Folk et al. (1992), suggesting that attention is only allocated on the basis of physical salience when it is consistent with attentional templates. Furthermore, Sawaki & Luck (2010) have shown that not only do task-irrelevant singleton distractors not elicit an N2pc, and thus do not appear to be attended, they in fact produce a Pd; indicating active suppression. This study highlights the importance of considering active suppression as well as capture when discussing attentional control. In particular, the study supports the view that top-down and bottom-up attentional control interact in modulating the topography of priority maps. Irrelevant but physically salient stimuli appear to be actively suppressed when they conflict with top-down attentional templates. More recent electrophysiological research analysing the time-course of cross-frequency interactions in top-down and bottom-up mediated pathways supports the view that top-down influences causally modulate bottom-up representational strength (Richter, Thompson, Bosman, & Fries, 2017).

All the evidence reviewed so far suggests that the interaction between top-down and bottom-up attentional control determines selection in busy visual scenes. However, in the last ten years attentional capture by stimuli that are inconspicuous and irrelevant to current goals has been reported (Awh et al., 2012; Failing & Theeuwes, 2017). I refer here to stimuli with learned reward associations. In this review two classes of theory to account for these effects will be considered. The first suggests that rewards influence attention through a mechanism that interacts with top-down and bottom-up control in the formation of perceptual priority maps (e.g., Awh et al., 2012). The second suggests separable roles of motivation and attention in the control of cognition (Raymond & O'Brien, 2009), with rewarding stimuli impacting the former.

Value-associated Stimuli – Super-distraction

A classic example of these learned reward associations capturing attention was conducted by Anderson et al. (2011) using a modified version of the additional singleton task outlined above (Theeuwes, 1991, 1992), but in a training-test method where the experiment is conducted in two distinct parts (e.g., Raymond & O'Brien, 2009). In Anderson et al. (2011), participants initially complete a simple visual search task where the target on any given trial is always inside either a red or a green circle and distractors are surrounded by differently coloured circles. Unbeknownst to the participant at the start of the task, on 80% of trials they receive a large monetary reward when the target circle is red and a small monetary reward when it is green. These contingencies are reversed for half of participants. Participants then engage in a subsequent additional singleton task. Here, they must locate a shape singleton to identify a visual target, but crucially all the search items are differently coloured. On a proportion of the trials one of the distractors is presented in the previously high or low reward associated colour; on remaining trials, no reward associated colours are present. See Figure 1.1 for an example of the training and test trials. Anderson and colleagues found slower RT when a previously high-reward distractor was present than when no reward associated colours were in the display. This value driven attentional capture (VDAC) from the previously high reward colour occurred despite the value associated distractor being task-irrelevant and physically non-salient compared to the rest of the distractors in the visual search display. This effect, therefore, seems to be outside the bounds of both top-down and bottom-up attentional control (Awh et al., 2012; Failing & Theeuwes, 2017). VDAC has also been shown when a colour was conditioned to no-reward; in this case, RTs were slowed by the presence of the previously high-reward compared to the no-reward distractor, ruling out accounts

purporting a sole role of selection history in the effect (e.g., Sha & Jiang, 2016) and pointing towards a reward-related slowing (Anderson & Halpern, 2017). However, the effect is also not specific to rewards and has been shown for punishment-associated distractors (Wang, Yu, & Zhou, 2013). Time and again, similar *super-distraction effects*, i.e. greater distraction by motivationally salient versus perceptually similar neutral stimuli, have been found (Anderson, 2015a, 2015b; Anderson, Faulkner, Rilee, Yantis, & Marvel, 2013; Anderson, Folk, Garrison, & Rogers, 2016; Anderson & Yantis, 2012; Alexia Bourgeois, Neveu, Bayle, & Vuilleumier, 2015; Bucker, Belopolsky, & Theeuwes, 2015; Della Libera & Chelazzi, 2006, 2009; Failing, Nissens, Pearson, Le Pelley, & Theeuwes, 2015; Hickey, Chelazzi, & Theeuwes, 2010a, 2010b; Hickey & Peelen, 2015; Hickey & Van Zoest, 2012; Le Pelley, Pearson, Griffiths, & Beesley, 2015; MacLean, Diaz, & Giesbrecht, 2016; Maclean & Giesbrecht, 2015; Munneke, Belopolsky, & Theeuwes, 2016; Munneke, Hoppenbrouwers, & Theeuwes, 2015; Pearson, Donkin, Tran, Most, & Le Pelley, 2015; Qi, Zeng, Ding, & Li, 2013; Roper, Vecera, & Vaidya, 2014; Rutherford, O'Brien, & Raymond, 2010; Theeuwes & Belopolsky, 2012; Wang et al., 2013).

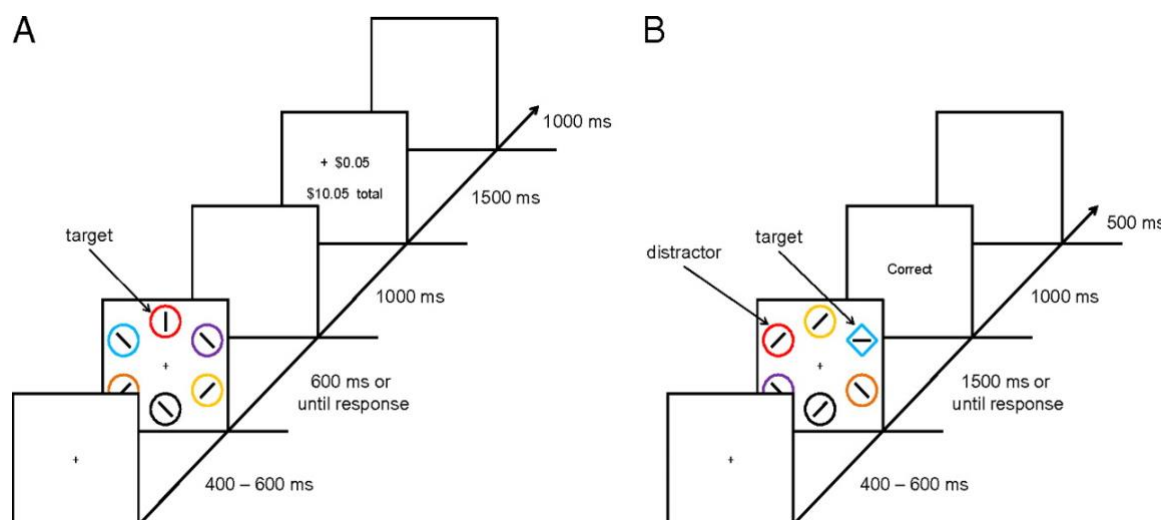


Figure 1.1. Example trial from the training task (A) and the test task (B) used to demonstrate value-driven attentional capture by Anderson et al. (2011). Taken from Anderson et al. (2011).

Super-distraction effects have generally been accounted for by supposing that motivational salience modulates representational strength on the attentional priority map by lending greater weight to stimuli predictive of rewards. In this way, motivationally salient stimuli capture attention. This has led some researchers to posit a reward-driven control dynamic as a third branch of attentional control, alongside bottom-up and top-down attentional control (Anderson et al., 2011; Awh et al., 2012; Della Libera & Chelazzi, 2006; Failing & Theeuwes, 2017; Kiss, Driver, & Eimer, 2009). This third mechanism may be the same mechanism that mediates task contingent involuntary orienting (Folk et al., 1992). Specifically, stimuli matching reward predicting features may modulate bottom-up attentional control in the manner that top-down attentional sets are purported to modulate them. Electrophysiological evidence has demonstrated that the N2pc appears earlier and is larger in amplitude to high reward targets compared to low reward targets, and this amplitude difference correlates with the performance improvement found for high-reward targets (Kiss et al., 2009).

Indeed, at the very earliest stages of visual processing, within 100 ms of stimulus presentation, it has been shown that the prospect of rewards modulates vision. Specifically, the P1 component of the ERP, which is always observed in response to visual stimulation and strongly influenced by low-level stimulus features such as luminance (Luck, 2005), has also been observed to be reward modulated (Hickey et al., 2010a; Maclean & Giesbrecht, 2015). Hickey et al. (2010a) used a variant of the additional singleton task (Theeuwes, 1992) where participants had to search for a shape singleton in the presence of a colour singleton distractor and correct performance was randomly rewarded with either a high or a low reward. Importantly, the colour of the target and shape singleton could either stay the same from trial

$n-1$ to the subsequent trial or they could switch. When there was no colour change, RT was faster following a highly rewarded trial $n-1$ compared to a low rewarded trial $n-1$. When the colour of the target and distractor singleton switched, RT was slowed following a high compared to a low reward. Comparable effects were also found in the electrophysiological data examining the lateralized P1. Following a high reward trial and a colour switch, the P1 contralateral compared to ipsilateral relative to the distractor singleton was increased; following a high reward trial and no colour swap the P1 contralateral to the target was greater than the ipsilateral P1. Given the timing of the P1 component, the time-course of the effect is consistent with the notion that rewards modulate bottom-up attentional control. According to Hickey, Chelazzi, & Theeuwes (2011) this P1 effect suggests that perception is altered by rewards, and this precedes the deployment of attention. However, an alternative interpretation would be consistent with a mechanism similar to that of contingent involuntary orienting (Folk et al., 1992). In the Hickey et al. (2010a) paradigm the attentional set from trial $n-1$ is replicated on trial n following a reward (Thorndike, 1898), i.e., the participant must attend to the rewarded colour. Thus, attention is endogenously driven to objects with the previous target's colour whether it be target or distractor. Consistent with this idea, motivational salience is thought to endogenously amplify visual processing from the earliest level of visual cortex (Bayer et al., 2017). In this study, the location of a target was cued by a 100% predictive directional cue that also acted as an incentive cue, informing the participant whether a reward would be available on that trial. They found that in response to the search array the amplitude of the C1 increased when the cue predicted a reward versus no-reward (Bayer et al., 2017). In this experiment, incentive cues rather than the reward on the prior trial biased spatial attentional selection. However, in Hickey et al. (2010a), a similar mechanism

may underlie the object-based attentional selection of previously rewarded targets. Similar to this account, some researchers have suggested that rather than rewards directly biasing perception in a bottom-up manner, instead rewards amplify the representational strength of reward associated stimuli via a reward-specific mechanism that competes with bottom-up attentional capture and top-down attentional control in the formation of the attentional priority map (Awh et al., 2012; Chelazzi et al., 2014; Failing & Theeuwes, 2017). However, the mechanism underlying the perceptual competition is currently poorly specified. Such accounts can be collectively referred to as *Selection History accounts*.

Selection History Account

Selection History has been proposed to be the mechanism underlying super-distraction (Awh et al., 2012; Failing & Theeuwes, 2017, see Figure 1.2). In particular, stimuli that have previously resulted in the receipt of a reward following attentional deployment are likely to drive future attentional selection. Selection History as a concept has its basis in Thorndike's (1898) 'law of effect', which states that actions resulting in a satisfying outcome are likely to be repeated if the situation repeats. In particular, Selection History states that stimuli that previously resulted in a reward following attentional deployment have a lingering bias that alters attentional priority maps when the stimuli are re-encountered (Failing & Theeuwes, 2017). The novelty in the notion of the Selection History account as applied to visual selective attention is its emphasis on those situations when attentional deployment is inconsistent with top-down goals, but cannot be explained by physical salience, yet the stimulus has selection history (Awh et al., 2012; Failing & Theeuwes, 2017; Kadel, Feldmann-Wüstefeld, & Schubö, 2017). In the previous demonstration of super-distraction effects by

Hickey et al. (2010a), selection history was shown to modulate performance on a trial-by-trial basis. In this example, selection history is apparently a weak bias and easily reset when contingencies change moment-to-moment. However, when training of stimulus-reward contingencies is consistently repeated across many, many trials, the impact of rewarded selection history has been shown days and even months after reward learning (Anderson et al., 2011; Anderson & Yantis, 2013; MacLean & Giesbrecht, 2015), suggesting that value-based selection history can exert a robust attentional bias.

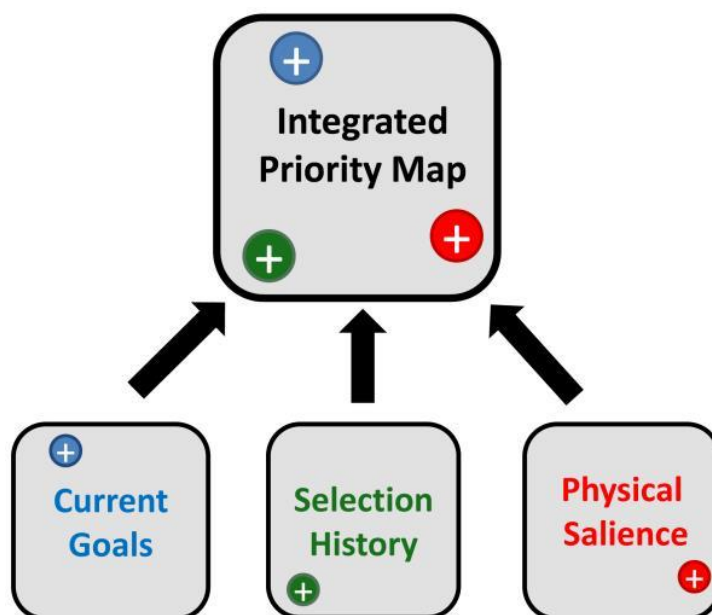


Figure 1.2. Representation of the Selection History account of attentional bias. Taken from Awh et al. (2012).

Super-distraction, though, is not ubiquitously observed. A manipulation as simple as changing the screen background between training and test is sufficient to eliminate VDAC (Anderson, 2015b). This is despite the top-down goal, the reward history, and the physical salience of the reward-associated distractor remaining constant. In this study, the initial training, the layout and meaning of all stimuli, and the task were identical between training and test and the background change was fully irrelevant to the test task. VDAC is also

eliminated when the task-relevance of shape and colour are reversed relative to the typical VDAC paradigm, i.e., shape predicts reward in the training task and in the subsequent test procedure search is for a unique colour, but a previously rewarding shape is present as a distractor on a proportion of trials (Wang et al., 2013). In these studies, despite the selection history for the value associated distractor remaining unchanged between conditions there was no evidence of VDAC. These findings raise doubts about the Selection History account of super-distraction being sufficient.

There are three main lines of evidence against the reward Selection History theory. The first relates to a key tenet of the account that a rewarded behaviour is likely to be repeated when the stimulus is re-encountered in similar circumstances. Yet, evidence does not support this. For example, Sali, Anderson, & Yantis (2014) again used the same task as Anderson et al. (2011), but this time training used only one target, repeated on every trial. Correct responses to the sole target were rewarded with a high reward on 75% of trials and a low reward on remaining trials. Selection during training, therefore, is completely unambiguous; on every trial the participant searched for the same target and was rewarded for being correct. Surprisingly, in the subsequent test task, no VDAC was observed. Therefore, despite the target during training fulfilling all the criteria for Selection History, it did not modulate attentional deployment during test. One potential explanation is that during training participants attributed the reward receipt to correct performance rather than associating it with the stimulus. In this view, the distractor has no motivational salience during the test task. Nevertheless, this finding is difficult to reconcile with the notion of Selection History as a mechanism sufficient for super-distraction.

The second line of evidence relates to the influence of low-value associated distractors in attentional control. A conventional approach to investigating super-distraction in attentional control is to initially condition one stimulus to a high reward and another to a low reward (or no reward). These stimuli are then both tested either in isolation or simultaneously in the subsequent test task. When both previously rewarded stimuli appear in the same trial the stimulus associated with the larger reward should gain greater priority and thus bias competition, as is often the case (Bucker, Silvis, Donk, & Theeuwes, 2015; Failing & Theeuwes, 2014). In other trial types when there is no direct competition between previously rewarded stimuli, the bias arising from selection history should favour any previously rewarded stimulus, but the bias should be stronger for the most highly rewarded stimulus (Anderson, 2016). However, evidence for this is lacking. In many studies, the low reward-associated stimulus does not capture attention compared to a neutral stimulus, even when the neutral stimulus has no selection history (Anderson, Kuwabara, et al., 2016; Anderson et al., 2013; Anderson & Halpern, 2017; Anderson et al., 2011). This is also at odds with notions of rewarded selection history being sufficient for attentional control.

The third set of experiments to question the rewarded Selection History account involves participants with subclinical depression. Typical VDAC has been found to be eliminated in participants with subclinical depression compared to controls (Anderson, Leal, Hall, Yassa, & Yantis, 2014). Similarly, in a variation of the VDAC task, where the target could also be reward-associated, controls showed worse performance when the reward-associated stimulus was the distractor compared to when it was the target. This effect was eliminated in participants with subclinical depression (Anderson, Chiu, DiBartolo, & Leal, 2017). Importantly, however, selection history, in the absence of rewards, was shown to bias

attentional capture in participants with subclinical depression. In particular, over a period of 4-days participants searched for a green target, establishing a strong selection history for this stimulus. In the subsequent test task, participants with subclinical depression showed comparable performance decrements as controls when the distractor compared to the target was in the previously selected colour (Anderson et al., 2017). Therefore, the authors suggest that super-distraction and selection history rely on independent mechanisms as only super-distraction is affected by depression (Anderson et al., 2017).

Habitual Control Account

Consistent with this latter evidence, a somewhat related account of super-distraction postulates that selection history alone is not sufficient to bias attentional control (Anderson et al., 2017). Instead, during learning, it has been suggested that stimuli predicting reward garner a habitual attentional orienting response that reactivates whenever the stimuli are subsequently encountered (Anderson, 2016; Anderson et al., 2016). Instead of altering attentional priority maps, this account suggests that stimulus-response biases underscore super-distraction.

Similar, to the development of reward-driven effects on attentional control in training-test procedures, habitual control is thought to be established when actions are repeated in the pursuit of the same goal, in the same context until an automatic stimulus-response association is formed (Graybiel, 2008; Wood & Runger, 2016). Once habits are formed they are typically instantiated automatically as the default action based on the stimulus-response association, although there is some debate about the interaction between habit-based control and goal-directed control when the two are in conflict (Aarts & Dijksterhuis, 2000; Balleine &

O'Doherty, 2010; Wood & Neal, 2007). In particular, in healthy participants habits are generally the default mode unless they conflict with goal pursuit in which case more deliberate control is utilized (although see Wood & Runger, 2016 for exceptions). This is an issue when describing super-distraction in terms of a habitual response for two reasons. First, VDAC does not appear to be automatic. Rather than automatically biasing attention super-distraction appears to be subject to many factors discussed in the critique of Selection History accounts of super-distraction (e.g., Anderson et al., 2015; Sali et al., 2014; Wang et al., 2013). Second, animal research has shown that habits continue despite reward devaluation (Graybiel, 2008), whereas VDAC has been shown to be subject to extinction (Anderson et al., 2016; Roper et al., 2014), although by no means all experiments show this influence of devaluation on super-distraction. Prioritizing processing of stimuli based on associated reward as a habitual response offers a more mechanistic explanation than the Selection History account, yet it also is not sufficient. There are some outstanding issues about the extent to which super-distraction can be described as a habitual account as it does not account for the instances where super-distraction is not found.

One aspect of the habitual-based account of super-distraction that may be a fruitful avenue for future accounts of super-distraction is the emphasis on reward-associations modulating cognitive control mechanisms in favour of reward-associated stimuli rather than by modulating attentional priority maps. As discussed above the topography of attentional priority maps is modulated by both bottom-up and top-down factors (Desimone & Duncan, 1995). Cognitive control is closely aligned to the idea of top-down control. In essence, cognitive control determines the settings for top-down control in line with internal goals, but its reach extends beyond the role of adjusting attentional priority maps. Additionally,

cognitive control mechanisms activate entire neural networks related to goals, including those that code relevant stimulus-response contingencies, i.e. predicted outcomes for different behavioural options. Such predictions may be used to bias attentional priority maps, choose and plan motoric responses (e.g., press right for an orange target), and alter expectations (Buschman & Kastner, 2015). Thus, cognitive control settings are heavily reliant on previous experience. Notions of super-distraction as a habitual response are consistent with rewards acting at the level of cognitive control, and this mechanism then generating the “attend to me” signal for reward-associated stimuli. This is compared to accounts such as Selection History that imply a direct role of reward on attentional processes, independent of modulations in top-down, cognitive control. A higher-level bias, involving cognitive control, in reward processing is supported by the plenitude of results showing reward driven effects on many areas of cognition, including working memory, decision making, response inhibition, task switching, and attentional selection (Braver et al., 2014). Placing the impact of rewards in the context of cognitive control also aligns with the known neurophysiology of both rewards and cognitive control.

The Role of Dopamine

Both reward processing and cognitive control are heavily dependent on dopamine (DA) mediated pathways in subcortical and prefrontal structures (Braver et al., 2014; Cools, 2008). In respect to rewards, positron emission tomography (PET) has been used to demonstrate individual differences in the magnitude of super-distraction effects; VDAC is strongly predicted by increased endogenous DA release in the right anterior caudate during the reward learning training phase (Anderson, Kuwabara, et al., 2017). Likewise, during the

test phase on reward-associated distractor present trials elevated DA release in the right anterior and posterior caudate, and the right posterior putamen also predicted increased VDAC (Anderson, Kuwabara, et al., 2016). Interestingly, the latter study also found evidence that the ability to ignore reward-associated stimuli was associated with the suppression of DA release in the same striatal regions (Anderson, Kuwabara, et al., 2016). Similarly, studies where reward is predicted by an incentive cue show that rewarding events generate phasic DA activity in the substantia nigra and the ventral tegmental area (Schultz, 2000), both of which are heavily connected and supply DA to the striatum through the mesolimbic and nigrostriatal pathways. Consistent with Anderson, Kuwabara, et al. (2016) the omission of expected rewards also depresses DA neurons in these regions in primates (Schultz, 2000). Phasic DA release following rewards and DA depression following reward omission has been linked to prediction error signalling, which is considered to be a teaching signals for learning (Schultz, 2000; Schultz, Dayan, & Montague, 1997). Importantly, in animal studies it has also been shown that over time DA activity related to reward receipt becomes linked to the cue that predicts the reward such that DA activity is elicited by the cue, an effect known as autoshaping (Flagel, Watson, Robinson, & Akil, 2007; Ljungberg, Apicella, & Schultz, 1992) or the establishment of cue incentive salience (Robinson & Berridge, 1993). Such incentive salience likely represents the neural basis of super-distraction following extinction, with the cues themselves becoming 'liked' (Berridge, 2007; DiFeliceantonio & Berridge, 2012; Volkow, Wang, Fowler, Tomasi, & Telang, 2011). Interestingly, in rats there are often large individual differences as to whether DA activity is initiated by the cues. In other rats, DA release continues to activate solely on receipt of the reward (e.g., Flagel et al., 2007). Similar individual

difference in humans may underlie the positive correlation observed between DA release during learning and subsequent VDAC (Anderson, Kuwabara, et al., 2017).

fMRI evidence similarly points to a role of DA rich subcortical structures in reward responsiveness. Again, using the VDAC paradigm, BOLD activity in the striatum has been observed to be greater on reward distractor present trials compared to reward distractor absent trials during the test phase (Anderson, Laurent, & Yantis, 2014). In a second experiment where reward was omitted during the training phase no differences were found in striatal activity between the previously selected and unselected distractors, suggesting that the elevated striatal activity was specifically reward driven (Anderson, Laurent, et al., 2014). Both these fMRI data in humans and the animal research above point to a link between enhanced striatal activity and the motivation to engage with or processing of reward predicting stimuli.

Indeed, even in complex naturalistic scenes, such as pictures of busy roads, the presence of a reward-associated distractor category (e.g., cars) in the scene elicits activation in the DA midbrain (Hickey & Peelen, 2015). However, in this study increased midbrain activity was associated with suppression of reward-associated distractor information, as measured using multivoxel pattern analysis in the visual cortex (Hickey & Peelen, 2015). Given the poor temporal resolution of fMRI, the time course of the effect is unclear. One possibility is that the midbrain sensitivity was related to the processing of the reward-associated stimulus before top-down factors initiated the suppression. This would be consistent with ERP evidence showing that when VDAC is reduced behaviourally, a Pd signal to high value associated distractors can be observed, whereas large VDAC effects are associated with a N2pc to the same distractors (Qi et al., 2013). These data demonstrate the potentially suppressive nature of top-down control on the motivation to process reward-associated stimuli.

Neuroanatomy of Reward Processing

Hickey & Peelen (2015) not only showed a strong link between midbrain sensitivity and the strength of visual representations in the visual cortex for rewarding stimuli, they also demonstrated that a wider network involving the orbitofrontal cortex (OFC), dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC), and parietal lobe also predict the reward modulated strength of the information in the visual cortex. The OFC is thought to be critically involved in predicting the probability and relative magnitude of different outcome values as well as coding the experienced outcome (Li, Vanni-Mercier, Isnard, Mauguière, & Dreher, 2016; Tremblay & Schultz, 1999). For example, in monkeys, neural responses in the OFC were found to be sensitive to the reward history of two conditioned stimuli, both associated with liquid rewards. OFC neurons were found to track the relative reward magnitude of the two conditioned stimuli (Saez, Saez, Paton, Lau, & Salzman, 2017). Specifically, when the amount of liquid reward conditioned to a stimulus remained constant, OFC activity in response to the stimulus altered depending on whether a second stimulus was conditioned with a lesser or greater reward. The authors suggest that this tracking of relative reward magnitude in the OFC reflects the motivational significance associated with the stimulus (Saez et al., 2017). The DLPFC, likewise, is involved in predicting reward outcomes from different actions (Marcos, Nougaret, Tsujimoto, & Genovesio, 2018). Monkey studies have also found the DLPFC to be sensitive to the magnitude of rewards with increased neuronal activity in response to larger rewards (Leon & Shadlen, 1999). ERP evidence in humans has also shown that the medial frontal negativity (MFN), which corresponds to ACC activity, is responsive to the magnitude of rewards and this responsiveness predicts behavioural adaptations to previously rewarding distractors (Hickey et al., 2010a). The MFN

was originally proposed to be an index of the motivational impact of outcomes (Gehring & Willoughby, 2002) and this corresponds well with Hickey et al. (2010a). All the aforementioned areas have strong reciprocal connections with the striatum and can be considered as part of a wider reward processing network involved in motivated cognition as these areas are also conventionally considered in the context of cognitive control even in the absence of explicit rewards.

The Role of the Anterior Cingulate Cortex

In particular, the ACC and DLPFC are strongly linked to adaptation in cognitive control, although they serve dissociable functions. The ACC has been associated with the monitoring of inputs and performance, whereas the DLPFC is likely involved in the implementation of a control strategy (Bush, Luu, & Posner, 2000; MacDonald III, Cohen, Stenger, & Carter, 2000). As more research is conducted into ACC functioning its role has become broader. Initially, findings that the ACC was more responsive to novel word presentations than practiced words on a verbal response task suggested that its main role may be in orchestrating effortful rather than automatic responses (Raichle et al., 1994). Other early theories of the ACC highlighted its role in error monitoring (Carter et al., 1998). The evidence supporting the ACC in error detection is strong and much of the support for this idea comes from the error related negativity (ERN, also known as the error negativity). The ERN is a negative deflection of the ERP that occurs following an error. Its neural generator is most likely in the ACC (Dehaene, Posner, & Tucker, 1994; Falkenstein, Hohnsbein, Hoormann, & Blanke, 2000; Gehring, Goss, Coles, Meyer, & Donchin, 1993). Likewise, on correct trials the correct response negativity (CRN) has also been found. The CRN is thought to have similar properties to the ERN, and also

has its neural generator in the ACC (Hajcak, Moser, Yeung, & Simons, 2005). One possibility to align CRN findings with the theory that the ACC monitors errors was to suggest that CRN and ERN activity represented instances where errors were likely, such as during response competition (Brown & Braver, 2005; Carter et al., 1998). Indeed, such evidence inspired one of the most influential accounts of ACC function, i.e., conflict monitoring theory (Botvinick, Braver, Barch, Carter, & Cohen, 2001). It proposes that the ACC is engaged in monitoring for conflicts in information processing. Here, conflict refers to response competition; when stimuli activate multiple potential responses, information processing must select the most appropriate response. When conflict arises, the ACC gauges the need for strengthened cognitive control biases to overcome it (Botvinick et al., 2001). Indeed, the conflict monitoring hypothesis accounts well for the ERN, as errors and conflicts are likely to coexist (Carter et al., 1998). In addition, the frontal N2 component of the ERP, which like the ERN is thought to be generated by the ACC, has consistently been shown during pre-response conflict in tasks such as the flanker task (van Veen & Carter, 2002; Yeung, Botvinick, & Cohen, 2004).

The Flanker Task, Conflict Adaptation, and the ACC

In the flanker task a central target is flanked by two identical distractors, one either side of the distractor. Importantly, the distractors (flankers) can either represent the same (congruent) response as the central target or the alternative (incongruent) response. Incongruent flankers slow RT compared to congruent flankers, an effect known as the flanker effect (Eriksen & Eriksen, 1974, see Figure 1.3 for an example flanker trial). The slowing on incongruent trials reflects the need to overcome the conflict that arises from activation of two competing responses, one from the flanker and the other from the target (Eriksen, 1995).

Consistent with this interpretation, the influence of the flankers is maximal when flankers precede the target by around 100 ms (Flowers & Wilcox, 1982; Mattler, 2003), demonstrating that flankers have greatest impact when their response is activated prior to target processing. Furthermore, the frontal N2 is considerably larger on incongruent than congruent trials (Folstein & Van Petten, 2008), supporting a role of response conflict on incongruent trials.

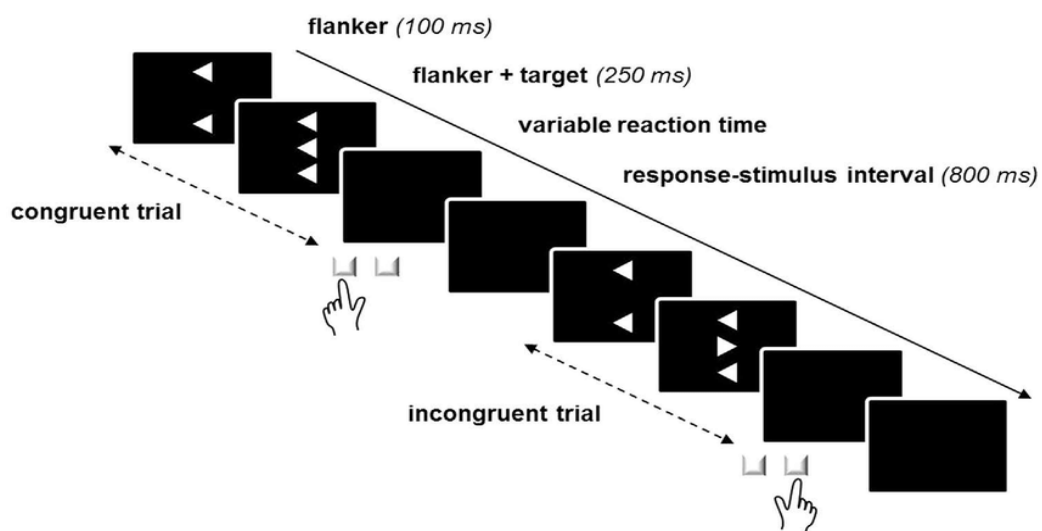


Figure 1.3. Example trial sequence from an arrow flanker task. Participants must respond to the direction of the central arrow. The example sequence is of a congruent followed by an incongruent trial. Adapted from Seer et al. (2017).

In addition to being a useful measure of response competition the flanker task is also a paradigm suited to investigating fluctuations in cognitive control through the analyses of sequential trial effects. The interference from incongruent flankers is reduced and RT are faster when such trials are preceded by an incongruent compared to a congruent trial. Likewise, the benefit from congruent flankers is also reduced and RT are slower when congruent trials are preceded by an incongruent rather than a congruent trial. The reduced flanker effect after incongruent versus congruent trials is known as the conflict adaptation (CA) effect (Gratton, Coles, & Donchin, 1992, see Figure 1.4). Together, these two modulations of the flanker effect that make up the CA effect suggest that conflict signals induce

strengthened cognitive control to overcome similar, future conflict. The strengthened cognitive control is thought to overcome conflict by boosting the representational strength of the target, and relatively reducing the strength of flanker representations (Egner & Hirsch, 2005). This effectively benefits performance on a further incongruent trial but is to the detriment of performance on a subsequent congruent trial (although see, Mayr, Awh, & Laurey, 2003). Importantly, such conflict adaptation effects have also been demonstrated in other tasks involving conflict arising from response competition, such as the Simon (Stürmer, Soetens, Leuthold, Schröter, & Sommer, 2002) and Stroop (Kerns et al., 2004) tasks.

In the Simon task, the participant must respond using the directional keys on the keyboard as to the colour of the target (e.g., press 'up' when the target is orange). Importantly, the target can either be presented above or below fixation. Therefore, participants must inhibit the prepotent response activated by the location of the target to respond to the target colour. When the target response and its location are congruent, RT are faster than when the target response and its location are incongruent, an effect known as the Simon effect. Consistent with the conflict adaptation effect in the flanker task, the Simon effect is also reduced following incongruent trials versus congruent trials (Stürmer et al., 2002). Therefore, the behavioural evidence from a variety of tasks involving response competition support the notion that conflict elicits modulations in the allocation of cognitive control.

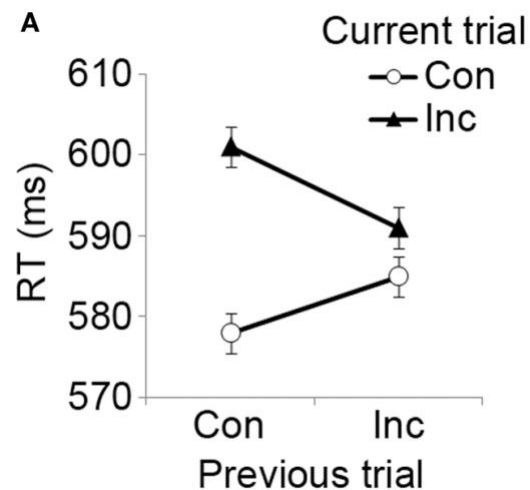


Figure 1.4. Classic conflict adaptation result. The congruency effect (incongruent - congruent) is larger following a congruent compared to an incongruent trial. Taken from Egner, Ely, & Grinband (2010).

The N2 amplitude following congruent and incongruent trials in the flanker task has also been found to correspond with this interpretation of the conflict adaptation effect. The N2 is larger to incongruent flankers after a congruent compared to after an incongruent trial (Clayson & Larson, 2011). The reduced N2 following incongruent trials supports the view that the behavioural CA effect is likely to, at least in part, be the result of conflict-driven enhancements of task-relevant cognitive control signalled via the ACC. fMRI evidence further supports this notion, showing increased BOLD activity in the ACC on incongruent trials following congruent compared to incongruent trials (Kerns, 2006; Kerns et al., 2004). Furthermore, lesions to the cingulate cortex produce a diminished CA effect (Sheth et al., 2013). Together these studies point to a clear role of the ACC in detecting conflict, as ACC activity was increased to conflict signals when the current strength of cognitive control was not sufficient to reduce response competition.

The role of the ACC, however, is not restricted to monitoring conflict. It has also been implicated in emotional and motivational processing (Bush et al., 2000). Botvinick (2007)

proposed that ACC monitors aversive signals, with conflict merely being an example of an aversive event (Dreisbach & Fischer, 2012). This idea reconciles conflict monitoring theory with other accounts of ACC function that assign it a role in monitoring the outcomes of strategic decisions and guiding future decision making (Botvinick, 2007; Bush et al., 2002). This notion is supported by studies of conflict adaptation, measured using the lateralized readiness potential (LRP) in the Simon task. In this task, an early LRP is found when the previous trial is congruent, showing a readiness to respond to the location of the stimulus, but the LRP is reduced when the prior trial is incongruent, demonstrating increased control over responses (Fröber, Stürmer, Frömer, & Dreisbach, 2017). Interestingly, the same LRP effect has been shown to scale with self-reported unpleasantness on the previous trial. When the previous trial is reported as unpleasant, no early LRP is evident on the subsequent trial, but early LRPs are evident following pleasant trials. Unfortunately, it is not clear what the participants were indicating as being unpleasant about the trial. Previous research has shown that face stimuli associated with inhibitory responses are rated as lower in trustworthiness than stimuli not associated with inhibition (Kiss, Raymond, Westoby, Nobre, & Eimer, 2008). Consistent with this finding, Fröber et al. (2017) found incongruent trials, which require inhibition, to be more likely to be assigned a more unpleasant rating than congruent trials. Therefore, the congruency on the prior trial was probably an important determinant of the Fröber et al. (2017) findings. Another possibility is that participants were responding to the success of the cognitive strategy on the prior trial, which could either be to utilize or ignore target location information. The chosen strategy would likely be informed by the congruency of the prior trial (e.g., the conflict adaptation effect). The self-reported pleasantness could be viewed as an index of intrinsic feedback (positive affect) for the previous strategic choice, thus motivating

future strategic decisions. In support of this view, behavioural conflict adaptation is known to be reduced when trials are followed by monetary gain, again demonstrating that strategies that result in a payoff appear to be repeated (e.g., Thorndike, 1898), despite the cognitive costs (i.e., conflict) experienced (van Steenbergen, Band, & Hommel, 2009). Further evidence consistent with this notion has shown that ACC activity is also enhanced during positive feedback for actions under volitional control and this activity guides future choices depending on the value of the action (Walton, Devlin, & Rushworth, 2004). These data demonstrate that modulations of cognitive control in response to recent events are dependent on emotional/motivational drivers that estimate the cognitive costs and benefits of strategic choices rather than conflict, *per se*, and that these modulations may be mediated by activity in the ACC.

Cognitive costs, though, are not the only drivers determining the biases instigated by cognitive control. Benefits or anticipated rewards probably also play an important role. As demonstrated earlier, DA is critically involved in driving incentivized cognition. DA is also abundant in the ACC, which is a target for projections from the midbrain (Schweimer & Hauber, 2006). Consistent with this, ACC activity is reactive to the receipt of rewards and also to expected rewards, especially when the rewards are perceived to be contingent on behavioural choices (Amiez, Joseph, & Procyk, 2006; Walton et al., 2004). In rats, lesions that disconnect neural communication between the ACC and the nucleus accumbens disrupts autoshaping, as do bilateral lesions to the ACC, demonstrating the importance of ACC-striatal connectivity in stimulus-reward learning and incentive salience (Parkinson, Willoughby, Robbins, & Everitt, 2000). Similarly, human neuroimaging supports a role for the ACC in predicting reward magnitude (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005), and in

particular the pooling of reward information across different possible decisions by coding reward prediction errors (Wallis & Kennerley, 2011). Accordingly, it has been proposed that this DA system, incorporating striatal projections to the ACC, is responsible for motivating the selection of a cognitive action plan to pursue goals by coding the predicted rewards and incentive salience of multiple options (Holroyd & Yeung, 2012). The ACC's role in the system is the "gate-keeper" that computes expected reward and costs associated with different response options and promotes the optimal choice (Rushworth & Behrens, 2008; Rushworth, Walton, Kennerley, & Bannerman, 2004; Shenhav, Botvinick, & Cohen, 2013). In my dissertation I take this idea and apply it to the cognitive operations that are potentially executed in response to visual stimuli, and how value-associations may bias the selection of a cognitive operation.

Expected Value of Control Hypothesis

Recently, these ideas have been formalized by Shenhav and colleagues into a model called the Expected Value of Control (EVC, Kool, Shenhav, & Botvinick, 2017; Shenhav et al., 2013, 2017; Shenhav, Straccia, Cohen, & Botvinick, 2014; Trapp, Shenhav, Bitzer, & Bar, 2014). Key to the theory is that the dorsal ACC (dACC) manages whether cognitive control is to be exerted, determines the strength of that control, and selects the cognitive strategy to be used for engagement with information (Shenhav et al., 2013). The theory suggests that these decisions are primarily determined by two factors, 1) the expected payoff, and 2) the cost of exerting control or not (Kool et al., 2017). The expected payoff in its simplest form can be considered as the expected value, either intrinsic (e.g., related to task performance) or extrinsic (e.g., monetary reward), of engaging in any given action. The costs of engaging

control largely relate to the mental effort required to implement and sustain the control. Determining factors in the calculation of costs include the cognitive, motoric, and metabolic expense required, all of which hinge on the supposition of limited resources (Shenhav et al., 2017). For example, working memory is a cognitive resource required to sustain a strategy of control, and the limitations in the capacity of working memory are well known (Luck & Vogel, 1997). Thus, it is cognitively costly to unnecessarily utilize these limited resources. In addition to these costs of utilizing control, costs can also be incurred by not implementing control. The prevailing cost of not biasing control is cross talk in information processing. Response conflict is the result of cross talk, i.e., when two streams of information require similar neural resources to process they interact impairing accurate processing of one or both streams of information (Bergen, Medeiros-Ward, Wheeler, Drews, & Strayer, 2013).

I return to the flanker task to consider these ideas. In the flanker task there are two appropriate cognitive strategies, 1) attend to flankers and target, and 2) attend to the target and ignore distractors. However, the cost of each strategy is dependent on the congruency of the trial. The latter strategy is costly not only in terms of the increase in demands required to sustain control, but also in relation to the opportunity costs on congruent trials (Kurzban, Duckworth, Kable, & Myers, 2014; Shenhav et al., 2017). Specifically, placing less emphasis on flanker processing means that potentially beneficial information is being lost from congruent flankers. The former strategy, on the other hand, is most costly on incongruent trials where cross talk occurs as a result of the simultaneous processing of flankers and target. The resultant response conflict is not only cognitively costly to resolve, but also motivationally costly because of its potentially aversive nature (Botvinick, 2007). Consistent with the notions of the EVC theory, different cost profiles should be associated with each strategy depending

on the congruency of the previous trial. This explains the need for shifts in the strategic allocation of control depending on the congruency of the prior trial.

Motivational Competition

Here, I propose an account of super-distraction that incorporates the ideas of the EVC hypothesis. Key to the theory is that high-level cognition and behaviour are regulated by an unconscious competition among complex representations of discrete motivational states. In this motivation-competition view, motivational states can be automatically instantiated by sensory cues (or external objects) that signal upcoming opportunities to achieve goals. They can, of course, also be provoked by internally generated, ‘top-down’ signals. Importantly and in contrast to perceptual priority frameworks, goals, not sensory cues, are at the heart of each representation, enabling a single cue to instantiate multiple, and potentially competing motivational states. The representation of each motivational state specifies a motivational *direction* and *intensity*. Motivational direction refers to the cognitive operations or behavioural actions associated with achieving that goal (Eder, Rothermund, De Houwer, & Hommel, 2015; Greenwald, 1970; Hommel, Müsseler, Aschersleben, & Prinz, 2001). Intensity refers to the strength of each state relative to the strength of all other concurrently active motivational states. As in the EVC model, *intensity* depends on a trade-off between predicted goal value and the predicted cognitive, motoric, and metabolic cost of achieving the goal. This dependence on prediction means that intensity is determined by both relevant prior experience and the current context (Botvinick & Braver, 2015; Dijksterhuis & Aarts, 2010; Inzlicht, Schmeichel, & Macrae, 2014; Muraven & Baumeister, 2000; Shadmehr, Huang, & Ahmed, 2016; Westbrook & Braver, 2015). These ideas are somewhat similar to

computational notions of 'state representations' used in formal reinforcement learning theories (Wilson, Takahashi, Schoenbaum, & Niv, 2014). In this motivational competition framework, motivations actively and dynamically compete for access to the high-level cognitive machinery needed to control behaviour. This competition ensures that only the most intense motivation wins control (Shenhav et al., 2013), reducing the costly periods of indecision.

A key line of research supporting this motivational competition notion of visual processing priority (i.e., motivated cognition) comes from studies of effortful behaviour. Perhaps unsurprisingly, both animal and human research shows that subjects are more willing to exert cognitive effort when the personal predicted payoff (reward) is larger. Although unsurprising, this concept forms the backbone of the EVC hypothesis. For example, rats in a T-maze where they can choose to work for a high reward by climbing a barrier or receive a low reward without scaling a barrier prefer the high reward option. However, the same rats after intra-ACC infusion of a D1 receptor antagonist show a preference for the low reward option (Schweimer & Hauber, 2006). Similarly, rats with a temporarily deactivated ACC show reduced willingness to exert cognitive effort for a high reward on a visuospatial attention task, instead preferring the low reward but easier version of the task compared to when the ACC is functioning typically (Hosking, Cocker, & Winstanley, 2014). In addition, when rats reach satiation they no longer prefer the high reward/high effort choice, instead preferring to receive less sucrose for the less demanding cognitive task as the ultimate value of the reward diminishes (Cocker, Hosking, Benoit, & Winstanley, 2012), demonstrating that the computation of cost-benefit is sensitive to internal states. Humans are also more likely to choose more demanding cognitive tasks, such as more a demanding working memory task,

when incentives for doing so increase (Kool, McGuire, Rosen, & Botvinick, 2010; Kool et al., 2017; Westbrook, Kester, & Braver, 2013). In addition, humans are also more likely to increase effortful attentional preparation when incentives for success on an upcoming visual search task are high versus low (Sawaki, Luck, & Raymond, 2015). Furthermore, as with rats and consistent with the literature discussed earlier demonstrating both reward and cost sensitivity in the dACC, human research into effortful behaviour has also shown the dACC to be ideally suited for the final cost-benefit computation that forms the basis of the competition between motivational states. Accordingly, the dACC is responsive to the net value of decision options (Croxson, Walton, O'Reilly, Behrens, & Rushworth, 2009; Shenhav et al., 2013). Moreover, the motivational competition model is not only consistent with the behavioural and neuroimaging data it is also biologically plausible, given the theorized roles and known projections between the striatum, dACC, insular, DLPFC, and OFC amongst other regions.

Implicit in the motivational competition hypothesis, as in classic theories of top-down control, is the necessity to incorporate prior experience and learning into the mechanism determining the allocation of control. Motivational intensity can be determined by immediately prior information, such as during CA, and also more long-term conditioning, as is the case in VDAC where stimulus-reward associations are conditioned over many trials both just prior to or even weeks before subsequently re-encountering the same stimuli (Anderson et al., 2011; Anderson & Yantis, 2013). In both CA and VDAC the motivational direction being considered (i.e., to reduce flanker processing after an incongruent trial, or to attend to value-associated distractors) is elicited based on the previous encounters with the stimuli, whether it be an immediately preceding encounter or one requiring long-term memory. The motivational intensity of both strategies is also reflected in these previous encounters. In the

context of VDAC, during learning every encounter with the high-value colour reinforces both the large expected payoff of attending to that colour and the opportunity costs of not immediately attending to the high reward colour (i.e., missing the reward). This strategy is again elicited in the subsequent test-task when the high value colour is perceived, slowing RT. As with rats that gradually reduce the estimates of expected payoff of sucrose rewards as they become satiated (Cocker et al., 2012), human participants gradually devalue the perceived benefits of attending to the high reward colour as they learn that the reward is no longer forthcoming, leading to extinction of VDAC (Anderson, Kuwabara, et al., 2016; Roper et al., 2014). The model is also highly sensitive to the magnitude of rewards, given the importance of the expected payoff, and therefore accounts for the lack of attentional capture from low value-associated stimuli where the motivational intensity of this state is reduced compared to high value-associated stimuli. Moreover, although not large there is also a cost of attending to the colour in the VDAC test task in terms of the slowing of target processing. This adds to the rate of extinction and counteracts the expected payoff of attending to low value colours. A prediction that can be made from this motivation-based model of VDAC is that increases in the cost of colour processing in the test task, for example by increasing cross-talk from colour processing, would reduce VDAC. This prediction is tested in Chapter 4.

Importantly, currently active cognitive control mechanisms influence the motivational competition by modulating predicted costs and benefits of achieving specific goals, thus controlling motivational intensity. Mechanisms that inflate a predicted cost or devalue a predicted benefit reduce motivational intensity, whereas mechanisms that underestimate a predicted cost or inflate a predicted benefit enhance motivational intensity.

Consistent with this notion, individual difference studies show that the strength of current cognitive control can have a suppressive influence on states that have heightened predicted payoffs. Specifically, individuals who have a higher working memory capacity are less susceptible to VDAC (Anderson et al., 2011). Working memory is often associated with improved executive function and the ability to sustain proactive task relevant processing (Engle, 2002). One possibility is that individuals with high working memory capacity are more capable of modulating the intensity of exogenously activated motivational states (those instantiated by sensory cues) consistent with task-relevant goals. In VDAC this would suggest that high working memory capacity individuals effectively dampen the motivational intensity of colour processing in the test task in a proactive fashion because of a strong motivation to process shape. Consistent with this notion, individuals scoring highly on the BAS_{Drive} subscale of the Behavioral Inhibition System/Behavioral Activation System Scale (Carver & White, 1994), thought to index the ability to maintain task-relevant motivations, show reduced reward priming (Hickey et al., 2010b). Furthermore, individuals who demonstrate increased ability to remain focused on goal-directed behaviours, in this case measured by increased mindfulness, also show reduced VDAC (Levinson, Stoll, Kindy, Merry, & Davidson, 2014). Analogously, impulsivity, the inability to maintain current motivations, is associated with increased VDAC (Anderson, Kronemer, Rilee, Sacktor, & Marvel, 2016). Again, the neural basis of this suppressive influence on the motivational intensity of exogenous states also been demonstrated. Specifically, the DLPFC has long been considered crucial not just for the maintenance and updating of working memory, but also in coding top-down task relevant behaviours in response to behavioural goals (Braver, Paxton, Locke, & Barch, 2009; Curtis & D'Esposito, 2003; MacDonald III et al., 2000). Recent evidence has linked the strength of

connectivity between the DLPFC and striatal regions, such as the caudate, in the expected value of incentive stimuli. When smokers are presented with smoking related cues, weaker connectivity between the DLPFC and the caudate predicted increased cravings and increased cue responsivity in the caudate (Yuan et al., 2017), demonstrating the potentially suppressive interactions between goal-directed control in the DLPFC and incentive salience in the caudate.

Proactive and Reactive Control in Motivational Competition

A distinction between exogenous and goal-directed motivations accords well with other theories of how control is instigated. Recently, control dynamics have been dichotomized into two distinct types, proactive and reactive control (Braver, Gray, & Burgess, 2007; Braver, 2012). Although the distinction between the two types of control is often blurred, proactive control is characterized by preparatory control over attention to minimize, for example, predicted conflict in accordance with behavioural goals, whereas reactive control generally refers to attentional control implemented post-stimulus processing. CA could be classified as both reactive and proactive. The strategy to either process or ignore flankers is initiated reactively based on the congruency of the prior trial, but this strategy is then used proactively on the subsequent trial. However, typically CA is regarded as a reactive phenomenon (Funes, Lupiáñez, & Humphreys, 2010a, 2010b). Regardless, as discussed above the distinction may also be useful when considering competition in motivated cognition both between and within goal-directed (proactive) and exogenous (reactive) motivational states.

Exogenous motivational states such as those initiated by the value-associated stimulus in VDAC and other super-distraction effects can generally be considered as being reactive. The goal of attending to the reward associated stimulus is only instigated post-stimulus onset

because of the expected payoff developed through training, although some preparatory cues preparing the observer for the presence of reward associated stimuli are likely given the similarity between the training and test contexts (Anderson, 2015). In this view, VDAC is the result of the motivational competition between proactive task-relevant processing (i.e., attend shape) and the exogenous motivation associated with the value laden stimulus (i.e., attend colour). However, motivational competition is not restricted to proactive vs. reactive strategies. Instead, the competition can arise from two potentially reactive strategies, such as conflict adaptation and value-driven attentional capture. For example, in the flanker task, following an incongruent trial, the motivational intensity of the strategy to attend to the flankers is low because of the cognitive costs associated with the response conflict; thus, flankers are ignored. However, if the flankers were value-associated during a prior training task the cost of attending to the flankers would be negated by the increase in the predicted payoff. Thus, the expected value of attending to the flankers would be increased relative to the value of ignoring the flankers. This is in-keeping with a motivational competition account of cognitive control with the strategy that has the largest expected value effectively winning control in a winner-takes-all manner. These predictions are tested in Chapter 2.

Motivational Competition in Adolescents

In view of the proposed dependence on reactive mechanisms in the allocation of control to value-associated stimuli and indeed the reliance on estimating the predicted benefits associated with allocating control based on learned value-associations, adolescence is likely to be a fruitful developmental epoch for investigating these mechanisms. Adolescence is typically defined as the developmental period between the ages of 12-17 years (Spear,

2000) although in terms of neural development adolescence can be considered to continue into the mid-20s when brain development reaches maturity. A defining characteristic of adolescence in the developmental literature is that they are more likely to engage in risky behaviours. As a consequence, teenagers are at a greater risk of mortality and more susceptible to developing addictions (Dahl, 2004). This is underscored by an increase in impulsivity that is attributed to imbalances in neural maturation (Chambers, Taylor, & Potenza, 2003; Ernst, Pine, & Hardin, 2006; Somerville, Jones, & Casey, 2010; Steinberg, 2010). Neuroanatomical studies in adolescents have revealed that the synaptic density in reward processing regions (e.g., striatal regions) follows a quadratic trajectory, peaking at around 14 years of age. However, areas thought to be involved in more proactive control (e.g., DLPFC), including the density of connections from cortical to subcortical regions, develop linearly throughout adolescence only reaching full maturity in early adulthood at around 25 years of age (Giedd, 2004; Giedd et al., 1999; Gogtay & Giedd, 2004; Luna, Marek, Larsen, Tervo-Clemmens, & Chahal, 2015).

The observed imbalance in neural maturation has spawned many dual-systems models of adolescent risk-taking, concentrating on immature proactive control and hyper-sensitive reward processing (Ernst et al., 2006; Geier & Luna, 2009; Pfeifer & Allen, 2012; Somerville et al., 2010; Steinberg, 2010). Another perspective suggests that because proactive control is weak in adolescents, they become over-reliant on reactive control strategies. Even by 'late' adolescence, the contingent negative variation of the ERP, thought to index response preparation, is attenuated compared to adults in epochs prior to a response (Killikelly & Szűcs, 2013; Padilla, Pfefferbaum, Sullivan, Baker, & Colrain, 2014). However, the subsequent P3b activity, activated post-stimulus onset during the response execution epoch is increased

compared to in adults (Killikelly & Szűcs, 2011). Similarly, Andrews-Hanna et al. (2011) used a modified version of the Stroop task, where the ratio of incongruent (e.g., naming the ink colour of the word blue in red ink) to neutral trials (e.g., naming the ink colour of a non-colour word in red ink) was increased. Under such conditions, adults show increased DLPFC activity compared to conditions of equal incongruent and neutral trials because the task requires sustained proactive control to focus attention on the relevant features (Andrews-Hanna et al., 2011). However, adolescents (mean age = 15.6 years) do not show the same increases in DLPFC activity as adults under these conditions. Instead, adolescents show increased ACC activity compared to adults after conflict. This would be consistent with teenagers responding reactively to each instance of conflict rather than taking global condition statistics into account (Andrews-Hanna et al., 2011). In support of this conclusion, the experiment also found that lower DLPFC activity in adolescents predicted self-report measures of increased impulsivity. Furthermore, behaviourally adolescents also show poorer proactive control. They are slower and less accurate during anti-saccade tasks compared to adults, demonstrating an inability to maintain task-relevant response tendencies, instead initiating responses post-stimulus onset (Hwang, Velanova, & Luna, 2010; Kramer, De Sather, & Cassavaugh, 2005). Together these ERP, fMRI and behavioural studies suggest a propensity for adolescents to respond reactively to exogenous rather than internally generated motivations (Andrews-Hanna et al., 2011; Killikelly & Szűcs, 2013; Solomon et al., 2014).

Despite the apparent differences in how control is allocated in adolescents compared to adults, by late adolescence (~16 years) no difference in the ability to detect cognitive costs reactively has been reported (Ladouceur, Dahl, & Carter, 2007). In late adolescents, the ERN and N2 elicited by incorrect responses and conflict, respectively, during the flanker task are

similar to those found in adults (Ladouceur et al., 2007). However, in the same study late adolescents did show an increased P_E , an ERP with a neural generator also in the ACC, which is responsive to motivational aspects of error monitoring (Falkenstein et al., 2000), compared to adults (Ladouceur et al., 2007). One possibility is that late adolescents are more sensitive to motivational feedback that drives reactive control; Chapter 3 investigates this possibility.

Alongside the increased propensity for reactive control, adolescents also appear to overestimate the expected value of exogenous motivational states. Specifically, it is evident when examining the adolescent brain's responsivity to reward contingencies that they are especially sensitive to motivational cues. Adolescents generally show increased striatal activity in both the anticipation and receipt of rewards compared to adults (Braams, van Duijvenvoorde, Peper, & Crone, 2015; Ernst et al., 2004; Geier & Luna, 2009; Luna, Padmanabhan, & Hearn, 2010; Neuroscience & Galvan, 2010; Padmanabhan, Geier, Ordaz, Teslovich, & Luna, 2011; Van Leijenhorst et al., 2010, although see Bjork et al., 2004; Bjork, Smith, Chen, & Hommer, 2010); although the increased activity is not valence specific. Instead, the activity appears to be related to the motivational intensity of the outcomes rather than the outcome's positive nature (Galván & McGlennan, 2013). Accordingly, in rats, adolescents are much more likely to attribute incentive salience to stimuli. They exhibit an increased tendency for sign-tracking than young adults, consistent with an inflated sense of the expected payoff leading to the allocation of inappropriate reactive control (Anderson, Bush, & Spear, 2013; DeAngeli, Miller, Meyer, & Bucci, 2017). In humans, there is also evidence that adolescents are more likely to inflate the expected value of reward-associated motivations. VDAC is not only increased in adolescents compared to adults, but also persists long beyond VDAC has extinguished in adults (Roper et al., 2014). The latter finding that VDAC survives

extinction in adolescents but not adults shows that teenagers fail to modulate the expected value of reward-associated control when it is costly to task-relevant goals. The primary finding that VDAC is larger in adolescents demonstrates an increased propensity for teenagers to act on exogenous motivations (i.e., attend the high value-associated colour). As a result of adolescents' increased sensitivity to reward-driven behaviours they can offer an important contribution to the study of cost-benefit trade-offs in the allocation of control. Especially, in the understanding of how expected payoffs may influence control without the suppressive influence of strong goal-directed control; Chapter 5 contributes to knowledge in this area.

The motivational competition approach to adolescent cognition extends existing dual-system frameworks of adolescent risk-taking by offering a more mechanistic appraisal of the underlying computations that afford adolescents' allocation of control. The motivation model predicts increased behavioural activation by rewarding stimuli in adolescents because they inflate the predicted payoffs as a result of enhanced striatal sensitivity to rewards. This then feeds into the computation of motivational intensity, which is not diluted by goal-driven control mechanisms because of immature frontal connectivity to mid-brain DA transmission.

In sum, attentional frameworks (e.g., Selection History) of reward-driven distraction are insufficient because they do not offer a mechanistic account of the underlying processes. Instead, it has been proposed that rewards bias attention not by altering attentional priority maps, but rather by supposing that value-associated stimuli initiate separate goals that have specific learned control dynamics, reactively, post-stimulus onset. The motivational competition account proposes that multiple motivational states are constantly and concurrently competing for control of cognition, and that this competition is resolved by computing cost-benefit trade-offs for each motivation. Cognition is then determined by the

motivational state with the greatest relative motivational intensity. Value-associated stimuli garner increased motivational intensity because of the learned reward. The motivational competition account is supported across behavioural, electrophysiological and imaging research, and a plausible neural basis largely reliant on connectivity between the dACC, striatum, and DLPFC has been proposed. Furthermore, the model is also applicable in explaining developmental differences, such as enhanced reward sensitivity in adolescence.

Chapter 2. Value-based Modulation of Visual Attention

Depends on Competition Among Motivational States

Abstract

Task irrelevant, but motivationally salient stimuli sometimes interfere with performance more than similar, but motivationally neutral stimuli. Current explanations for these super-distraction effects posit that motivational salience enhances a stimulus' perceptual representation, improving its competitiveness for gaining control over attention. Here, I suggest that competition among stimulus- and task-instantiated motivational states explains these effects better than perception-based competition. To investigate, I conducted four experiments on healthy young adults using a colour-flanker task involving (a) neutral distractors, (b) distractors with motivationally salient shapes (imbued in a prior shape-money conditioning task), or (c) perceptual salience (manipulated by brightness). Of particular interest was whether well-studied sequential trial effects would depend similarly or differently on motivational versus perceptual flanker salience. Although perceptual strength accounts of super-distraction predict similar effects, I report opposite effects. Specifically, performance interference effects attributable to distractor motivational salience were only observable when conflict (colour incongruence) had been experienced on the previous trial and not after no-conflict trials; whereas effects attributable to perceptual salience were absent after conflict trials but present after no-conflict (congruent) trials. An additional experiment showed that when flanker value associations were made more difficult to access during the flanker task, their effect on performance disappeared, but, counter-intuitively, was reinstated when a concurrent secondary task was required. Collectively, these effects of motivational salience are inconsistent with conventional perceptual competition accounts, but are adequately explained by positing a competition among motivational states driven by costs versus benefits of cognitive engagement with stimuli.

Typical visual environments contain multiple objects, each with the potential to motivate different behaviours that may or may not be related to one's on-going task. For example, passing a fast-food restaurant while driving home might motivate a diversion via the drive-through. To maintain the goal of getting home, the driver must either suppress the perceptual processing of the goal-irrelevant stimulus (restaurant) or inhibit the motivational state it initiated ("I want food"). Currently, it remains unclear which option the brain uses to maintain goal-directed behaviour. However, most studies from the field of selective attention clearly favour the notion of perceptual suppression (Awh et al., 2012; A. Bourgeois, Chelazzi, & Vuilleumier, 2016; Chelazzi et al., 2014; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Le Pelley, Mitchell, Beesley, George, & Wills, 2016), and have largely ignored the possibility that regulation of motivational states may be involved.

Time and again, studies in visual attention have shown that motivationally salient but task-irrelevant stimuli can interfere with speeded performance on simple visual search or decision tasks to a greater extent than perceptually similar but motivationally-neutral stimuli. Response time (RT) slowing and enhanced error rates have been found with emotionally salient distractors (see Yiend, 2010, for a review), personally relevant distractors (Gronau, Cohen, & Ben-Shakhar, 2003; Humphreys & Sui, 2016; Sui, He, & Humphreys, 2012; Tong & Nakayama, 1999), task-irrelevant images related to personal addictions (Field, Mogg, Zetteler, & Bradley, 2004; Lubman, Peters, Mogg, Bradley, & Deakin, 2000; Noël et al., 2006; Stormark, Field, Hugdahl, & Horowitz, 1997), and of particular importance for the current study, distractors that have learned positive or negative value associations (Anderson et al., 2011; Bucker, Belopolsky, et al., 2015; Della Libera & Chelazzi, 2006; Failing et al., 2015; Hickey et al., 2010b, 2010a; Le Pelley et al., 2015; Munneke et al., 2016; Qi et al., 2013; Roper et al.,

2014; Rutherford et al., 2010). These *super-distraction effects*, i.e., greater distraction by motivationally salient versus perceptually similar neutral stimuli, have often been accounted for by supposing that motivational salience modulates the strength of perceptual representations (Awh et al., 2012; Chelazzi et al., 2014; Rutherford et al., 2010). Stronger representations are presumed to have a greater likelihood of capturing attention (Wei & Zhou, 2006; Yantis & Jonides, 1984), and hence motivational salience makes irrelevant stimuli super-distracting.

Such views have been encapsulated within the framework of an attention ‘priority map’ (Awh et al., 2012). Attention priority map theories generally posit that selective attention is determined by the relative perceptual representational strength of stimuli in the visual array, with the strongest representation (corresponding to the tallest peak on the priority map) gaining access to high level processing, i.e., capturing attention. In some views, peak height on the priority map is solely determined by sensory salience (Franconeri & Simons, 2003; Itti & Koch, 2000; Jonides & Yantis, 1988; Theeuwes, 1992), other models posit (or at least imply) that peak height is determined by a dynamic process of competition that uses ‘top-down’ task-specific expectations and task requirements to modulate the map’s topography (e.g., Bichot et al., 2010; Desimone & Duncan, 1995; Folk et al., 1992; Ptak, 2012; Sawaki & Luck, 2010). Such models of perceptual competition accommodate super-distraction effects by positing that mechanisms sensitive to prior experience can boost the representational strength of irrelevant but motivationally salient stimuli (Awh et al., 2012; Wang et al., 2013).

A significant problem for this perception-based view is that the extant evidence supporting it is not uniformly strong. A large number of studies report situations in which

motivationally salient distractors neither produce interference effects in attention (e.g., Roper et al, 2014; Sali et al., 2014; Sha & Jiang, 2016). Moreover, the presence of super-distraction effects is often subject to substantial individual differences (Hickey et al, 2010b; Anderson et al, 2011; 2013), being present in some but by no means all participants. Yet despite the accumulation of this substantial evidence to the contrary, the notion that super-distraction effects result from automatic boosts to the strength of perceptual representations remains a widely-held view.

Here I propose an alternative motivated cognition framework for explaining super-distraction effects based on the idea that sensory cues and top-down signals generate motivational states (goals) that compete for control over high-level cognition. The motivational competition is resolved in favour of the motivational state with the greatest motivational intensity (Shenhav et al., 2013), which is determined by the predicted costs and benefits of each state. This competition ensures that only the most intense state at any moment controls cognition. As in other views of cognitive control, competition for control over behaviour is internally monitored (Botvinick et al., 2001; Kerns et al., 2004; MacDonald III et al., 2000) so that experience of past conflict enhances the predicted cost of a future related goal, effectively dampening motivational intensity for that goal. Put together, the notion of a motivation-based competition allows specific predictions regarding the role of cognitive conflict in super-distraction effects. Importantly these predictions contrast directly with those made using a conventional perceptual competition framework.

The aim of the experiments reported here was to test these predictions by assessing value-based super-distraction effects in a simple attention task. Specifically, I used a value-learning task to imbue the shape of abstract symbols with monetary value (wins, losses, or no

value) and then used these stimuli in a colour flanker task (Eriksen & Eriksen, 1974). Super-distraction effects in the latter task were assessed by contrasting performance in conditions in which the flankers were value-associated (value-flanker conditions) with those when they had no-value associations (no-value flanker conditions). On each trial a central target symbol appeared concurrently with two flanking distractor symbols that preceded it briefly; participants made a speeded two-alternative forced choice about the colour of the central target. Some trials were congruent, i.e., all stimuli had the same colour, making responses to any item correct. Other trials were incongruent, i.e., target and flankers had different colours, making responses to flankers incorrect. The degradation of performance (indexed by RT and percent correct choices) on incongruent relative to congruent trials is known as the congruency effect (CE; Eriksen, 1995) and reflects flanker distraction. (See Table 2.1 for a list of performance definitions used in the flanker task).

Table 2.1. Definitions used in the flanker task.

Term	Definition
Congruent trial	Flankers and target have the same colour
Incongruent trial	Flanker and target have different colours
Congruency effect (CE)	RT incongruent trial – RT congruent trial
CE _{con}	CE after a congruent trial
CE _{incon}	CE after an incongruent trial
Conflict adaptation (CA)	CE _{con} – CE _{incon}
Super-distraction effect (SDE)	CE _(value/bright flankers) – CE _(no-value/dim flankers)

Numerous studies have shown that CE depends on the congruency of the prior trial (Gratton et al., 1992); CE is large after a congruent trial (CE_{con}) and small after an incongruent

trial (CE_{Incon}). This difference in CE magnitude ($CE_{Con} - CE_{Incon}$) is referred to as Conflict Adaptation (CA) and is thought to reflect a mechanism that uses the conflict experienced on a preceding incongruent trial to modify top-down control settings for a subsequent trial (Botvinick et al., 2001; Egnér & Hirsch, 2005; Ghinescu, Schachtman, Ramsey, Gratton, & Fabiani, 2016; Kerns et al., 2004; Pastötter, Dreisbach, & Bauml, 2013; Ullsperger, Bylsma, & Botvinick, 2005). Comparisons of CE and CA with value versus no-value flankers thus provides a measure of super-distraction. Here I use these measures to test the different predictions made by perceptual versus motivation-based models of processing priority.

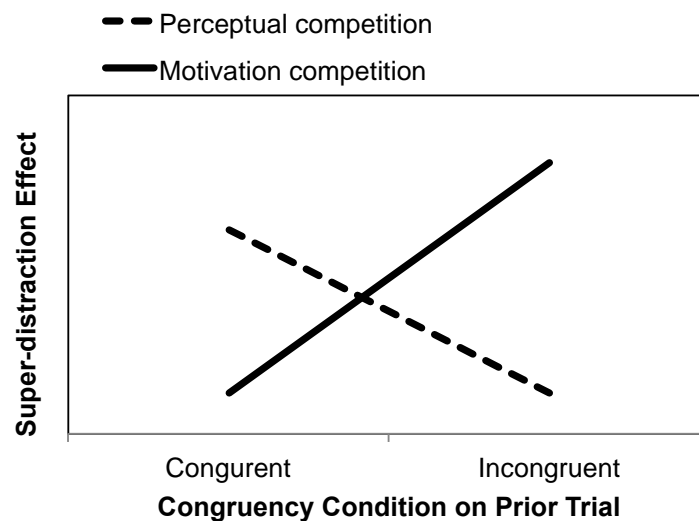


Figure 2.1. Predicted super-distraction effects for flanker task performance after congruent versus incongruent trials using a processing priority framework based on perceptual (dashed line) or motivation-based (solid line) competition.

Perceptual competition models predict that both CE_{Con} and CE_{Incon} should be larger with value flankers than with no-value flankers (a positive super-distraction effect), regardless of the congruency of the prior trial due to the enhanced likelihood of attention capture by these motivationally salient stimuli. However, this difference should be larger after congruent trials when flanker suppression is weak or absent, allowing value-associations to enhance the perceptual priority of flankers leading to increased attentional capture. After incongruent

trials, flankers should be suppressed, weakening the effect of value associations, leading to a smaller super-distraction effect (see Figure 2.1).

The motivational competition hypothesis on the other hand makes different predictions. To explain, it is easier first to consider a motivation-competition interpretation of flanker effects, such as CA, without considering the role of value associations. In this view and consistent with previous theories of conflict triggered control adaptations (Dreisbach & Fischer, 2012, 2015), motivational intensity for identifying target colour (i.e., the main task of the experiment) should remain constant regardless of the preceding trial, but motivation to identify flanker colour should vary with the congruence of the preceding trial. Thus, competition between the two motivational states (identify target colour, identify flanker colour) should vary correspondingly (Egner & Hirsch, 2005; Ullsperger et al., 2005). After a congruent trial, motivational intensity to code flanker colour should be high due to higher predicted benefit, enhancing CE. After an incongruent trial (higher predicted costs) motivation should be low, with conflict from flankers being inherently aversive (Botvinick, 2007; Dreisbach & Fischer, 2015), reducing CE and thereby accounting for CA effects (Gratton et al., 1992).

Of interest here is how flanker value might modulate these effects. Notions of incentive salience (Robinson & Berridge, 1993) posit that value-flankers offer greater predicted benefits than no-value flankers and should thus heighten motivational intensity for processing flankers. However, the effect of this added benefit should only become evident after an incongruent trial when motivation to code flanker colour is generally low allowing motivation to process value-associated flanker features to be relatively stronger. This intensity gain should be evident for value flankers and be absent for no-value flankers. Thus, CE_{Incon}

should be larger with value-flankers than with no-value flankers, producing a large positive super-distraction effect. In contrast, after a congruent trial the motivational intensity to code flanker colour is already strong, even without value, because of the benefit experienced on the prior trial. Thus, the relative intensity increase from value flankers versus no-value flankers is negligible and CE_{Con} should be unaffected by flanker value producing no super-distraction effect. This prediction is particularly contradictory with a perceptual competition framework of super-distraction effects that still predicts an enhanced perceptual priority from value flankers and thus a positive super-distraction effect on CE_{Con} (See Figure 2.1).

I tested these and related predictions in four experiments. In Experiments 1 and 2, I directly contrasted the effects of motivationally salient distractors (Experiment 1) with those of perceptually salient distractors (Experiment 2). In Experiment 1, participants began the study by learning to associate orange and purple symbols with monetary wins, losses, or no value. Only symbol shape, not colour, was predictive of outcome value. In Experiment 2, the value-learning task was omitted entirely. Both studies used the same flanker task except that in Experiment 2, flankers were either dim or bright instead of being value or no-value associated. I predicted that the results from Experiment 1 (motivationally salient distractors) would be consistent with the motivation-based framework (as shown in Figure 2.1) and inconsistent with the perceptual competition framework. I predicted the reverse pattern for the results of Experiment 2. In Experiments 3 and 4, a value learning session preceded the flanker task as in Experiment 1, except that here all symbols were white. The aim was to reduce the transfer of value associations to the coloured symbols used in the flanker task (Le Pelley, 2004). I predicted that colour flankers would only minimally instantiate motivation to activate flanker value associations, eliminating value effects on CA. Indeed, I observed this

effect in Experiment 3. Experiment 4 used the same learning/flanker stimuli as Experiment 3, but this time manipulated motivational state during the flanker task by loading visual-colour working memory during each trial. The aim was to increase the cognitive cost of coding colour in the flanker task and thereby reduce motivational intensity for this goal. According to the motivational competition hypothesis, this should effectively boost the latent motivation for coding flanker shape driven by value associations, allowing super-distraction effects to re-emerge. Perceptual competition models make no such predictions. In Experiment 5, bright versus dim flankers were again used, but similar to Experiment 4 a concurrent WM task was also performed. The reasoning was that a WM load should not impact the influence of physical salience, so I expected to replicate Experiment 2. To anticipate, the results favour the notion of competition among motivational states and are poorly accounted for by perceptual competition models.

General Methods

Participants

Students from the University of Birmingham participated in exchange for course credits or money plus cash earned during the value-learning task (up to an extra £5). All participants (see Table 2.2) had normal or corrected-to-normal vision, no history of neurological disorder, and were naïve both to the purpose of the experiment and to Japanese Hiragana ideograms. Informed consent was obtained from all participants. All procedures used here were approved by the University's Ethical Review Committee. Sample sizes for Experiments 1 – 3 were calculated based on the effect size obtained by van Steenbergen et al.

(2009) who also examined the conflict adaptation effect depending on reward conditions, albeit they were interested in the influence of performance dependent rewards rather than the influence of value-associated distractors. They reported a Cohen's $d = .71$ for the comparison of CE_{Con} and CE_{Incon} . I therefore assumed an effect size of $d = .71$, a power of 0.80, and a two-tailed test. The result was a required sample size of at least 13 to observe the conflict adaptation effect. For Experiment 4, the sample size was based on a $\eta^2 = .33$ reported by Ahmed & de Fockert (2012) for a three-way interaction with a between-subjects factor of WM-group. Again, assuming a power of 0.80, and a two-tailed test a sample size of at least 20 participants was required. G*Power 3.1 was used for the calculation of sample sizes.

Table 2.2. Participants' Demographic Information and Mean Questionnaire Scores from all Experiments (standard error in parenthesis).

	Exp. 1	Exp. 2	Exp. 3	Exp. 4		Exp. 5
				WM	No-load	
<i>N</i>	15	15	15	21	21	21
Females	11	15	13	14	16	16
Right-handed	11	11	13	21	20	18
Age (years)						
Mean	22.5 (3.0)	19.1 (1.1)	20.8 (1.5)	21.4 (1.8)	22.6 (2.1)	19.3 (.2)
Range	18 - 29	18 - 21	20 - 25	18 - 25	19 - 27	18 - 21
BIS/BAS						
BIS	21.4 (.8)	22.9 (.8)	21.4 (1.0)	19.7 (.8)	20.6 (.9)	20.3 (.6)
BAS reward	18.4 (.4)	17.2 (.6)	15.8 (.9)	16.3 (.7)	17.0 (.7)	17.2 (.5)
BAS drive	10.9 (.7)	9.8 (.5)	9.9 (.6)	10.0 (.6)	12.1 (.6)	10.7 (.5)
BAS fun seeking	12.0 (.6)	11.2 (.5)	10.9 (.6)	11.7 (.5)	11.7 (.6)	11.9 (.4)
BIS-11						
Attention	9.5 (.7)	9.7 (.5)	10.3 (.5)	10.2 (.5)	11.2 (.7)	11.0 (.7)
Cognitive instability	6.5 (.6)	6.7 (.4)	6.9 (.4)	6.6 (.3)	7.1 (.5)	6.4 (.4)
Motor	15.6 (.9)	15.3 (.8)	15.0 (.6)	15.9 (.7)	16.0 (.8)	15.3 (.6)
Perseverance	8.1 (.5)	7.5 (.5)	6.9 (.4)	7.5 (.4)	8.0 (.4)	7.2 (.5)
Self-control	12.0 (.9)	11.1 (.6)	12.6 (.8)	12.0 (.5)	12.3 (.7)	12.4 (.7)
Cognitive complexity	10.7 (.8)	11.7 (.8)	10.7 (.6)	10.5 (.6)	11.6 (.5)	12.5 (.5)

Apparatus

Stimulus presentation and data recording were controlled using custom software developed with PsychoPy (Peirce, 2007, 2009) controlling a Stone PC-1210. Responses were entered using a standard keyboard. Stimuli were presented in RGB colour space on a gray (Experiments 1, 3, and 4: 128, 128, 128) or black background (Experiments 2 and 5: 0, 0, 0) of a 68 cm LCD monitor with a screen resolution of 1920 x 1080 and a refresh rate of 60 Hz. Viewing distance was approximately 70 cm. Testing was conducted in a quiet room with ambient lighting and without the aid of a chin rest.

Stimuli

Japanese ideograms (PJ Hiragana font) subtending approximately $1.9^\circ \times 1.4^\circ$, presented in white (255, 255, 255), purple (99, 84, 99), or orange (119, 84, 0) served as stimuli. Unless otherwise stated, stimuli were equiluminant regardless of colour. In both tasks, symbols appeared along the horizontal meridian; flanker-task targets appeared centrally and flanker as well as learning-task symbols were presented laterally left or right by 4° .

Procedure

Value-Learning Task. See Figure 2.2a. Each trial began with a fixation cross (750 ms), followed by a brief (250 ms) presentation of two symbols, one on either side of fixation, and then a blank screen until response. Symbols were selected from a set of six (Experiments 1 and 3) or three (Experiment 4). Each was assigned a point value of 0 (No-Value), 500 (Win), or -500 (Loss); value-symbol assignments were counterbalanced across participants. Participants were told to earn as many points as possible by selecting (unspedeed) the symbol with the largest point value. They used the index or middle fingers of the right hand and the '1' or '2' key to choose the left or right symbol, respectively. Immediately after response, each symbol's numerical value replaced its symbol for 500 ms. The value of the chosen symbol, i.e., that trial's outcome, remained visible for an additional 500 ms. A running total of points earned was continuously presented on the vertical midline 8° below fixation and updated after each choice.

The two symbols presented on each trial could either be matched or mismatched in value. Each possible mismatched symbol (win vs. no-value, loss vs. no-value, and win vs. loss) pair was equally likely; the location of the optimal choice on mismatched pairs was equally likely to be left or right. Matched trials (included in Experiments 1 and 3, and excluded in

Experiment 4) required an arbitrary response and were used to provide experience of outcome for each symbol; data from these trials were not analysed. Participants completed three blocks of 108 trials in Experiment 1 and 3, or three blocks of 80 trials in Experiment 4. The cumulative point total was visible during inter-block rest breaks. Points earned were converted into cash and given to participants at the end of the learning session. Eighteen practice trials using the same procedure but with Roman letters and explicit value assignments (A = 1, B = 2, and C = 3) were completed prior to the learning session.

Test Scales. After completing the learning phase, participants completed the Munsell D-15 colour vision test; all participants performed normally. They then completed the Behavioural Inhibition/Behavioural Activation System Scale (BIS/BAS, Carver & White, 1994) and the Barratt Impulsiveness Scale (BIS-11, Patton, Stanford, & Barratt, 1995). Differences among participant groups in different experiments were non-significant and were non-significantly correlated with any measure of super-distraction reported here. Data obtained from the personality inventories are reported in Table 2.2. Immediately after completing the questionnaire participants engaged in the flanker task.

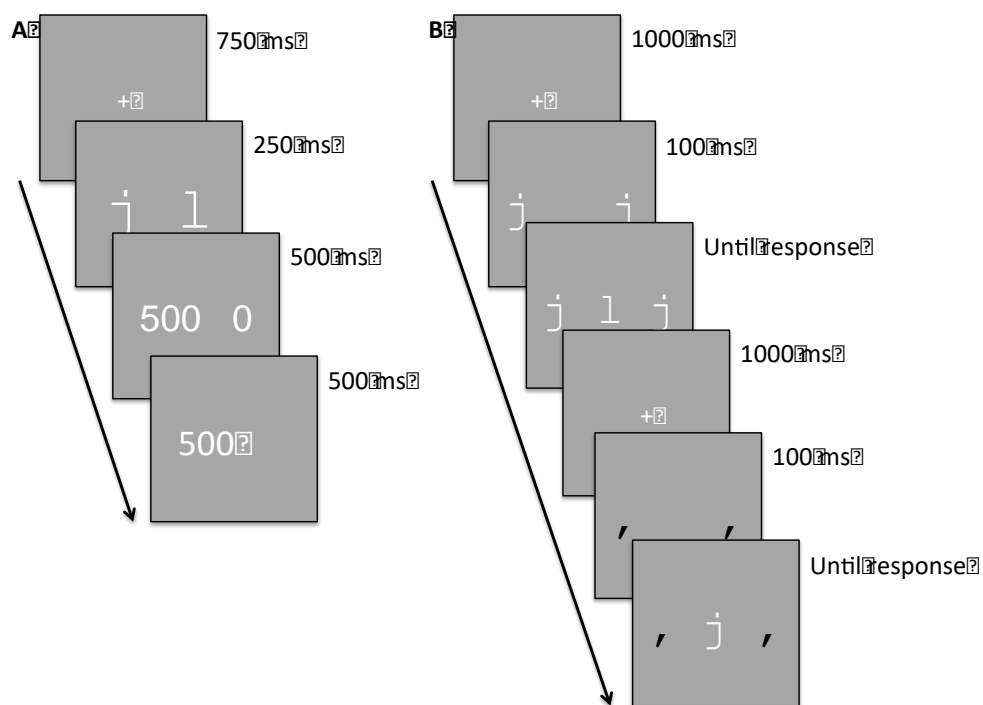


Figure 2.2. A. Example trial during the Learning Task. In Experiment 1 symbols were displayed in either orange or purple, whereas in Experiments 3 and 4 they appeared in white, as shown here. The task was to earn as many points as possible by choosing one of the two symbols. Numbers show the point value corresponding to each symbol and the final frame shows the outcome received on that trial. B. Example of two successive trials in the Flanker Task. Here the symbols always appeared in orange (depicted here as white) or purple (depicted here as black). The task was to report the colour of the target (central symbol) as fast and accurately as possible. The example shows an incongruent trial preceded by a congruent trial.

Flanker Task. See Figure 2.2b. Each trial began with a fixation cross (1000 ms) that was followed by an initial presentation of flankers (two identical symbols in the same colour) on either side of an empty centre area for 100 ms. See Figure 2.2b. This was immediately replaced with a three-item array comprised of the previous flankers plus a central target all of which remained visible until response. The task was to report the target's colour by pressing the '1' or '2' key with the index or middle finger of the right-hand, as quickly and accurately as possible. The assignment of key to colour was counterbalanced across participants. Response time (RT) from target onset and error rates was recorded. No feedback was given, and no points were awarded or lost.

The symbols used were the same as those experienced in the learning task. On half of trials flankers and target had the same colour (congruent trials); on remaining trials, they were colour mismatched (incongruent trials). Each possible combination of flanker symbol/colour and target symbol/colour was equally likely to occur. This created colour congruent (C) or colour incongruent (I) trials with flankers that had no-value associations, win associations, or loss associations (Experiments 1 and 3) or flankers that were dull or bright (Experiment 2). Critically, the experiments produced four different two-trial sequences: congruent-congruent (CC), incongruent-incongruent (II); congruent-incongruent (CI) and incongruent-congruent (IC).

Participants completed 144 (Experiments 1 and 3) or 128 (Experiment 2) trials of each combination of flanker value (or brightness) X congruency, without regard to sequence type, split equally between four blocks and presented in a pseudo random order (Experiments 1 and 3: 864, Experiment 2: 512 trials in total). The trial structures for the flanker task in Experiments 4 and 5 are described in their own section.

Data Analysis

Value-Learning Task. Proportion optimal choice was calculated for each participant across the entire session. Thirteen out of 85 (15%) participants failed to achieve greater than 75% correct meaning that acquisition of value associations could not be assumed in these cases. All their data was excluded, including that reported in Table 2.3. Proportion optimal choice for each block was then calculated for each remaining participant. Repeated-measures ANOVAs on these data with block (1, 2, or 3) as within-subjects factor were conducted (Experiments 1 and 3). Memory condition was included as a between-subjects factor for Experiment 4.

Flanker Task. Two participants in Experiment 3, one in Experiment 4, and three in Experiment 5 had mean RTs and/or error rates greater than 2.5 SD above the group mean, resulting in their data from being excluded from further analysis. All incorrect trials (Experiment 1 = 4.6%, Experiment 2 = 6.2%, Experiment 3 = 4.7% of trials; see Experiment 4 and Experiment 5 for details) and trials faster than 300 ms or slower than 5000 ms were excluded (Experiment 1 = 0.2%, Experiment 2 = 0.5%, Experiment 3 = 0.1%, Experiment 4: WM = 0.04%, No-load = 0.3%, Experiment 5 = 0.1% of trials), means and SD's were then calculated for each flanker value X prior trial congruency X current trial congruency condition for each participant. RTs slower than 3 S.D. above the individual conditions means were also excluded (Experiment 1 = 1.9%, Experiment 2 = 2.1%, Experiment 3 = 2.0%, Experiment 4: WM = 2.2%, No-load = 2.0%, Experiment 5 = 2.2% of trials). In Experiments 1 and 3 individual means based on remaining data were analysed with a 2 x 2 x 3 repeated-measures analysis of variance (ANOVA) with current flanker congruency, previous flanker congruency, and current trial flanker value (no-value, win or loss) used as within-subjects factors. In Experiment 4, the within-subjects factor of flanker value only had 2 levels (no-value or win); in Experiments 2 and 5 it was replaced with flanker brightness (dull or bright). Error rates were similarly analysed. Significant three-way interactions of RT data were followed-up by calculating CE_{Con} and CE_{Incon} for each flanker value. Additionally, conflict adaptation (CA) effects for each current trial Flanker Value were also calculated as shown in Table 2.3.

Significance of CA was tested using one-sample t-tests. Comparisons of CA values across conditions used one-way ANOVAs. All follow-up planned pairwise comparisons were corrected for multiple comparisons by the False Discovery Rate procedure (Benjamini & Hochberg, 1995). Alpha levels were set at .05 throughout.

Experiment 1

The aim of this experiment was to assess the presence of super-distraction effects in the flanker paradigm. Super-distraction involved comparing performance on trials with value-associated flankers with that when flankers were equally familiar but not associated with a motivationally salient outcome. Sequential trial effects were of particular interest (Gratton et al., 1992); specifically, the experiment was designed to test the effect of flanker value on the interaction of prior trial congruence and current trial congruence, as perceptual and motivational competition theories of processing priority predict different outcomes for this triple interaction effect.

Method

Procedure

Value-Learning Task. Six symbols were conditioned to three different values (win, no-value, loss; two to each value). One of the two symbols denoting each value was viewed in purple and the other in orange, meaning that shape, not colour, predicted symbol value. This symbol-colour-value conjunction remained consistent throughout the experiment. Each symbol was equally likely to be presented at either location. On 108 trials both symbols had the same value; on half of these value-match trials symbol shape also matched and on remaining trials shapes were mismatched. Symbol value (and shape) was mismatched on 216 choice trials (72 for each possible choice pair, i.e., Win/Loss, Win/No-Value, and Loss/No-Value), with half having colour-matched symbols and half having colour-mismatched symbols.

Flanker Task. Symbols had the same colour-shape conjunctions as seen in the value-learning task.

Results and Discussion

Value-Learning Task. See Table 2.3 for value-learning task performance for all experiments reported in Chapter 2. Performance in this Experiment improved significantly across blocks $F(2, 28) = 64.679, p < .001, \eta^2 = .822$) and averaged 87% correct (S.D. = 6%).

Table 2.3. Mean Proportion of Optimal Choices as a Function of Block during the Value-Learning Task for Experiments 1, 2, and 3.

Block	Exp. 1	Exp. 3	Exp. 4	
			WM	No-load
1	.76 (.02)	.75 (.02)	.80 (.04)	.83 (.03)
2	.90 (.02)	.84 (.02)	.95 (.01)	.96 (.01)
3	.93 (.02)	.89 (.02)	.96 (.01)	.98 (.01)
Overall	.87 (.02)	.83 (.02)	.91 (.02)	.92 (.01)

Note. There was no Value-Learning Task in Experiments 2 and 5. Standard error in parenthesis.

Table 2.4. Mean RT as a Function of the Trial Type for All Experiments.

Trial Type	Exp. 1	Exp. 2	Exp. 3	Exp. 4		Exp. 5
				WM	No-load	
No-value/Dull						
CC	449 (12)	524 (12)	483 (10)	545 (20)	477 (13)	589 (16)
CI	515 (14)	577 (10)	547 (11)	605 (22)	525 (10)	601 (11)
IC	472 (12)	540 (9)	504 (11)	583 (20)	495 (13)	596 (15)
II	503 (12)	578 (14)	547 (11)	601 (17)	529 (11)	635 (16)
CA effect	34 (7)	15 (11)	21 (9)	42 (9)	15 (10)	-27 (12)
Win/Bright						
CC	456 (13)	506 (11)	483 (10)	557 (23)	480 (12)	563 (14)
CI	507 (13)	573 (11)	543 (9)	600 (23)	525 (10)	619 (14)
IC	463 (12)	543 (11)	508 (11)	569 (19)	510 (13)	598 (16)
II	510 (12)	586 (10)	542 (11)	608 (20)	528 (11)	640 (15)
CA effect	4 (6)	24 (9)	26 (8)	4 (12)	26 (10)	14 (11)
Loss						
CC	449 (11)		489 (9)			
CI	509 (13)		547 (10)			
IC	462 (11)		516 (12)			
II	516 (13)		552 (10)			
CA effect	6 (5)		21 (8)			

Note. There were four trial sequences, congruent-congruent (CC), congruent-incongruent (CI), incongruent-congruent (IC), and incongruent-incongruent (II). The conflict adaptation (CA) effect was calculated as ((CI-CC)-(II-IC)). There was no loss condition in Experiments 2, 4, and 5. Standard error in parenthesis.

Flanker Task. Group mean RTs for the main conditions of this and all other experiments reported in Chapter 2 are reported in Table 2.4. As expected the statistical analysis showed significant effects indicating the presence of CA. Specifically, RTs were slower (by 51 ms) when target and flanker colour were incongruent versus congruent ($F(1, 14) = 103.280, p < .001, \eta^2 = .881$); they were faster (by 7 ms) when the previous trial was congruent versus incongruent ($F(1, 14) = 16.453, p < .005, \eta^2 = .540$); and, critically, the effect of current and prior trial congruence interacted significantly ($F(1, 14) = 12.193, p < .005, \eta^2 = .466$). Importantly for the current study, the 3-way interaction (current congruency X prior

congruency X flanker value) was also significant ($F(2, 28) = 8.364, p < .005, \eta^2 = .374$)¹, indicating the presence of a super-distraction effect and justifying the analysis of value effects on CE_{Con} and CE_{Incon} , as well as CA.

Both CE_{Con} and CE_{Incon} for Experiments 1-3 reported are presented in Figure 2.3; super-distraction effects are shown in Figure 2.4A; and CA effects are presented in Table 2.4. All analyses of CE_{Con} , CE_{Incon} , and CA effects in Experiment 1 revealed non-significant differences between flankers with win- versus loss-associations, consistent with previous studies showing that effects of motivational salience on attention are independent of value valence (e.g., O'Brien & Raymond, 2012; Rothermund, Wentura, & Bak, 2001; Schmidt, Belopolsky, & Theeuwes, 2015; Wang et al., 2013)² as would be expected given that the stimuli are only secondary reinforcers to wins and losses in the value-learning task; consequently, these conditions were collapsed into a single value-associated flanker condition for all further analyses.

¹ Although not related to the aims of the experiment a similar ANOVA using the prior trial flanker value (value vs. no-value) as a factor instead of current trial flanker value showed no significant main effects or interactions involving prior trial flanker value (all $ps > .36$). A further ANOVA using target value (value vs. no-value) in place of flanker value showed no significant effects involving target value (all $ps > .53$). However, in both ANOVAs typical effects associated with CA were found to be significant.

² An ANOVA of RTs excluding the No-Value condition showed the main and all interaction effects involving value to be non-significant (all $ps > .137$).

Value-based Modulation of Visual Attention Depends on Competition Among Motivational States

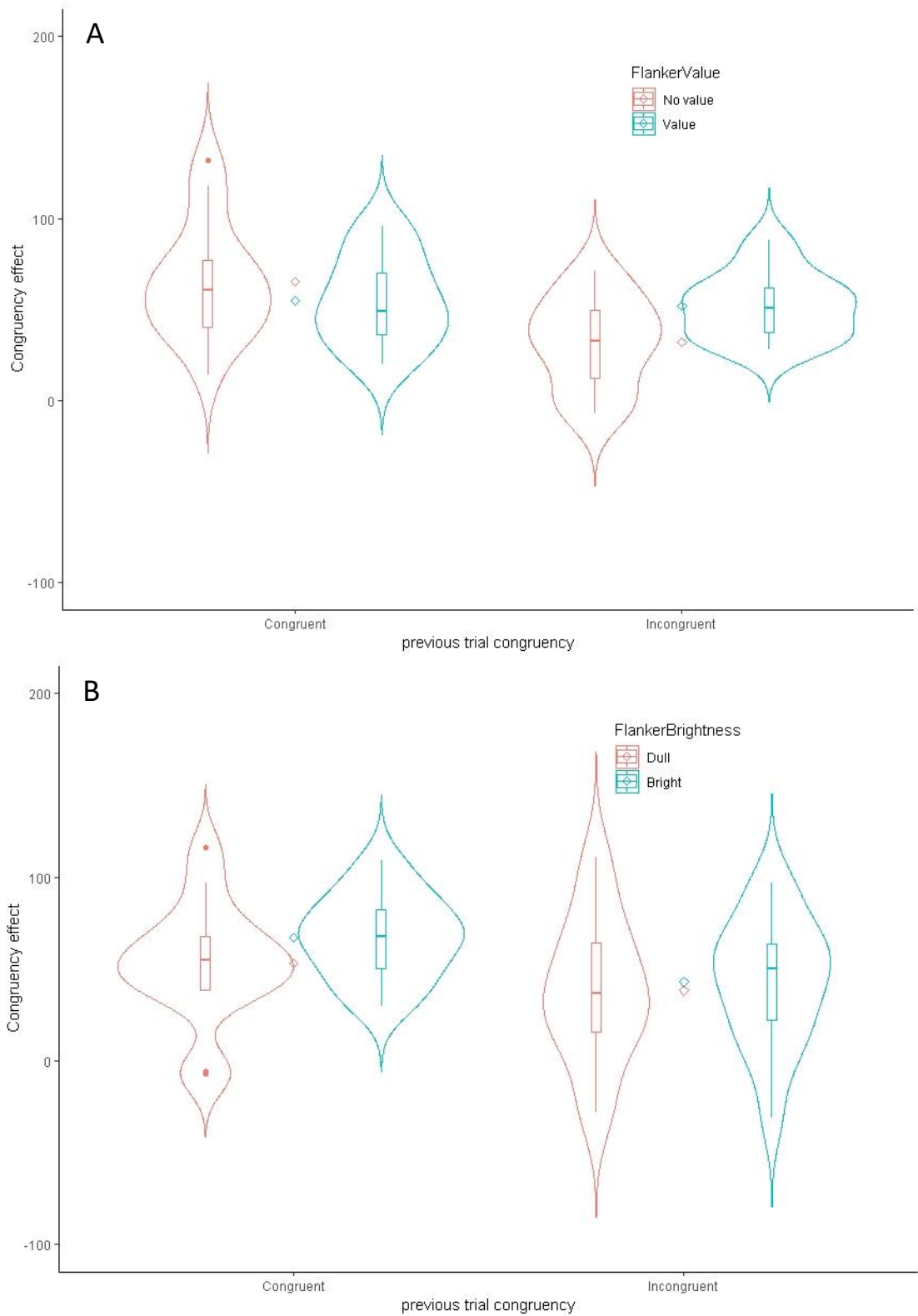


Figure 2.3. Group mean CE_{Con} and CE_{Incon} plotted separately for each current trial flanker value or brightness condition in Experiment 1 (A) and Experiment 2 (B), respectively.

In line with the predictions of the motivational competition hypothesis as shown in Figure 2.1, a super-distraction effect (see Figure 2.4) was present following an incongruent trial. CE_{Incon} was 20 ms larger when flankers had value versus no-value associations ($t(14) = 3.013, p < .01$). Although the perceptual competition hypothesis predicts that CE_{Con} should be larger with value versus no-value flankers, here I found that CE_{Con} with value flankers was in fact slightly smaller than that with no-value flankers; however, this difference was not significant ($t(14) = 1.788, p = .095$) in line with predictions (See Figure 2.1).

For no-value flankers, CE_{Incon} was 34 ms smaller than CE_{Con} ($t(14) = 4.556, p < .001$) resulting in a significant (and typical) CA effect ($t(14) = 4.560, p < .001$). However, when flankers were value-associated CE_{Incon} and CE_{Con} did not differ, resulting in a non-significant CA effect ($t(14) = 1.160, p = .266$). Thus, CA was significantly larger (by 30 ms) in the no-value compared to the value flanker condition ($t(14) = 3.704, p < .005$).

Analysis of error rates revealed a significant effect of current trial congruency, with errors on incongruent trials being 0.19 more probable than on congruent trials ($F(1, 14) = 18.909, p < .005, \eta^2 = .575$). No other effects reached significance (all p 's $> .25$).

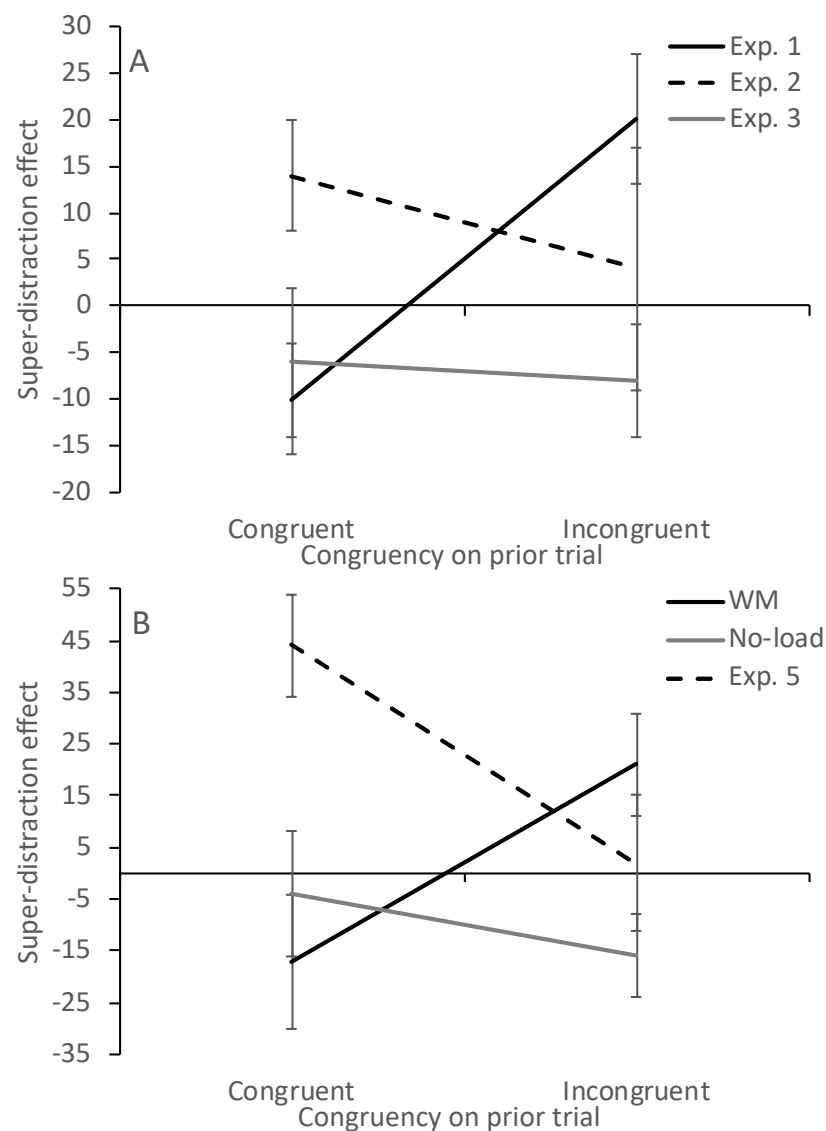


Figure 2.4. Group mean super-distraction effect for each current trial flanker value/brightness condition. A. Experiments 1 – 3. B. Experiments 4 (WM and No-load) and 5. Error bars represent ± 1 s.e.

The pattern of results here clearly show that previously learned, irrelevant value associations are able to influence processing priorities even when they offer no prospect of monetary outcomes, confirming previous reports of such effects using value-associated stimuli as irrelevant pre-target stimuli in a non-rewarded attention task (Rutherford et al., 2010). Importantly, these data show that value-associated flankers did not capture attention under all conditions. Unlike most previous reports of value-based attention capture where

sequential trial effects are not considered, and distractor effects are presumed on all trials, I found that value-dependent distraction depended on the conflict of the prior trial. This finding raises serious challenges for extant accounts of value-based attention capture that posit modulation of a perceptual priority mechanism. However, the findings of this experiment are consistent with the notion that value associations influence the motivational intensity driving specific cognitive operations.

Experiment 2

To more directly differentiate motivational and perceptual salience, I conducted a second flanker experiment, this time manipulating only flanker brightness and omitting the value learning phase of the experiment. The aim was to assess how perceptual salience, as opposed to motivational salience of flankers might influence CE_{Con} and CE_{Incon} in the flanker task. Perceptual competition models predict that the difference between CE_{Con} and CE_{Incon} will be greater for bright versus dim flankers. In this view, brighter stimuli should generate higher peaks on a perceptual priority map and thus be more likely to capture attention increasing interference in a bottom-up fashion. Such effects should be exacerbated by a preceding congruent trial when attention to flankers is not suppressed. The motivational competition hypothesis predicts a similar outcome. The rationale for the current experiment was therefore not to distinguish between perceptual and motivational models, but rather to distinguish the effects of physical versus motivational salience on flanker effects.

Method

Stimuli

Stimuli in the flanker task in the experiment differed in two important ways from Experiment 1. First, although all symbols were still always presented in orange or purple, they were presented as dim (Purple [87, 75, 87]; Orange: [120, 86, 1]) or bright (Purple [168, 145, 168]; Orange [201, 145, 2]). Second, only two different symbols were used. This was used to reduce perceived complexity due to lack of visual experience with the hiragana (no value learning task) and to focus the task more closely on colour discrimination.

Procedure

Value-Learning Task. There was no value-learning task.

Flanker Task. One of the two symbols always appeared as bright and the other as dim and symbol-brightness assignments was counterbalanced across participants. Each symbol was presented in orange or purple equally often. The target and flanker symbol/luminance, target and flanker colour, and congruency were all fully crossed within the flanker task.

Results and Discussion

Flanker Task. As in Experiment 1, the statistical analysis of RT showed significant effects indicative of CA. Specifically, RTs were slower (by 50 ms) when target and flanker colour was incongruent versus congruent ($F(1, 14) = 69.219, p < .001, \eta^2 = .832$); they were faster (by 17 ms) when preceded by an congruent versus an incongruent trial ($F(1, 14) = 31.308, p < .001, \eta^2 = .691$); and as in Experiment 1 these current and prior trial congruency effects interacted significantly ($F(1, 14) = 11.049, p < .01, \eta^2 = .441$). However, unlike Experiment 1, the three-

way interaction (flanker brightness X prior trial congruency X current trial congruency) was non-significant ($F(1, 14) = .372, p = .552, \eta^2 = .026$), indicating that flanker brightness had a non-significant effect on CA. Yet, the planned comparison of the super-distraction effect (defined here as CE with bright flankers minus CE with dim flankers) after a congruent trial was significant ($t(14) = 2.295, p < .05$). This is in stark contrast to Experiment 1 that showed super-distraction effects only after incongruent trials.

These between-experiment differences are supported by an ANOVA on mean RT using Experiment (1, 2) as a between-groups factor in addition to the previously described within-subjects factors. The analysis showed a significant four way-interaction (prior trial congruency X current trial congruency, X flanker value/brightness X and salience type; $F(1, 28) = 4.924, p < .05, \eta^2 = .150$). Importantly, CA was significantly larger (by 21 ms) with flankers high in physical salience compared to those high in motivational salience ($t(28) = 2.205, p < .05$) and super-distraction effects after congruent trials were significantly larger in Experiment 2 (by 25 ms) than in Experiment 1 ($t(28) = 2.897, p < .01$).

Errors in the current experiment were modestly more likely (by .024) when the current trial was incongruent compared to congruent ($F(1, 14) = 9.312, p < .01, \eta^2 = .399$), and more likely (by .018) when the previous trial was incongruent compared to congruent ($F(1, 14) = 15.955, p < .005, \eta^2 = .533$). No other error effects reached significance (all $ps > .25$).

The pattern of results obtained in Experiments 1 and 2 show clear dissociation between motivational and perceptual salience. This dissociation is not easily accounted for by views positing that motivational salience enhances the strength of perceptual representations. Such views predict a similar pattern of effects for both experiments, notwithstanding the possibility that the magnitude of physical and motivational salience may

have been dissimilar. Finding salience effects that were opposite in direction is however consistent with the view that motivational salience affects processing priorities using mechanisms distinct from those affected by physical salience.

Experiment 3

If processing priorities depends on a competition among motivational states, then flanker stimuli that are only weakly linked to motivationally salient outcomes should be less effective at disrupting performance than stimuli with stronger, more accessible value associations. Experiment 1 presented coloured stimuli during the learning task and even though colour was not predictive of value, all value-learned shapes were either orange or purple, as seen later in the flanker task. This should have facilitated activation of value-associations leading to the pattern of super-distraction effects seen in that experiment. In the current experiment, I sought to weaken the link between learned value and flanker stimuli by eliminating colour using only white symbols in the value learning task, but retaining colour in the flanker task as in Experiment 1. Considering that associative transfer is more efficient when the relevant features remain consistent (Le Pelley, 2004), I predicted weak activation of value associations and thus weak motivational intensity for processing flanker shape. This should reduce or eliminate super-distraction effects. Note that a similar prediction can be made based on the notion that value associations boost perceptual representational strength. Although this experiment does not serve to distinguish these accounts, its follow-up (Experiment 4) uses findings from this study to further contrast the motivation-based and perception-based frameworks for explaining value effects on visual processing.

Method

Procedure

Value-Learning Task. The same procedure as used Experiment 1 was followed except that all symbols appeared in white. Six symbols, two producing each outcome (win, loss, no-value) were used,

Flanker Task. One symbol assigned to each value in the value-learning task was presented in orange and the other in purple, mirroring the conditions of Experiment 1.

Results and Discussion

Value-Learning Task. Performance improved significantly across blocks $F(2, 28) = 33.210, p < .001, \eta^2 = .703$) and averaged 83% correct (S.D. = 6%).

Flanker Task. As in the previous two experiments, the statistical analysis of RT showed significant effects indicative of CA. RTs were slowed by 49 ms when target and flanker colour were incongruent compared to congruent ($F(1, 14) = 122.651, p < .001, \eta^2 = .898$); were faster (by 13 ms) when the prior trial was congruent versus incongruent ($F(1, 14) = 30.533, p < .001, \eta^2 = .686$); and these effects significantly interacted ($F(1, 14) = 17.967, p < .005, \eta^2 = .562$). However, in contrast to Experiment 1, the 3-way interaction (current congruency X prior congruency X flanker value) was non-significant ($F(2, 28) = .137, p = .872, \eta^2 = .010$), as were all other effects involving flanker value (flanker value: $F(2, 28) = 2.554, p = .096, \eta^2 = .154$; current congruency x flanker value: $F(2, 28) = 2.201, p = .129, \eta^2 = .136$; previous congruency x flanker value: $F(2, 28) = 1.360, p = .273, \eta^2 = .089$). To underscore, comparisons

of CE showed that neither CE_{Con} ($t(14) = .759, p = .461$) nor CE_{Incon} ($t(14) = 1.309, p = .212$) were significantly affected by flanker value (see Figure 2.5).

An ANOVA on mean RT using Experiment (1, 3) as a between-subjects factor showed a significant four way-interaction (prior trial congruency X current trial congruency X flanker value X and Experiment); ($F(1, 28) = 4.515, p < .05, \eta^2 = .139$). Importantly, with value flankers CA was 20 ms larger in Experiment 3 than it was in Experiment 1 ($t(28) = 2.166, p < .05$; See Table 2.4). Additionally, super-distraction effects (Figure 2.4) after incongruent trials were significantly larger in Experiment 1 than in Experiment 3 (by 28 ms, $t(28) = 3.103, p < .01$).

As in the previous two experiments, errors were significantly ($p = .031$) more likely when the current trial was incongruent compared to congruent ($F(1, 14) = 20.157, p < .005, \eta^2 = .590$). An interaction effect of prior trial congruency x current trial congruency was marginal ($F(1, 14) = 3.954, p = .067, \eta^2 = .220$), and all other effects were non-significant (all p 's $> .18$).

Absence of an effect of flanker value in this experiment could mean that value associations were not activated at all because participant did not generalize learning with white symbols to coloured symbols. Alternatively, coloured flankers may have only very weakly activated symbol value associations, resulting in a weak motivational intensity to process symbol shape. The next experiment investigated the latter possibility.

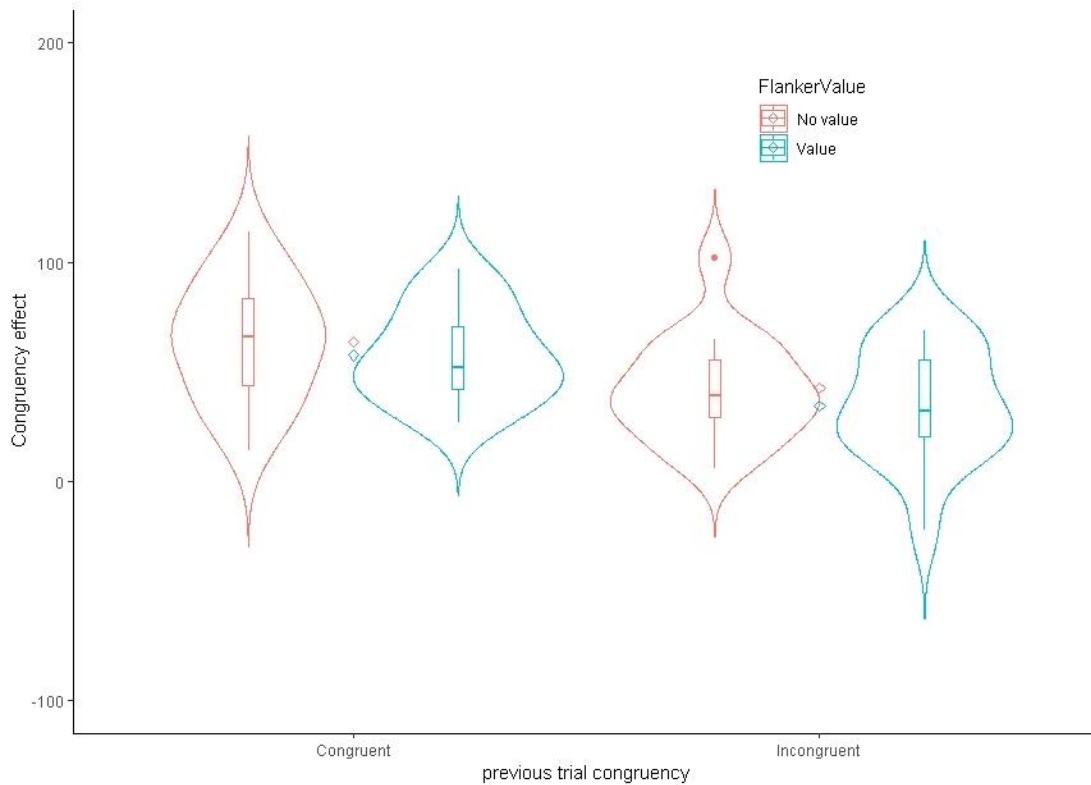


Figure 2.5. Group mean CE_{Con} and CE_{Incon} for each current trial flanker value in Experiment 3.

Experiment 4

The motivation-based framework postulates that the cognitive operation or action with the greatest motivational *intensity* will control behaviour. In the flanker task used in all the experiments reported here, the ‘attend colour’ motivation should be relatively high compared to the drive to ‘attend shape’ because colour is the relevant feature for the task. In Experiment 1, I enhanced shape-directed motivation using value associations that were easily activated in the flanker task by virtue of close correspondence between the stimuli in the learning and flanker tasks. In Experiment 3, I lowered this correspondence by using only white symbols in the learning task and thus weakened the activation of value associations in the flanker task. This presumably caused super-distraction effects to disappear because motivation to process flanker shape was weak.

It was reasoned that adding a secondary task that required colour processing should decrease the motivation to process flanker colour, consequently increasing the relative intensity to process flanker shape. This was based on the observation that task-irrelevant processing in an attention task is increased when the processing requirements in a concurrent working memory (WM) task matched those of the target processing in the attention task (Kim, Kim, & Chun, 2005). Specifically, when a concurrent WM load and target processing in a modified-Stroop task both relied on verbal processing, but the distractor in the Stroop task required spatial processing, distractor interference was increased compared to when there was no WM task (Kim et al., 2005). This was not because of the increased cognitive load (e.g., Lavie, 2005), but was dependent on the WM feature overlapping with, and thus increasing the cost of, target processing. In particular, in a second experiment they also showed that when the dominant feature in the WM task matched that of the distractor in the Stroop task, Stroop interference was reduced compared to without a WM load (Kim et al., 2005). Similarly, when discriminating the orientation of a shape, a line segment distractor that matched the orientation of several line segments of the target when it was oriented one way but not the other causes increased motivation to suppress (i.e. increased cost of processing) the distractor compared to when the task was to simply detect a shape (i.e., no cost of processing the distractor, Hickey et al., 2009).

To test this account, Experiment 3 was repeated but this time demanding, colour-based, concurrent secondary task was added during flanker trials. The aim was to decrease the motivational intensity for processing flanker colour, allowing the intensity of the motivation to process flankers as boosted by value associated shapes to gain relative strength and thus influence response. Thus, super-distraction effects should once more emerge. The

second aim here was to replicate the null findings from Experiment 3 in a second group of participants who performed the task with an undemanding, orientation-based secondary task that did not involve a concurrent colour-based WM load.

With this in mind, participants in Experiment 4 underwent value learning using white letters only. Half of participants then conducted the flanker task whilst at the same time being engaged in a colour-based visual WM task. Remaining participants were required to do a secondary, orientation task that did not involve carrying a concurrent WM load demand. It was predicted that the WM group should show effects of flanker value (similar to Experiment 1) whereas the no-load group should produce results similar to those found in Experiment 3, i.e. show no super-distraction effect.

Method

Stimuli/Apparatus

Stimuli used in the WM task and orientation judgment task were multicoloured arrays (each 5° square) comprised of 25 small squares (1° square) each randomly filled with one of 10 equiluminant colours. The stimuli set comprised 16 unique arrays that were used as study and test stimuli.

Procedure

Value-Learning Task. In contrast to Experiments 1 and 3, only three white symbols were used in the learning task, one for each value (win, loss, no-value). No matched trials were presented and each of the three mismatched symbol combinations were equally likely.

Flanker Task. As in Experiment 3, all symbols were equally likely to appear in either purple or orange. The flanker task was as described for Experiments 1 and 3 with the following exceptions. Only symbols with no-value or win associations were used; each was equally likely to appear in orange or purple. All flanker trials were presented as 2-trial sequences with each trial pair beginning and ending with a WM study and test array, respectively. Each 2-trial sequence began with a fixation cross (1000 ms) followed by a 400 ms display of the WM array. Two flanker trials with the same timings as used previously were then presented. Finally, a test array was presented rotated either 5° clockwise or anticlockwise for 2000 ms or until response. Participants in the WM group were asked to press the space bar using their left hand if the test and study array differed and to withhold response if they did not. Participants in the No-WM group were instructed to ignore the study array and to press the space bar with the left hand if the test array was rotated clockwise and to withhold a response if it was rotated anticlockwise. The direction of rotation of the test array and its match/mismatch with the study array was pseudorandomly chosen on each trial such that for each group a space bar response was correct on half of trials and a no-go response was correct on remaining trials. Participants completed 10 blocks of 64 flanker trials (32 two-trial sequences per block). Flanker congruency, previous flanker congruency, flanker value, and correct secondary task response type (go, no-go) were fully crossed such that in each session there were 20 repetitions of each.

Data Analysis

RTs and error rates from the second flanker trial in the trial sequence were analysed as reported in the General Methods. Additionally, trials were removed for the first trial sequence in every block (3.1% in both groups), if responses on the second flanker trial (WM =

2.2%, no-load = 3.3%), the first flanker trial (WM = 2.9%, no-load = 3.8%), or the WM/orientation task (WM = 12.9%, no-load = 3.5%) were incorrect. A mixed-effects ANOVA with group as the between-subjects factor and flanker congruency, previous flanker congruency, and flanker value as within-subjects factor was conducted.

Results and Discussion

Value-Learning task. Overall error rates did not differ between groups ($F(1, 40) = .734$, $p = .397$, $\eta^2 = .018$) and averaged 91% (S.D. = 0.02) and 92% (S.D. = 0.01) in the WM and no-load groups, respectively. Performance improved significantly across blocks ($F(2, 84) = 46.563$, $p < .001$, $\eta^2 = .526$) and this rate of improvement did not depend on Group ($F(1, 40) = .077$, $p = .926$, $\eta^2 = .002$).

Flanker Task. RTs were 78 ms slower for the WM group compared to the No-WM Group ($F(1, 40) = 11.889$, $p < .005$, $\eta^2 = .229$), consistent with previous findings (de Fockert, Rees, Frith, & Lavie, 2001; Lavie, 2005; Lavie, Hirst, De Fockert, & Viding, 2004). Critically, the four-way interaction of group X current trial congruency X prior trial congruency X flanker value was also significant ($F(1, 40) = 7.265$, $p < .05$, $\eta^2 = .154$), justifying separate ANOVAs on the RT data from each group.

As in the previous experiments, the statistical analysis of RT showed significant effects indicative of CA for both groups. RTs were slower when the current trial was incongruent versus congruent [WM Group: 40 ms, $F(1, 20) = 20.921$, $p < .001$, $\eta^2 = .511$; No-WM Group: 37 ms, $F(1, 20) = 61.052$, $p < .001$, $\eta^2 = .753$]; RTs were faster when the prior trial was congruent versus incongruent [WM Group: 13 ms, $F(1, 20) = 6.227$, $p < .05$, $\eta^2 = .237$; No-

WM Group: 14 ms, $F(1, 20) = 12.049$, $p < .005$, $\eta^2 = .376$] and these two effects interacted significantly in both cases [WM Group: $F(1, 20) = 7.155$, $p < .05$, $\eta^2 = .263$; No-WM Group: $F(1, 20) = 7.141$, $p < .05$, $\eta^2 = .263$]. Critically, the three-way interaction involving flanker value was only significant in the WM Group ($F(1, 20) = 8.616$, $p < .01$, $\eta^2 = .301$), and not the No-WM Group ($F < 1$).

As shown in Figure 2.6, for the WM group CE_{Incon} was significantly larger (by 21 ms) with value versus no-value flankers ($t(20) = 2.098$, $p < .05$), producing a super-distraction effect (See Figure 2.4) comparable to the 20 ms effect obtained in Experiment 1 (Figure 2.4). Here, as in Experiment 1, CE_{Con} was unaffected by the value of the flankers ($t(20) = 1.306$, $p = .206$). Further replicating Experiment 1, the WM group showed CA with no-value flankers, CE_{Incon} was significantly smaller (43 ms) than CE_{Con} ($t(20) = 4.756$, $p < .001$), resulting in a significantly larger CA effect for no-value versus value flanker conditions ($t(20) = 2.938$, $p < .01$).

For the No-WM group, comparisons of CE showed that neither CE_{Con} value ($t(20) = .309$, $p = .761$) nor CE_{Incon} ($t(20) = 1.893$, $p = .073$) were significantly affected by flanker value, resulting in no super-distraction effects (Figure 2.4). Moreover, there was no effect of value on CA ($t(20) = .895$, $p = .381$), replicating Experiment 3.

Furthermore, super-distraction effects after congruent trials did not differ between no-WM and WM groups ($t(20) = .857$, $p = .402$), but after incongruent trials super-distraction effects were significantly larger in the WM group than the no-WM group (by 37 ms, $t(40) = 2.819$, $p < .005$).

Across both groups, errors were .02 more probable when the current trial was incongruent versus congruent ($F(1, 40) = 8.074$, $p < .01$, $\eta^2 = .168$). There was also a marginal interaction between current trial congruency x group ($F(1, 40) = 3.640$, $p = .064$, $\eta^2 = .083$);

Value-based Modulation of Visual Attention Depends on Competition Among Motivational States

driven by a slightly larger CE in the No-WM Group compared to the WM Group by .02. No other effects, including any involving group, reached significance (all p 's > .15).

Value-based Modulation of Visual Attention Depends on Competition Among Motivational States

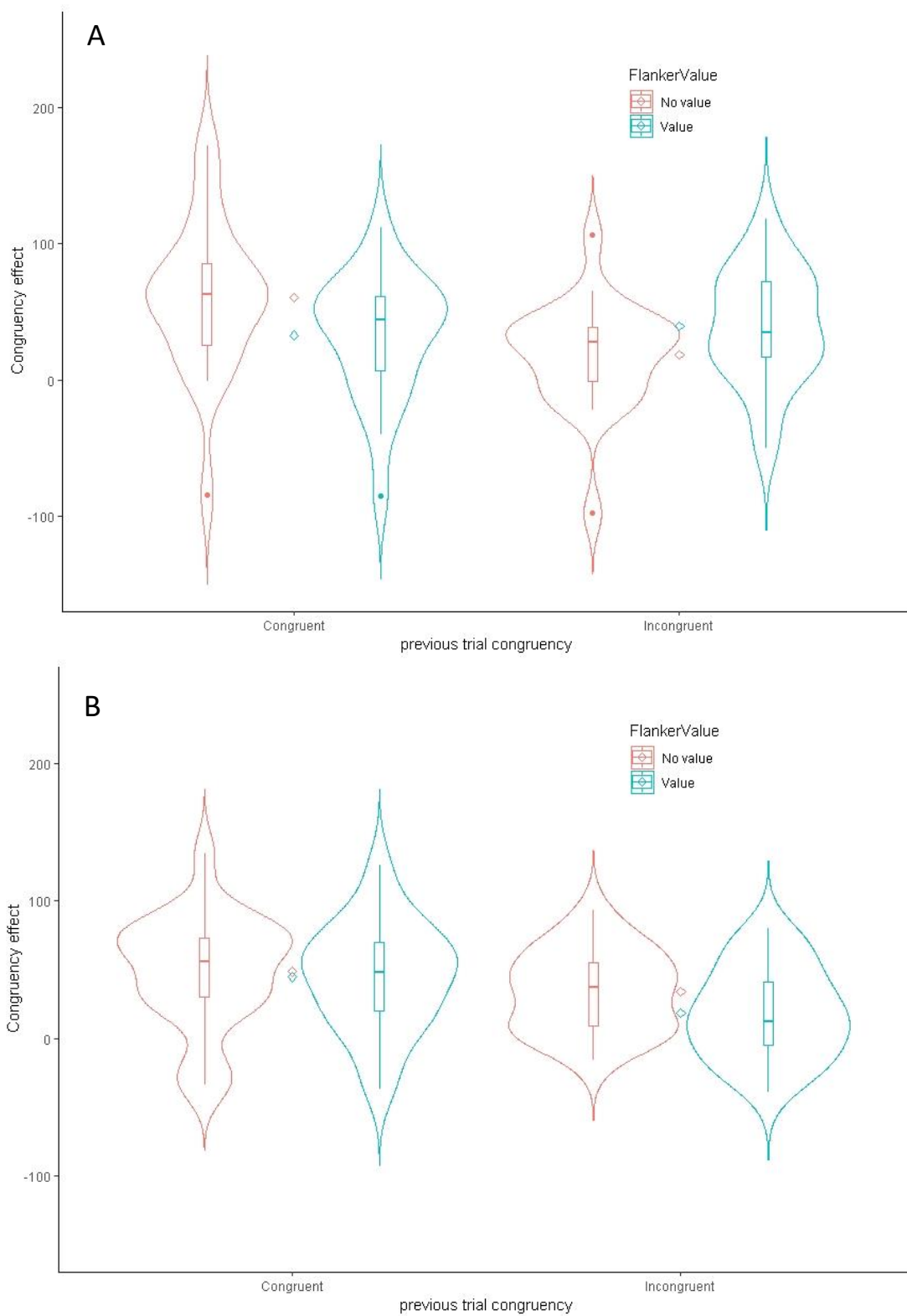


Figure 2.6. Group mean CE_{Con} and CE_{Incon} plotted separately for each current trial flanker value in the WM load (A) and the No-load (B) conditions in Experiment 4.

The results from this experiment are important because they provide replications of the effects in Experiment 1 and 3, thereby bolstering confidence in these findings. Furthermore, they show an interesting and counter-intuitive effect, namely that carrying a colour-based WM load allows distractors with shape-based value associations to interfere with performance on a colour-based attention task. In contrast when no such WM load is being carried, such previously learned colour associations have no effect on performance.

Given that the secondary task was more difficult in the WM compared than the no-load group one possibility is that the different pattern of performance between the two conditions could be related, at least in part, to the differential demands of the secondary task, independent of the colour-based nature of both tasks in the WM group. This possibility is reasonable but not explanatory as although finding greater distraction effects with a more demanding concurrent WM load has been previously reported (Lavie, 2005; Lavie et al., 2004), the notions of perceptual and cognitive load that have been used to account for them cannot explain differences observed here with value versus no-value flankers in the WM group. Specifically, the cognitive load in both reward conditions is identical; yet the pattern of flanker interference effects was clearly dependent on the value-association. Similarly, the perceptual and cognitive loads in the flanker task of Experiments 1 and 3 were the same, yet distinct differences in super-distraction effects were observed.

Experiment 5

Perceptual competition models do not predict an increase in super-distraction effects after an incongruent trial with a concurrent colour-based WM load, as seen in Experiment 4. Regardless of a concurrent WM load, perceptual competition models predict that salient

stimuli produce higher peaks on a perceptual priority map and thus capture attention increasing interference in a bottom-up fashion. After a congruent trial when attention to flankers is freely available such effects are exaggerated resulting in a larger super-distraction effect than after incongruent trials, as seen in Experiment 2. With a colour-based WM load, predictions made by perceptual competition models do not differ as the WM load does not influence the physical salience of stimuli. They still predict that super-distraction will be larger after a congruent trial. Similar to the rationale of Experiment 2, here I again attempted to distinguish the effects of physical salience compared to motivational salience (Experiment 4; WM group) on flanker effects. In this experiment the flankers were again either bright or dim, and the flanker task was performed alongside the colour-WM task. It was predicted that the results would mirror those found in Experiment 2.

Method

Stimuli/Apparatus

Stimuli in the flanker task were the same as in Experiment 2. Stimuli used for the concurrent WM task were the same as in the WM group in Experiment 4.

Procedure

Value-Learning Task. There was no value-learning task.

Flanker Task. Only two symbols were used; one was always bright and the other dull to match the symbols/salience associations from Experiment 4. Otherwise, the flanker task was the same as that used in Experiment 4.

Data Analysis

Data were analysed as in Experiment 4. Trials were removed for the first trial sequence of every block (3.1%), if responses on the second flanker trial (2.5%), first flanker trial (3.7%), or the WM task were incorrect (15.1%). A repeated-measures ANOVA with the factors; flanker congruency, previous flanker congruency, and flanker brightness was conducted on remaining data.

Results and Discussion

Flanker Task. RTs were 37 ms slower when the current trial was incongruent versus congruent ($F(1,20) = 31.515, p < .001, \eta^2 = .612$). RTs were 24 ms slower when the prior trial was incongruent compared to congruent ($F(1, 20) = 15.704, p < .005, \eta^2 = .440$). The two-way interaction between current trial congruency and flanker brightness was also significant ($F(1, 20) = 9.511, p < .01, \eta^2 = .322$), driven by a larger congruency effect when the flankers were bright compared to dull by 23 ms ($t(20) = 3.084, p < .01$). Importantly, the three-way interaction between prior trial congruency, current trial congruency, and flanker brightness was also significant ($F(1, 20) = 5.846, p < .05, \eta^2 = .226$).

As shown in Figure 2.7 and consistent with Experiment 2, CE_{Con} was significantly larger (by 44 ms) with bright versus dull flankers ($t(20) = 4.453, p < .001$), producing a large super-distraction effect. CE_{Incon} was unaffected by flanker brightness ($t(20) = .330, p = .745$), consequently no super-distraction effect was present. In addition, the super-distraction after congruent trials was significantly larger (by 42 ms) than after incongruent trials ($t(20) = 2.418,$

$p < .05$). This is in sharp contrast to the results obtained in Experiment 4 (WM group) where the direction of super-distraction effects found was opposite.

Error rates were low on the second trial in the sequence (.02). However, errors were .02 more probable when the prior trial was incongruent compared to congruent ($F(1, 20) = 13.743, p < .005, \eta^2 = .407$). Errors were also marginally more likely (by .01) when the current trial was incongruent versus congruent ($F(1, 20) = 4.162, p = .055, \eta^2 = .172$). No other effects reached significance (all $ps > .493$).

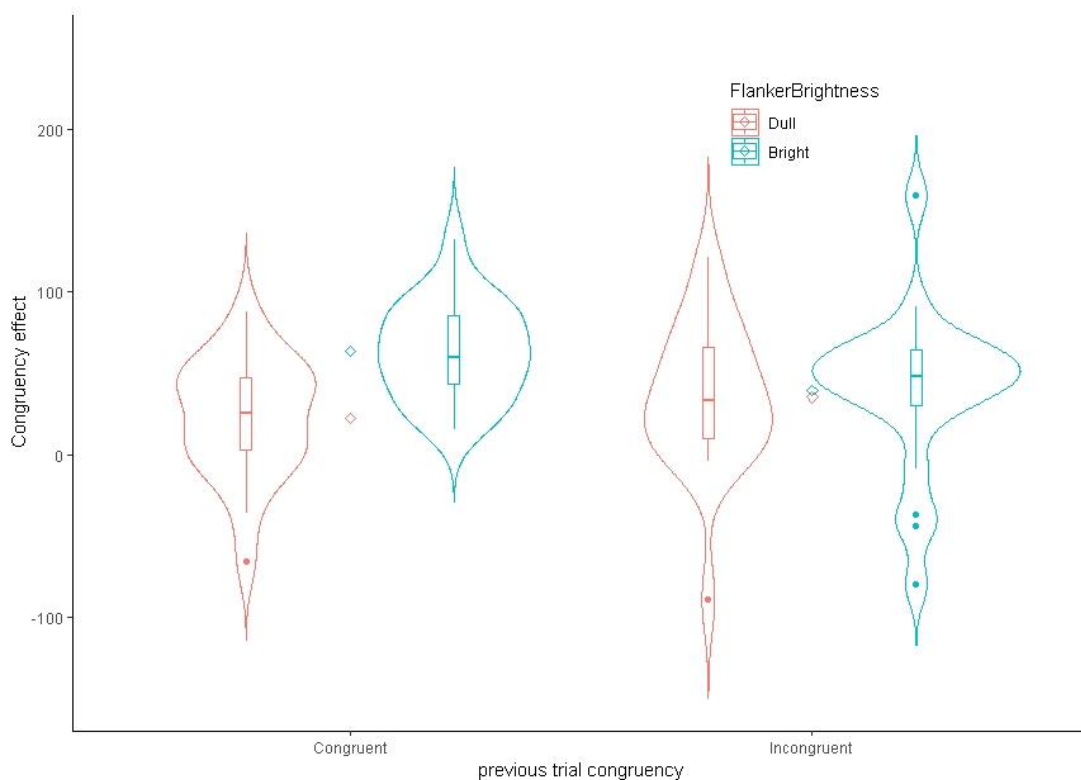


Figure 2.7. Group mean CE_{Con} and CE_{Incon} plotted separately for each current trial flanker brightness in Experiment 5.

The results from this experiment corroborate the findings from Experiment 2. The increased super-distraction after congruent compared to incongruent trials with physically salient flankers is consistent with the predictions of perceptual competition models. The findings further demonstrate that the effects of motivational salience and physical salience

are not consistent. The results of this experiment also rule out an alternative interpretation of the data from Experiment 4. In Experiment 4, as errors on the WM/orientation task were larger in the WM group compared to the no-WM group it was not clear whether the increased influence of valued flankers was motivationally mediated or simply the result of a more demanding secondary task. Given the results of Experiment 5, the latter interpretation can be ruled out as the WM task here was as demanding as that in the WM group in Experiment 4, however the pattern of results is clearly not the same. Therefore, it is not simply the presence of a demanding secondary task that results in increased super-distraction after incongruent trials. Instead, the results are consistent with shifts in the motivational intensity to process flanker colour induced by the concurrent colour-based WM task increasing the relative intensity to process flanker shape.

General Discussion

In five experiments, the speed and accuracy of behavioural responses in a simple colour flanker task were examined, specifically exploiting well-studied sequential trial phenomena that show greater flanker interference (i.e., CE) after congruent trials than after incongruent trials (Gratton et al, 1992). In Experiments 1, 3, and 4, meaningless symbols were first imbued with value or no-value associations, and then later these conditioned symbols were used as stimuli in the flanker task, with the aim of comparing CE effects when flankers had value versus no value. In contrast to these experiments on motivational salience, Experiments 2 and 5 had no learning component but instead used bright versus dim flankers so that the effects of perceptual salience could be directly assessed. In Experiment 1, learning

involved symbols that had the same colour as those seen subsequently in the flanker task; in Experiment 3 and 4, learning involved only white symbols, but the subsequent flanker task only used coloured symbols (as in Experiment 1). Experiment 4 (but not 3) required one group of participants to engage in a colour-based WM task concurrently with the flanker task, with another group carrying no such WM load (replicating conditions of Experiment 3). In all studies CE effects obtained with no-value (or dim) flankers were subtracted from those obtained with value (or bright) flankers. Of interest in each experiment was whether the resultant index of super-distraction ($CE_{\text{value(bright)}} - CE_{\text{no value (dim)}}$) depended on the congruency of the preceding trial. Sequential trial effects were of interest because two different accounts of the effects of motivational salience on visual performance, namely the perceptual competition account and the motivational competition account, make different predictions regarding the interactions between flanker value and prior trial congruency. These results come out strongly in favour of the motivational competition account.

The Perceptual-competition account

The more widely held perceptual competition account of value-based super-distraction proposes that motivational salience acts like perceptual salience boosting the strength of distractor perceptual representations and allowing stimuli to compete more effectively with target stimuli in a perceptual competition for attention (e.g., Chelazzi et al., 2014). This notion of perceptual competition, often described using a 'spatial processing priority map' analogy, predicts that the interactive effects of flanker value and prior trial congruency should be in the same direction in Experiments 1 and 2, although clearly, they were not. More specifically, this view predicts minimal super-distraction after incongruent

trials and large super-distraction after congruent trials in both experiments. Experiencing an incongruent trial on one trial is thought to enhance target focus on the subsequent trial (Ullsperger et al., 2005), an operation that should generally cause a reduction in CE effects and should neutralize any boost in distractor representational strength that arise from high value-associations (Experiment 1) or greater physical salience (Experiment 2). Thus, in both experiments CE effects and super-distraction should be small when the preceding trial is incongruent. Although such an effect was observed in Experiment 2, this effect was absent in Experiment 1. Perceptual competition theories also predict that after experiencing a congruent trial in which flankers provide redundant, target-congruent information, flanker processing should be facilitated (or at least not suppressed) on the subsequent trial; this should enable boosts in perceptual representational strength that arise from high value-associations or greater physical salience to have maximal impact, speeding responses on congruent trials and slowing responses on incongruent trials in both experiments. The net result should be large CE and large super-distraction effects after congruent trials. Again, this effect was found in Experiment 2 but not in Experiment 1. Instead large super-distraction effects were found after incongruent trials and non-significant effects after congruent trials. This effect and the clear differences between the results of the two experiments raise serious doubts about the viability of a perception competition account for explaining motivational salience or value-based effects on visual attention. To explain these findings, I suggest an alternative explanation based on a competition among motivational states that is grounded in the cognitive control literature (e.g., Shenhav et al., 2013; Braver et al., 2015).

The motivation-competition account

The motivation-competition account posits that control over high-level cognition and action results from a dynamic competition among concurrently active and largely unconscious motivational states. In this view, a motivational state is an activated neural network that represents a desired goal, a motivational direction (the series of cognitive operations and actions needed to achieve the goal), and an index of motivational intensity. The latter is a value derived by comparing predicted costs versus benefits of achieving the goal (Shenhav et al., 2013) in the current context and relies heavily on a combination of prior experience and current sensory processing. The most intense motivational state active at any point in time will win the motivation-based competition and control high-level processing (e.g., attention) and action. Competition is viewed here as an emergent property, possibly involving reciprocal inhibition so that as one state gains intensity, others lose power. Importantly, motivational states can be automatically activated by external cues if they signal an opportunity to achieve goals. This is an important feature of the motivational competition framework because it allows any external cue to potentially activate multiple motivational states. A cue's capacity to instantiate a motivation state, i.e., its incentive value (Robinson & Berridge, 1993), is determined by prior learning. Like biased competition models of attention (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001) motivation-based competition can be biased using cognitive control mechanisms. In this view, these neural mechanisms adjust the predicted costs (effort) and/or benefits associated with achieving specific goals (Hare, Camerer, & Rangel, 2009), thus modulating motivational intensity and biasing the competition.

An important distinction between the motivation-competition and the perception-competition view is that in the former a single sensory cue can activate multiple competing states with different motivational directions and intensities, whereas in the latter, each cue has only one representation that presumably embodies all its features (Duncan, 1984; Kahnemann and Treisman, 1984). For example, in the former framework, a coloured symbol could motivate colour recognition (i.e., be colour-directed) and/or shape identification (i.e., be shape-directed), whereas in the latter framework, a single representation holds both colour and shape information. Another critical distinguishing feature of the motivational competition notion is that it specifies a direct means by which prior history can be combined with current sensory information, a feature lacking in perceptual models (e.g. Awh et al., 2012)

How can the motivation-competition framework account for the main findings presented here? First, consistent with extant views on cognitive effort (Botvinick et al., 2001; Shenhav et al., 2013), prior conflict from a just prior incongruent trial in the colour-based flanker task should weaken motivation to attend flanker colour on the subsequent trial. As a result, flanker shape-directed motivation should be comparatively enhanced, allowing any boost from value-associations to make this motivational state competitive. Thus, greater RT slowing should be evident on subsequent incongruent trials with value but not with no-value flankers, specifically exacerbating CE effects with value flankers and thus producing a large super-distraction effect. Indeed, this is the result found in Experiment 1. Applying similar reasoning, flanker colour-directed motivation should be especially high after a colour-congruent trial due to low predicted effort and high benefit, allowing it to easily out-compete any shape-directed motive. Even with a boost from value associations, this motivational state would be relatively weaker and thus super-distraction effects should be absent. Finding no

effect of flanker value in this condition in Experiment 1 is therefore consistent with the motivational competition view.

The motivation-competition view also can explain the counterintuitive findings of Experiment 4 where making the flanker task more difficult enhanced value-based flanker effects. In Experiment 3 and 4 learning involved white symbols only whereas the flanker task used these symbols but presented them in orange or purple, as in Experiment 1. When WM was loaded with a coloured pattern in one condition of Experiment 4, the same value effects as seen in Experiment 1 were found. When the WM task was absent (Experiment 4: No-load condition; Experiment 3), prior value learning had no effect on the performance in the flanker task. Couched within the motivational competition framework, the findings of Experiment 4 are predictable. The colour-based WM load should have caused cognitive conflict for engaging with the colour-based flanker task, thus increasing the predicted effort of target and flanker colour processing. This should reduce motivational intensity for colour processing and thus explains the overall slowing in the WM load versus no-load condition. With colour-motives less intense, shape-directed motives instantiated by value associations would have become relatively more competitive, accounting for why the pattern of value-based effects seen in Experiment 1 once more emerged. This finding is important because it suggests that value-associated stimulus features are able to automatically activate motivational states that can easily take control over cognition and behaviour if other concurrent motivational states suddenly wane. This dynamic see-saw process can thus explain sudden impulsivities, including relapses from abstinence in addicts in the presence of addiction related cues.

Perceptual competition theories predict a different outcome for Experiment 4. They posit that the contents of WM can be used to pre-activate sensory representations biasing

them to be more competitive when matching stimuli are encountered (e.g. Desimone & Duncan, 1995). A WM load of a coloured pattern, as used in Experiment 4, should therefore have biased perceptual competition away from flanker and target related colours, explaining the general slowing for all conditions that was found. However, perceptual competition biased by the contents of WM (see Olivers, Peters, Houtkamp, & Roelfsema, 2011 for a review) does not predict a differential effect of WM load depending on flanker value, and although some work suggests a modulating role of prior history on attention biases by WM content (Kiyonaga, Egner, & Soto, 2012) no clear account for these effects have been previously put forward.

Another somewhat related view of value-based super-distraction postulates that during learning stimuli signalling motivationally salient outcomes garner habitual responses, or response tendencies, that become active whenever such stimuli are subsequently encountered (de Wit et al., 2012; Graybiel, 2008; Wood & Runger, 2016). In value-based attention capture paradigms, repeated exposure to reward predicting stimuli may establish an associative link that later enables automatic preferential attentional selection whenever these stimuli are present in visual arrays (Anderson, 2016). However, such automaticity is clearly absent in some situations. For example, in Experiment 1 responses on flanker trials that were preceded by a congruent trial showed no super-distraction effects leaving this account unsatisfying. A similar view, Ideomotor theory, goes a step further by postulating that associative links between cues, actions, and outcomes are bi-directional, with each element able to activate the other because of a common complex representation (Eder et al, 2015; Greenwald, 1970; Hommel et al, 2001). This notion is very close to what is referred to here as a motivational state but here I add the notion of competition between different motivational directions, especially when they involve different cognitive operations. It is this aspect of

competition that is necessary to explain super-distraction effects in the current series of experiments.

A difference between the current series of experiments and those previously conducted that favour a perceptual account of super-distraction effects is that I employed an operant conditioning procedure during learning whereas they typically utilize Pavlovian conditioning (e.g., Anderson et al., 2011). Given that my interpretation is framed around instrumental processes could the different learning contexts explain why a perceptual competition account is not sufficient for the current set of experiments? Although perceptual frameworks have typically accounted well for previous super-distraction effects in the literature, as mentioned above they cannot account for the current data. The motivational competition framework posited here though can not only encompass the current data, but I believe it also explains well super-distraction effects in the literature. Unpicking the consequences of operant versus Pavlovian conditioning during learning is an interesting future direction for the field.

Although the current data cannot speak directly to brain mechanisms supporting the notion of a motivational competition, numerous neuroscientific studies suggest a plausible neural architecture primarily involving frontal-striatal structures. Striatal mechanisms are known to play a role in the rapid instantiation of motivation states arising from motivationally salient stimuli (Robinson & Berridge, 1993, Schultz et al., 1997; Schultz, 2000), such as the value-associated distractors used here; these mechanisms are also known to be heavily modulated by signals from frontal cortex (Hare et al., 2009; Holroyd & Yeung, 2012). Perhaps motivational intensity is initially determined by these subcortical striatal mechanisms but can be quickly suppressed or amplified by frontal areas able to access information about predicted

value and predicted effort. Two areas that are associated with estimating effort and cognitive conflict are the dorsal anterior cingulate cortex (dACC; Botvinick et al, 2001; Shenhav et al., 2013) and the insula (Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010), although other structure may also be involved. The ventromedial pre-frontal cortex (vmPFC; e.g., Kable & Glimcher, 2007), orbitofrontal cortex (OFC; Li et al., 2016), and dorsolateral PFC (dlPFC) on the other hand are known to be involved in prediction of outcome value, with dlPFC modulating value estimates provided by the former structures when self-control is required (Hare et al, 2009). Collectively these frontal structures may form a network that not only estimates net benefits of concurrent motivation states but also enables dynamic competition so that a single state can emerge to control cognition and behaviour. In addition to reacting to the instantiation of a new motivation, the network could also act predictively when the current context is associated with reward outcomes from specific stimuli (Anderson, 2015). Such proactive adoption of a motivational direction towards reward associated stimuli would lead to stronger representations of these stimuli in early visual areas (Anderson, Kuwabara, et al., 2017; Anderson, Laurent, et al., 2014; Bayer et al., 2017; Hickey et al., 2010a; Hickey & Peelen, 2015).

In conclusion, these experiments have added to a growing body of empirical evidence showing that motivationally salient stimuli can unduly influence visual processing priorities, even when it is disadvantageous. However, these data advance theoretical understanding by showing that such effects cannot result from augmentation of perceptual representations that then effectively bias competition among stimulus representation. Instead, it is suggested that stimuli with motivationally salient associations can automatically instantiate motivation states that then compete to control cognitive operations and actions.

Chapter 3. Motivational Competition in Adolescents

Abstract

Adolescents are more likely to engage in risky behaviours. Underlying this propensity for risk taking, adolescents are thought to be hyper-sensitive to reward-associated stimuli and are more likely to activate motivational states (goals) reactively rather than in a proactive fashion. A consequence of these two is that adolescents show more goal flexibility because they are more sensitive to motivational states activated by external cues. Here, I investigated how adolescents resolve competition between externally driven and task-relevant motivational states. Adolescents (~17 years) and adults (~27 years) performed a colour-flanker task in which the task-relevant motivational state (whether to attend to the flanker colour) was constantly changing based on the response conflict experienced on the prior trial. Importantly, the shapes of some flankers were associated with value (imbued during a prior value-learning task with white shapes), thus conferring an externally driven, task-irrelevant motivational state to attend to the flankers. Results showed that only following response conflict (incongruent trials) were interference effects attributable to the value-association of the flankers found. This effect was only evident in adolescents but not adults. The results are discussed in relation to a motivational competition framework of adolescent risk-taking that emphasises adolescents inflating the perceived benefits of previously rewarding stimuli causing them to reactively initiate inappropriate goals.

Adolescence is a period of life often characterised by a propensity to engage in risky behaviours (e.g., substance use and dangerous driving) more so than at any other stage of life (Dahl, 2004; Kann et al., 2013). One contributing factor is likely to be societal; adolescence is when individuals begin to experience freedom in decision making as they take on greater individual responsibility for their own actions. However, the increased risk-taking is also often attributed to imbalances in cognitive development. Specifically, brain regions sensitive to the rewarding properties of stimuli are thought to develop much earlier than those required to maintain goal-directed cognitive control. This imbalance in neural maturation is most evident in mid-to-late adolescence (Casey, Jones, & Hare, 2008; Chambers et al., 2003; Geier & Luna, 2009; Luciana & Collins, 2012; Somerville et al., 2010; Spear, 2000; Steinberg, 2010). As a consequence of the imbalance, adolescents are thought to be hyper-sensitive to rewards and value-associated behaviours. Here, I investigate how attentional deployment to irrelevant value-associated distractors is affected by this proposed hyper-sensitivity to rewards in adolescents.

Neuroimaging research has shown that adolescents demonstrate greater activation in dopamine mediated midbrain regions, such as the ventral striatum, in response to rewards compared to both children and adults (Geier & Luna, 2009; Luciana & Collins, 2012; Somerville et al., 2010; Spear, 2000; Van Leijenhorst et al., 2010). Importantly, in adolescents, during an anti-saccade task, increases in BOLD activity in the ventral striatum on rewarded compared to unrewarded trials has been shown to predict better accuracy on rewarded versus neutral trials. In adults, rewards were not found to influence behavioural performance or ventral striatal activity (Padmanabhan et al., 2011). Such evidence suggests

that when rewards are contingent on goal-directed attention they improve attentional control in adolescents.

Although Padmanabhan et al. (2011) demonstrated improved performance in adolescents on rewarded versus unrewarded trials, baseline performance in the neutral condition was worse than in adults. Cognitive control coordinates activity throughout the brain to respond to stimuli relevant to current goals (Miller & Cohen, 2001). Sustained control is required to inhibit prepotent responses, such as in the anti-saccade task, and ignore task-irrelevant information. In adolescents, these sustained cognitive control abilities are still developing, and control is not thought to reach full maturity until early adulthood. However, adolescents are thought to compensate by utilising cognitive control in a more transient manner, as-and-when required (Andrews-Hanna et al., 2011; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; Hwang et al., 2010; Killikelly & Szűcs, 2013; Kramer et al., 2005; Luna, Garver, Urban, Lazar, & Sweeney, 2004; Padilla et al., 2014; Velanova, Wheeler, & Luna, 2009). Evidence has demonstrated that adolescents show a reduced BOLD response in brain regions (DLPFC) associated with sustained cognitive control compared to adults (Andrews-Hanna et al., 2011). Similarly, ERP evidence has shown that whereas response preparation activity (frontal CNV) is attenuated, activity (P3b) elicited by the stimulus is increased in late-adolescents compared to adults (Killikelly & Szűcs, 2013; Padilla et al., 2014).

These findings are consistent with extant views of cognitive control that assert a distinction between proactive and reactive control in goal initialization (Braver, 2012; Braver et al., 2007). First, proactive control reflects preparatory and sustained activation of behavioural goals consistent with task-demands that prioritise task-relevant stimuli. Reactive

control, on the other hand, mobilizes higher-level cognition in accordance with stimulus-driven goals, re-instantiated from prior encounters with the stimulus. As a function of being stimulus-driven, this latter control must be initiated post-stimulus onset and leads to only transient implementation of cognitive control (Braver, 2012). Importantly, different external cues or even different features (e.g., shape or colour) of the same cue can instantiate different and sometimes conflicting goals related to their cognitive analysis (e.g., identify colour, recognize shape). Recent models of cognitive control suggest that when such conflicts occur, it is resolved by an internal competition that depends on the intensity of the different motivational states (goals) to represent such information at a high level (Shenhav et al., 2013). If specific cues or cue features have been previously associated with reward, then they are likely to instantiate more intense motivational states due to greater predicted pay-off than cues with no prior reward history.

This motivational competition framework may offer an explanatory mechanism for the hyper-sensitivity to rewards often found in adolescents. Dopaminergic activity in the ventral striatum in response to reward cues is thought to closely relate to estimates of predicted pay-off (Robinson & Berridge, 1993). Therefore, the heightened reward sensitivity in adolescents coupled with the increased tendency to initiate control reactively, likely heightens the intensity of task-irrelevant, value-driven attentional biases in adolescents compared to adults (Ernst, Daniele, & Frantz, 2011; Romer, Reyna, & Satterthwaite, 2017).

Indeed, this assertion is consistent with current behavioural data showing a hyper-sensitivity in attention tasks to previously rewarding (Roper et al., 2014), emotionally significant (Grose-Fifer, Rodrigues, Hoover, & Zottoli, 2013) and personally significant (Braet & Crombez, 2003) task-irrelevant stimuli in adolescents. For example, Roper et al. (2014)

first imbued colours with a high or a low value, these same stimuli were then used as distractors in a subsequent visual search task. Search was for a unique shape, amongst homogeneously shaped distractors. Importantly, the colour of each stimulus was different, and on a proportion of trials one of the distractors could be in the previously high or low reward colour; on remaining trials no distractor was in a previously rewarding colour. No rewards were available in the visual search task. Replicating previous work (Anderson et al., 2011; Hickey et al., 2010a, b; Le Pelley et al., 2015; Rutherford et al., 2010), they found that adults were slowed by high value-associated distractors versus neutral distractors. However, such *super-distraction effects* extinguished after the first quarter of trials in adults. This is consistent with adults proactively updating their attentional set to ignore value-associated distractors. In adolescents, the super-distraction effect was greater than in adults and persisted throughout the experiment (Roper et al., 2014). These data are consistent with the motivational competition account. The increased super-distraction effects seen in adolescents suggest that they over-estimated the predicted payoffs associated with reward associated stimuli compared to adults. As a result, the stimulus driven motivational state that they instantiated inappropriately biased cognition.

Here, the aim was to directly assess whether adolescents show a strong, more persistent response to value-associated motivational states from external stimuli than adults in a paradigm that places task-relevant and externally generated (value-associated) motivational states in constant competition. In the current experiment, adolescents and adults completed a two-stage procedure. First, participants undertook a value-learning task where novel white symbols were imbued with a monetary value (win, loss, or no-value) so that only shape and not colour predicted reward outcomes. In a subsequent colour flanker

task (Eriksen & Eriksen, 1974) these same symbols were used as stimuli but were always presented in either orange or purple. The symbol shape was always irrelevant, and no further money could be earned in the flanker task. Participants had to make a speeded two-alternative forced choice about the colour of the central target. On half of trials the flankers were the same colour as the target (congruent); on remaining trials, they were opposite in colour (incongruent). The slowing of response times (RT) and increases in error rate on incongruent compared to congruent trials is known as the congruency effect (CE) and reflects distraction by flanker stimuli (Eriksen, 1995).

Of interest here was the common finding that CE depends on the congruency of the prior trial (Gratton et al., 1992); CE is larger after a congruent trial (CE_{con}) than after an incongruent trial (CE_{incon}). This difference in CE magnitude ($CE_{con} - CE_{incon}$) is known as conflict adaptation (CA). CA is thought to reflect a mechanism that regulates top-down control settings to minimize future potential conflict following the experienced conflict on a prior incongruent trial (Botvinick et al., 2001; Egner & Hirsch, 2005; Ghinescu et al., 2016; Kerns et al., 2004; Pastotter et al., 2013; Ullsperger et al., 2005). Comparisons of CE with value versus no value flankers on the trial following either conflict (CE_{incon}) or no conflict (CE_{con}) provides a measure of super-distraction.

The motivational competition account makes clear predictions about the pattern of super-distraction effects in this paradigm (as found in Chapter 3, Experiments 1 and 4). I will start by outlining the predictions for adolescents. As shown above adolescents have a tendency to reactively initiate motivational states and more easily activate motivational attraction to value-associated task-irrelevant distractors. Following a congruent trial, they should show no super-distraction (CE_{con}). Specifically, the task-relevant motivational state is

to attend to the colour of the flankers. The task-irrelevant motivational state is to attend to the value-associated shape of the flankers. Therefore, the two states align, and participants should show no super-distraction. Following an incongruent trial, the task relevant motivational state is to ignore the colour of the flankers because of the response conflict on the previous trial. However, the task-irrelevant motivational state is to attend them because of their value-associated shape, creating a motivational competition that requires resolution. Because of the predicted benefit of the learned value-association, this motivational intensity should remain heightened and super-distraction effects should be present after incongruent trials (CE_{Incon}). Different predictions are made for the adults. As demonstrated in Chapter 3 (Experiments 3 and 4) because the shape-based value-associations are completely task-irrelevant, in adults the motivational intensity of the shape-based motivational state is constantly reduced because it conflicts with the proactively defined attentional set. Therefore, at no point should the motivational state to attend to value-associated shapes win the motivational competition. As a result, no super-distraction effects are predicted for the adults after either congruent (CE_{Con}) or incongruent (CE_{Incon}) trials, and typical conflict adaptation should be observed regardless of the motivational salience of the flankers. Such findings would suggest that adolescents inflate the perceived benefits of externally driven value-associated motivational states that are activated reactively.

Method

Participants

16 adolescents (6 males; 16 – 17 years [mean = 16.87, SD = 0.4]; all right-handed) and 17 adults (7 males; 24 – 35 years [mean 26.67; SD = 4.3]; 14 right-handed) participated in exchange for money (£6 plus up to an extra £5 earned during the value-learning task). All participants had normal or corrected-to-normal vision, no history of neurological disorder, and were naïve to the purpose of the experiment and to Japanese Hiragana characters. Informed consent was obtained from all participants. Adolescents were students in further education (colleges for 16 – 18 year-old students) from Birmingham, UK. Adults were also from Birmingham, recruited via an online (Gumtree) advertisement. Participants were matched for educational attainment at age 15 - 16 through scores in a compulsory secondary education examination (GCSE, C grade = 5 points, higher scores represent higher grades) (adults = 6.1 vs. adolescents = 5.8). 65% of the adults had completed a university level qualification that based on a teacher report was equivalent to that predicted for the adolescent group (69%). One adult was removed from the analysis because the mean RT from this participant on the Flanker task was more than 4 SD above their group mean.

Apparatus

Stimulus presentation and data recording were controlled using custom software developed with PsychoPy (Peirce, 2007, 2009) controlling a Stone PC-1120. Responses were entered using a standard keyboard. Stimuli were presented in RGB colour space on a black (0,0,0) background of a 68 cm LCD monitor with a screen resolution of 1920 x 1080 and a refresh rate of 60 Hz. Viewing distance was approximately 60 cm. Testing was conducted in a quiet room with ambient lighting.

Stimuli

Japanese Hiragana characters (PJ Hiragana font) subtending approximately $1.9^\circ \times 1.4^\circ$, presented in white (255, 255, 255) during the value-learning task and orange (119, 84, 0) or purple (99, 84, 99) during the flanker task, were used as stimuli. The colours used in the flanker task were equiluminant. In both tasks, the symbols appeared along the horizontal meridian; laterally 4° to the left and right during the value-learning task and when presented as flankers in the flanker task; targets in the flanker task were presented centrally.

Procedure

Value-Learning Task. On each trial (see Figure 3.1), following a fixation cross (750 ms) two symbols were briefly presented (250 ms), one on either side of fixation. A blank screen immediately followed until response. On each trial symbols were selected from a set of 3 symbols; each with a point value of 0 (no-value), 500 (win), or -500 (loss); symbol/value assignments were counterbalanced between participants within each group; participants were unaware of the assignments at the start of the task. Participants were instructed to earn as many points as possible by selecting the symbol with the largest point value. The index and middle fingers of the right hand was used to press either the '1' or the '2' key to choose the left or right symbol, respectively. Immediately after a response, both symbols' values were presented in place of the respective symbol (500 ms). The value of the chosen symbol remained visible for a further 500 ms. A running total of the cumulative points earned was continuously presented centrally (8° below fixation) and updated after every choice.

The two symbols presented on each trial could be matched or mismatched. Each possible mismatched pair (win vs. loss, win vs. no-value, and no-value vs. loss) was equally likely and the optimal choice could be presented on the left or right with equal likelihood. Each

symbol pair on matched trials (win vs. win, no-value vs. no-value, and loss vs. loss) was presented on a third of these trials. Matched trials required an arbitrary response and were used to provide experience of receiving the outcome linked to each symbol; data from these trials were not analysed. Participants completed 180 trials (60 matched trials), split over 3 blocks. The cumulative points total and the amount of cash this would be converted into was presented during breaks. The cash earned was given to the participant at the end of the value-learning task. Eighteen practice trials using the same procedure but with Roman letters and explicit value assignments (A = 1, B = 2, and C = 3) were completed prior to the value-learning task.

Test-scales. During a 10-minute rest break following the completion of the value-learning task, participants completed the Munsell D-15 test of colour vision (all were successful), the Barratt Impulsiveness Scale (BIS-11, Patton, Stanford, & Barratt, 1995) and the Behavioural Inhibition/Behavioural Activation System Scale (BIS/BAS, Carver & White, 1994). Either after the 10-minutes had elapsed or when all tests had been completed participants started the flanker task.

Flanker task. Each trial (see Figure 3.1) began with a fixation cross (1000 ms) followed initially by the presentation of the flankers (two identical symbols of the same colour) on either side of an empty central area (100 ms). This was immediately replaced by the same flankers plus a centrally presented target, all of which remained visible until a response. Using the index and middle finger of their right-hand participants were instructed to press the '1' or the '2' key if the target was orange or purple, respectively, as quickly and as accurately as possible. Response time (RT) was recorded from the onset of the target. No feedback was given, and participants were aware that no further points would be awarded or deducted. The

symbols, used as targets and flankers, were the same as those experienced in the value-learning task. On half of trials flankers and targets had the same colour (congruent); on remaining trials, they were opposite in colour (incongruent). Each possible combination of flanker colour/symbol and target colour/symbol was equally likely to occur. This created congruent (C) and incongruent (I) trials with flankers that had no-value-, win-, and loss-associations. Critically, four different two-trial sequences were present: congruent-congruent (CC), congruent-incongruent (CI), incongruent-congruent (IC), and incongruent-incongruent (II).

Participants completed 648 trials in total split over 6 blocks, with 108 trials of each combination of flanker value x current trial congruency, presented in a pseudo random order.

Data Analysis

Value-Learning Task. Proportion optimal choice was calculated for each block. A mixed-design analysis of variance (ANOVA) with block (1, 2, or 3) as a within-subjects factor and age-group (adolescents versus adults) as a between subjects-factor was conducted. RT on matched trials were analysed with a 3 x 2 mixed design ANOVA with trial value (loss, no-value, win) as a within-subjects factor and age-group (adolescents vs. adults) as a between-subjects factor.

Flanker task. All incorrect trials and those with RT slower than 5000 ms were excluded. Remaining data were analysed with a 3 x 2 x 2 x 2 mixed-design ANOVA with current trial congruency (congruent vs. incongruent), prior trial congruency (congruent vs. incongruent), and current trial flanker value (no-value, win, or loss) as within-subjects factors and age-group (adolescents vs. adults) as a between-subjects factor. This was followed up with individual repeated-measures ANOVAs for each age-group, and significant three-way interactions here

were further followed up by calculating CE_{Con} and CE_{Incon} for each flanker value. Additionally, conflict adaptation (CA, $CE_{Incon} - CE_{Con}$) effects were also calculated for each flanker value. Follow-up planned pairwise comparisons were corrected for multiple comparisons using the False Discovery Rate procedure (Benjamini & Hochberg, 1995). Alpha levels were set at 0.05.

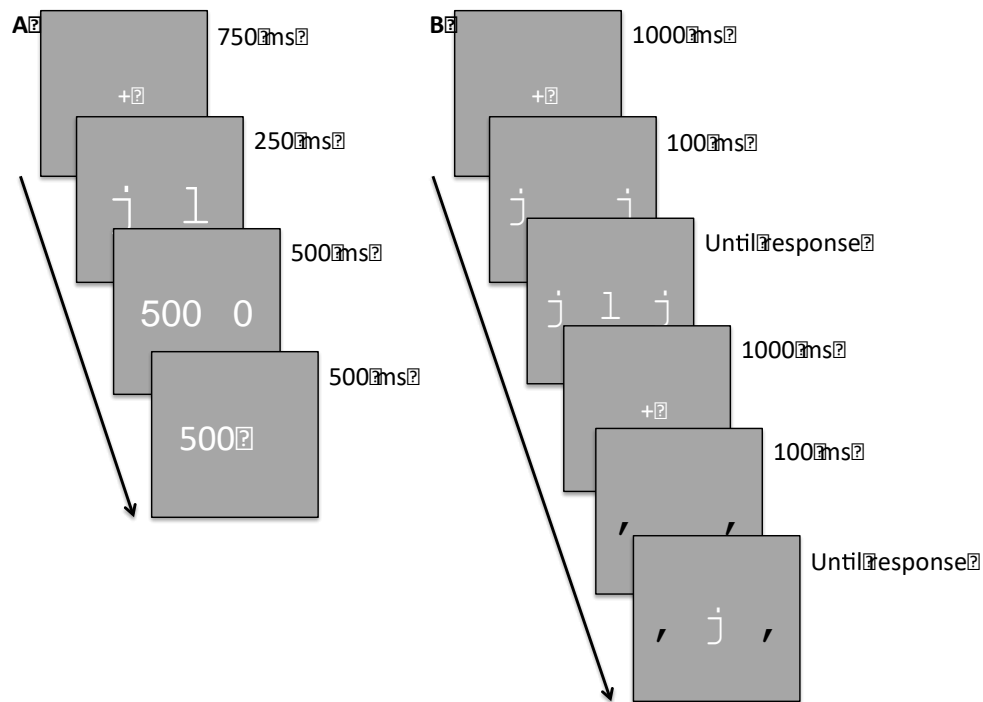


Figure 3.1. Example of a value-learning task trial (A), and a Flanker task trial sequence (B). The Flanker trial sequence represented a congruent followed by an incongruent trial.

Results

Value-Learning Task. Overall accuracy (see Table 3.1) did not differ between age-groups ($F(1, 30) = .360, p = .722$), averaging 86% (S.D. = 3%) and 87% (S.D. = 3%) in adolescents and adults, respectively. Accuracy improved significantly across blocks ($F(2, 60) = 33.574, p < .001, \eta^2 = .528$), but this rate of learning did not depend on age-group ($F(2, 60) = 2.920, p = .062, \eta^2 = .089$).

On matched trials, where both symbols were the same, RTs varied as function of trial value ($F(2, 60) = 16.063, p < .001, \eta^2 = .349$). RTs were significantly faster on win (513 ms) trials than no-value (640 ms, $t(31) = 4.078, p < .001$) and loss (691 ms, $t(31) = 4.850, p < .001$) trials. RTs were marginally slower on loss trials than no-value trials ($t(31) = 1.793, p = .083$). However, neither the main effect of age-group nor the interaction between trial value and age-group were significant (both $F_s < 1$).

Table 3.1. Mean percent optimal choices (standard error in parenthesis) as a function of block during the value-learning task.

Block	Adolescents	Adults
1	73 (5)	80 (3)
2	89 (3)	89 (3)
3	94 (2)	92 (3)
Overall	86 (3)	87 (3)

Flanker task. Table 3.2 shows RT for each condition and CA effects. Mean RT was slower by 85 ms for the adolescents compared to the adults ($F(1, 30) = 4.547, p < .05, \eta^2 = .132$). As is typical for CA (Gratton et al., 1992), RTs were slower by 54 ms on incongruent compared to congruent trials ($F(1, 30) = 71.817, p < .001, \eta^2 = .705$); they were faster when the prior trial was congruent versus incongruent by 12 ms ($F(1, 30) = 15.290, p < .001, \eta^2 = .338$); and, importantly, the effects of current and prior trial congruency significantly interacted ($F(1, 30) = 18.270, p < .001, \eta^2 = .378$). Critically for the current study, the four-way interaction (current congruency x prior congruency x flanker value x age-group) was also significant ($F(2, 60) = 3.935, p < .05, \eta^2 = .116$), justifying a separate analysis of super-distraction effects for both age-groups.

Table 3.2. Mean RT (with standard error in parenthesis) as a function of trial type.

Trial Type	Adolescents	Adults
No-value		
CC	597 (37)	512 (18)
CI	674 (40)	577 (18)
IC	624 (40)	540 (16)
II	639 (32)	580 (16)
CA effect	62 (24)	24 (8)
Win		
CC	604 (38)	503 (15)
CI	665 (45)	581 (19)
IC	612 (35)	537 (15)
II	680 (43)	581 (18)
CA effect	-7 (14)	35 (13)
Loss		
CC	598 (39)	501 (15)
CI	655 (39)	571 (21)
IC	612 (35)	544 (18)
II	662 (33)	569 (18)
CA effect	7 (18)	45 (17)

Note. There were four trial sequences; congruent-congruent (CC), congruent-incongruent (CI), incongruent-congruent (IC), and incongruent-incongruent (II). CA effects were calculated as $((CI - CC) - (II - IC))$.

To investigate the influence of the flanker-value valence, the ANOVA was repeated separately for both age-groups without the no-value condition. In the adult group, there was a marginally larger CE with win than loss flankers by 13 ms ($F(1, 15) = 3.269, p = .091, \eta^2 = .179$), but no other main or interaction effects reached significance for either adult or adolescent groups (all $ps > .109$). Therefore, the win and loss conditions were collapsed into a single value condition for all further analyses.

For each age-group, RTs showed significant effects consistent with conflict adaptation. RTs were slower when the current trial was incongruent compared to congruent (adults: 53 ms, $F(1, 15) = 70.430, p < .001, \eta^2 = .824$; adolescents: 53 ms, $F(1, 15) = 26.523, p < .001, \eta^2 = .639$); RTs were slower when the prior trial was incongruent versus congruent in the adults

(by 17 ms, $F(1, 15) = 23.909$, $p < .001$, $\eta^2 = .614$) but not in adolescents ($F(1, 15) = .452$, $p = .511$, $\eta^2 = .029$). In both age-groups the interaction between prior and current trial congruency was significant (adults: $F(1, 15) = 15.758$, $p < .005$, $\eta^2 = .512$; adolescents: $F(1, 15) = 7.286$, $p < .05$, $\eta^2 = .327$). Importantly, the three-way interaction was not significant in the adults ($F(1, 15) = 2.474$, $p = .137$, $\eta^2 = .142$) but was significant in the adolescents ($F(1, 15) = 5.949$, $p < .05$, $\eta^2 = .284$).

Consistent with the motivational-competition framework, in adolescents a super-distraction effect was present only when the prior trial was Incongruent (see Figures 3.2 and 3.3). CE_{Incon} was significantly larger with value versus no-value flankers by 45 ms ($t(15) = 3.024$, $p < .01$). However, CE_{Con} was unaffected by flanker value ($t(15) = 1.064$, $p = .304$). For the no-value flankers, the opposite pattern was found. CE_{incon} was significantly smaller than CE_{con} ($t(15) = 2.814$, $p < .05$), resulting in CA of 62 ms. However, CA was not present with value flankers ($t(15) = .048$, $p = .962$). Thus, CA was significantly larger in the No-value compared to the value flanker condition ($t(15) = 2.437$, $p < .05$). In the adult group, CE_{con} , CE_{incon} , and CA were unaffected by flanker value and no super-distraction effects were present (all $ps > .129$).

Moreover, a comparison between age-groups showed that super-distraction effects ($CE_{\text{value}} - CE_{\text{no-value}}$) after congruent trials did not differ ($t(30) = 1.452$, $p = .157$), but after an Incongruent trial super-distraction effects were significantly larger by 52 ms in the adolescents than the adults ($t(30) = 3.135$, $p < .01$). CA with value flankers was also significantly larger in adults than adolescents ($t(30) = 2.679$, $p < .05$).

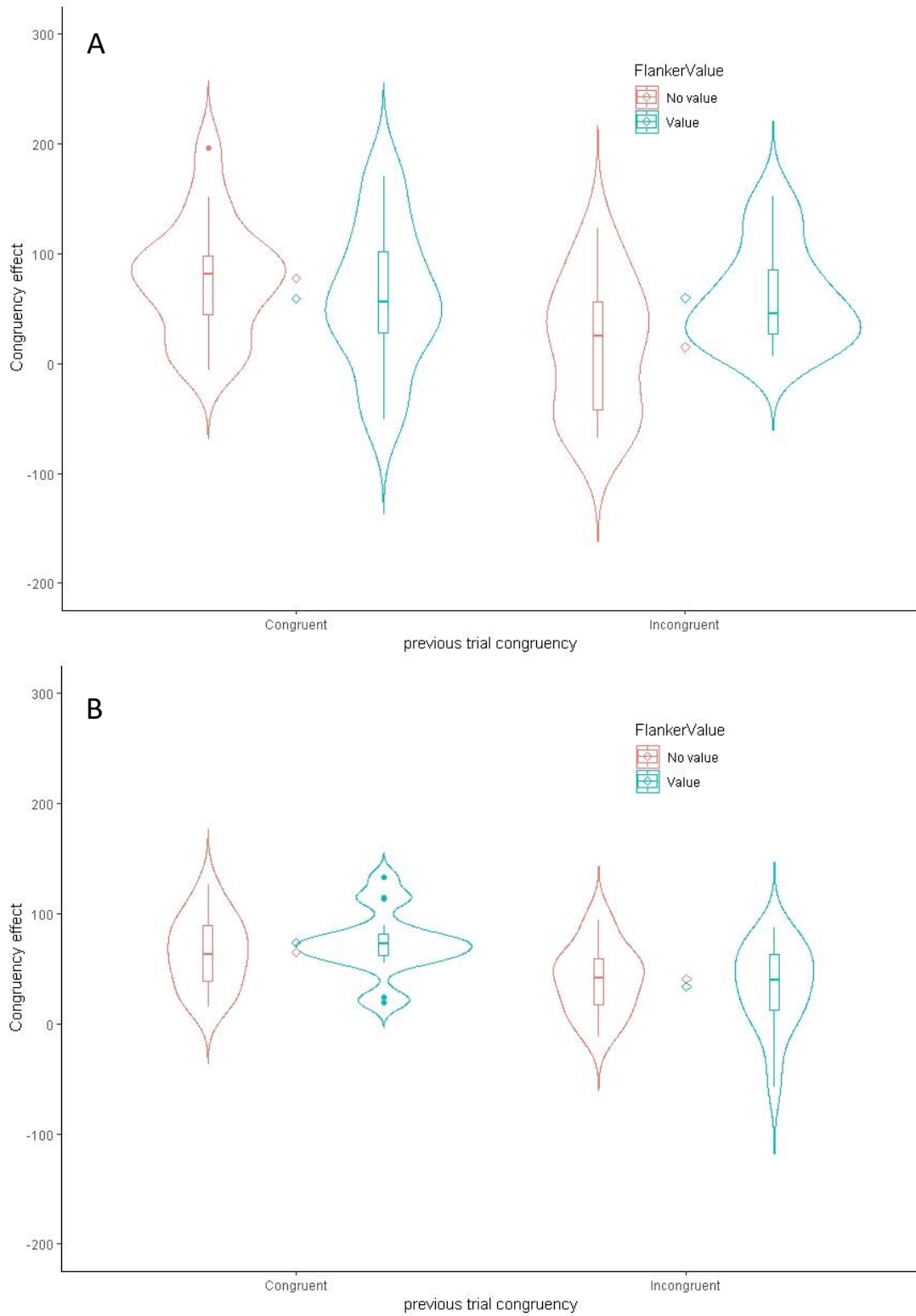


Figure 3.2. Congruency effects (incongruent – congruent) following a congruent and an incongruent trial for adolescents (A) and adults (B). Error bars represent ± 1 S.E.

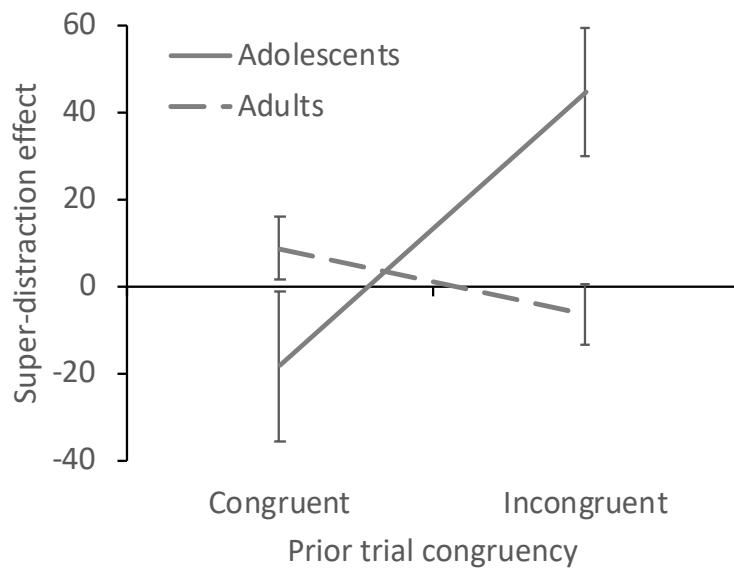


Figure 3.3. Super-distraction effects (Value - No-value) following a congruent and an incongruent trial for adolescents (solid line) and adults (dashed line). Error bars represent \pm S.E.

Overall accuracy was very high in the experiment (96.5%). Analysis of accuracy revealed a significant effect of current trial congruency, with accuracy on congruent trials being 1.3% higher than on incongruent trials ($F(1, 30) = 6.519, p < .05, \eta^2 = .179$). There was also a significant interaction between flanker value \times age-group ($F(1, 30) = 4.918, p < .05, \eta^2 = .141$). The interaction was driven by adolescents being 2.2% less accurate than adults with no-value flankers ($t(30) = 2.195, p < .05$); accuracy did not differ between the age-groups with value flankers ($t(30) = .972, p = .339$). No other effects reached significance (previous congruency: $F(1, 30) = .079, p = .780, \eta^2 = .003$; previous congruency \times age-group: $F(1, 30) = 2.414, p = .131$; current congruency \times age-group: $F(1, 30) = .073, p = .789, \eta^2 = .002$; previous congruency \times current congruency: $F(1, 30) = 2.220, p = .147, \eta^2 = .069$; previous congruency \times value: $F(1, 30) = .668, p = .420$; current congruency \times value: $F(1, 30) = .124, p = .727, \eta^2 = .004$; previous congruency \times current congruency \times age-group: $F(1, 30) = .906, p = .349, \eta^2 = .029$; previous congruency \times value \times age-group: $F(1, 30) = 1.608, p = .215, \eta^2 = .051$; current

congruency x value x age-group: $F(1, 30) = 1.213, p = .280, \eta^2 = .039$; previous congruency x current congruency x value x age-group: $F(1, 30) = 1.811, p = .189, \eta^2 = .057$).

Discussion

The results are consistent with adolescents being more susceptible to super-distraction effects, i.e., greater distraction by motivationally salient versus perceptually similar neutral stimuli, than adults. In particular, consistent with the motivational competition hypothesis, adolescents appear to inflate the perceived benefits of attending to value-associated stimuli.

Before discussing the increased super-distraction effects in adolescents, it is important to note that when flankers had no value-associations typical conflict adaptation was present in both adolescents and adults. Although, previous research has shown that in the flanker task electrophysiological recordings (ERN and N2) to response conflict are similar in adolescents and adults (Ladouceur et al., 2007), the current experiment is the first to directly assess conflict adaptation effects in these groups using the flanker task. Here, both groups demonstrated typical conflict adaptation effects (Gratton et al., 1992); CE_{Con} was greater than CE_{Incon} . Importantly, this shows that both groups were equally sensitive to the cognitive costs of response conflict when reactively adjusting the current motivational state. Consequently, my interpretation of super-distraction effects in adolescents is not confounded by differences in how the two groups responded to conflict. Group differences only emerged when the flankers had motivational salience, suggesting a crucial difference in the way adolescents perceived the predicted payoffs of task-irrelevant stimuli compared to adults.

The main finding from the current data was that motivationally salient flankers produced increased super-distraction effects in adolescents compared to adults. This is consistent with previous work also showing increased distraction by motivationally salient cues that were conditioned in a prior value-learning task, in adolescents compared to adults (Roper et al., 2014). However, the current data extend these findings. Only following an incongruent trial did super-distraction emerge in adolescents. Consistent with the motivational competition framework, the presence of super-distraction was dependent on competition between motivational states. Specifically, adolescents were not simply more motivated to attend to motivationally salient than neutral distractors, as evidenced by the lack of super-distraction after a congruent trial. However, following an incongruent trial, despite the utility of attending to the colour of the flankers being low, the perceived benefits of processing the shape of the flankers when they were value-associated brought the flankers back into competition for cognitive resources. This relative boost in motivational intensity for flanker processing based on the discrete motivational state instantiated by value-associated shapes explains why super-distraction is present following an incongruent trial.

In adults, super-distraction was not only smaller than in adolescents, it was completely absent. Based on previous work (Chapter 3) it is likely that this was because only the task-irrelevant shape of the stimuli predicted value, whereas the task-relevant colour of the stimuli had no association with reward. This is also consistent with Roper et al. (2014) who showed no super-distraction effects in adults, at least after a quarter of trials had been completed. One possibility, for both the current results and those of Roper et al. (2014) is that adults learn to incorporate the proactive knowledge that attending to shape is costly because it is irrelevant for the current task. Therefore, the motivational intensity to process shape is

relatively reduced, and as a result is uncompetitive in the motivational competition for cognitive resources. Adolescents, are less likely to incorporate proactive control than adults into decision-making (Andrews-Hanna et al., 2010; Killikelly & Szűcs, 2013; Padilla et al., 2014). Thus, adolescents inflate the perceived benefits of value-associated motivational states compared to adults and continue to reactively activate the learned goal.

Although the current study cannot speak directly to neural mechanisms, the idea that adolescents inflate the perceived payoffs of rewards is consistent with increases in ventral striatum activity in anticipation of rewards previously found in adolescents compared to adults (Geier et al., 2010). Dopamine levels in striatal regions are a likely mechanism to purvey signals of motivational intensity, especially when estimating the predicted benefits of discrete motivational states. Typically, in the human and nonhuman literature, dopamine levels in the ventral striatum are increased in adolescence compared to at all other stages of life (Telzer, 2016; Wahlstrom, Collins, White, & Luciana, 2010), marked by increasing dopamine receptor densities through mid-adolescence that reduce into adulthood (Crone & Dahl, 2012). Heightened dopaminergic activity in subcortical regions during adolescence is associated with laboratory risk taking (Botdorf, Rosenbaum, Patrianakos, Steinberg, & Chein, 2017; Braams et al., 2015), sensation-seeking, and impulsivity (Romer et al., 2017; Steinberg et al., 2008). All of these findings are consistent with adolescents inflating the perceived benefits in the calculation of motivational intensity, leading to increased goal flexibility and impulsivity (Barkley-Levenson & Galván, 2014; Casey, Getz, & Galvan, 2008; Crone & Dahl, 2012).

In conclusion, the results support a motivational competition account of adolescent super-distraction effects with an emphasis on adolescents inflating the predicted benefits of motivational states that were previously associated with a reward. Although further research

is required into the motivational competition framework of cognition in adolescents, the strength of the model is in quantifying a cost-benefit trade-off of cognition that can be targeted by interventions aimed at increasing the perceived personal benefits of prosocial behaviours (Telzer, 2016). A second feature of the model is that it assumes that inflating the perceived benefits of externally driven goals may be beneficial to adolescents in the long-term. Specifically, the resulting increases in goal flexibility can increase the richness of experience (Romer et al., 2017) that would feed into future computations of motivational intensity.

Chapter 4. Motivationally Driven Attentional Capture

Abstract

Visual search is sometimes slowed when a previously rewarded versus unrewarded distractor is present. This so-called “value-driven attention capture” (VDAC) is widely viewed as a perceptual phenomenon; positive reward history is thought to boost a stimulus’s representational strength regardless of current motivational contexts (e.g., task relevance), thus causing inappropriate attention capture (or VDAC). Alternatively, motivation could drive attention and account for VDAC via on-line computations of cost versus benefits for processing specific stimulus features. If so, then VDAC should depend on current motivational contexts, rather than on selection history alone. In this view, any concurrent secondary task, e.g., a working memory (WM) task, involving the reward-associated distractor feature should alter the cost/benefit trade-off for this feature and consequently modulate VDAC. However, if VDAC is driven by selection history alone, then such manipulations should have no effect. To investigate, I conducted a conventional two-phase VDAC experiment, but added a concurrent visual WM task to the second, non-rewarded visual search phase in which reward-associated distractors are presented. The WM task involved maintaining either (a) colour (the reward-associated feature), or (b) shape (the target-defining feature) information during each search trial. WM tasks were matched for difficulty. It was predicted that a colour WM task would increase the cost of processing the reward-associated distractor feature (colour), thus reducing motivation for processing it, and obliterating VDAC. In contrast, the shape WM task should increase shape processing costs, leaving motivation to process the distractor colour unaffected and enabling VDAC. Consistent with this motivation-driven account, VDAC was absent with a colour WM task but robust with a similarly difficult shape WM task. These effects show that selection history alone cannot account for VDAC; instead contextually determined motivational cost-benefit trade-offs appear to drive attention and reward-association effects on processing.

Visual selective attention is necessary to focus cognition on pertinent information in the visual percept. Recent models of attentional control extend the classic dichotomy between top-down, in which attention is guided by stimuli relevant to current goals, and bottom-up, when perceptual salience guides attention, control to include attentional selection guided by stimuli with previously rewarded selection history (Awh et al., 2012; Failing & Theeuwes, 2017). This proposed third branch of attentional control has largely been informed by studies that show *super-distraction effects*, i.e., greater distraction by motivationally salient versus perceptually similar neutral distractors. However, the mechanism through which motivationally salient stimuli compete for attentional control is poorly defined. To investigate the underlying cognitive mechanism, the constraints on value-driven attentional control need to be better understood.

Anderson and colleagues (Anderson et al., 2011) developed a paradigm that has been widely used to demonstrate super-distraction effects. The paradigm is a modified additional singleton task (Theeuwes, 1992), whereby participants first learn to associate a specific colour with receiving a small monetary reward and another colour with a larger monetary reward. In a subsequent visual search task for a shape singleton the presence of a distractor with the high-reward associated colour slows performance compared to when a distractor with a colour not associated with any outcome appears in place of the reward-associated colour. However, the same slowing is not found when the previously low-value distractor colour is used (Anderson et al., 2011).

This “value driven attentional capture” (VDAC) is inconsistent with classic top-down and bottom-up attentional control because the value-associated distractors are neither relevant to current goals nor physically salient, yet they capture attention (Anderson et al.,

2011; Awh et al., 2012). Common accounts suggest that "...arbitrary reward-related stimuli capture attention involuntarily and persistently as a result of associations that develop rapidly during learning." (pp. 10369, Anderson et al., 2011). It has been proposed that the involuntary attentional capture is adaptive to make observers aware of unexpected changes in the environment that may signal opportunity. These sentiments are captured in Selection History (Awh et al., 2012; Failing & Theeuwes, 2017) and Habitual Control (Anderson, 2016) theories of super-distraction.

The Selection History account suggests that super-distraction effects occur because a bias has built up to the target after repeated selection during learning. When rewarded for the selection, the bias is reinforced and develops quicker than without an explicit reward. According to Selection History accounts, super-distraction is a perceptual phenomenon, with the representational strength of previously selected stimuli increasing on attentional priority maps (e.g., Itti & Koch, 2000; Theeuwes, 1992; Ptak, 2012) that determine attentional capture. The increased representational strength allows previously selected stimuli to garner a competitive advantage over stimuli that are task-relevant or physically salient (Awh et al., 2012; Failing & Theeuwes, 2017). Selection History accounts suggest that it is through this mechanism that VDAC emerges. Likewise, the Habitual Control hypothesis (Anderson, 2016) suggests that an attentional habit develops during learning such that the stimulus develops an automatic attentional orienting response when re-encountered.

However, the automaticity of super-distraction has been questioned by previous failures to demonstrate VDAC (e.g., Sha & Jiang, 2016) and by studies demonstrating substantial individual differences in super-distraction (Hickey et al, 2010b; Anderson et al, 2011; 2013; 2016; 2017). Here, I assess whether VDAC is affected by two factors that are

known to influence the magnitude of distraction in conventional attention tasks. In Experiment 1, the impact of a concurrent working memory load is investigated. In Experiment 2, the influence of just prior distraction by rewards (sequential trial effects) is examined. The aim was to better understand the conditions required for super-distraction effects to emerge.

Experiment 1

When people have to perform two tasks at once, their performance suffers on one or both of the tasks. For example, distractor interference is increased in tasks requiring selective attention when working memory (WM) resources are being utilized to maintain information in a secondary task (de Fockert et al., 2001). Cognitive Load theory suggests that cognitive control mechanisms are required to maintain current attentional priorities and reduce distraction (Engle, 2002; Lavie et al., 2004). According to this theory, WM resources are necessary to resolve the perceptual conflict that arises between salient distractors and targets in visual search tasks (Lavie, 2005). A consequence of a taxing WM task, therefore, is that central resources that would otherwise reduce distraction from salient stimuli are occupied, resulting in large distraction compared to when under no WM load.

Consistent with the Cognitive Load account, Selection History and Habitual Control theories of super-distraction would predict increased VDAC when WM resources are loaded. According to these accounts, reduced WM resources should limit top-down biases that prioritize task-relevant stimuli. Reduced WM resources should also reduce the resources available for the suppression of salient task-irrelevant distractors, which in this case are motivationally salient. Therefore, if motivational salience boosts the perceptual

representations of stimuli then VDAC should increase with a concurrent WM load. In line with this prediction, reduced WM capacity has been shown to predict larger VDAC (Anderson et al., 2011). The first aim of the current experiment was to directly assess the impact of a concurrent WM load on VDAC.

The second aim was to investigate whether the type of information being held in WM influences VDAC. Despite WM capacity often being linked to a central executive (Morey & Cowan, 2004), WM resources can be also distinguished between verbal and visual domains (Baddeley, 1986; Luck & Vogel, 1997). Indeed, when maintaining a WM load, the degree of distractor interference in a concurrent visual attention task has been shown to depend on whether the information in the WM task and in the attention task require overlapping domain-specific processing units (Gil-Gómez de Liaño, Umiltà, Stablum, Tebaldi, & Cantagallo, 2010; Kim et al., 2005). Kim and colleagues used a WM sandwich task (e.g., de Fockert et al., 2001), whereby participants either had to perform a verbal or a spatial WM task. During the WM maintenance period, participants performed a modified Stroop trial where they had to identify the meaning of a word (“right” or “left”) while ignoring an arrow pointing either right or left. The target, therefore, required verbal processing, but the distractor was in the spatial domain. Consistent with Cognitive Load theory, they found that when the WM task was verbal (matching the target), there was increased distraction (larger congruency effect) from the arrow compared to when there was no WM task. However, when the WM task was spatial (matching the distractor), interference was reduced compared to without a WM task (Kim et al., 2005). This dissociation demonstrates that a WM load can both benefit and impair attentional control. Importantly, the distractor in Kim et al. (2005) was sometimes congruent and informative to the goal of identifying the target word. Their effect, therefore, represents

a modulation of goal-directed, strategic attentional control in response to the WM load. Specifically, when distractor processing is likely to interfere with WM maintenance because of the perceptual similarity between both sets of stimuli, the internal costs of processing the distractor are increased, making it less likely (Shenhav et al., 2013). The second aim of the current experiment was to investigate whether the same dissociation is found for VDAC when the motivationally salient distractor is always in conflict with goal-directed control (Anderson, 2016; Anderson et al., 2011; Awh et al, 2012).

Here, I expanded on Kim et al. (2005) by examining the influence of two different WM tasks, one matching the target domain (shape) and one matching the distractor domain (colour), on VDAC. A modified version of the VDAC task was used. Initial learning was consistent with that previously used by Anderson et al. (2011). However, during the test task, visual search trials were either sandwiched between a WM task requiring maintenance of a colour pattern or an irregular four-sided polygon. Another difference from the typical test task was that the target was always specified by a diamond amongst circles, rather than as the shape singleton (Anderson et al, 2011). This was to ensure maximum overlap between the shape WM task and the target processing in the visual search.

If super-distraction is driven by an involuntary attentional capture mechanism, independent of goal-directed control, then a concurrent WM load should increase VDAC regardless of the domain of the WM stimuli. If the magnitude of VDAC depends on the domain of the concurrent WM load, consistent with Kim et al. (2005), then it would suggest that the mechanism underlying super-distraction is strategic. In this case, when the WM domain matches that of the distractor feature in the visual search task (i.e., colour-based), VDAC

should be reduced compared when the WM domain matches that of the target feature (i.e., shape-based).

Method

Participants

Twenty-seven (all females; 22 right-handed; mean age = 21.0 years [S.D. = 4.6, range = 18 - 33]) naïve participants from the University of Birmingham took part in exchange for course credits or cash (£12, plus up to an additional £8 earned on the value-learning task). One participant failed the Munsell D-15 test of colour vision and was removed from all analyses; all remaining participants in both experiments had normal or corrected-to-normal vision and no history of neurological illness. A further two participants were removed from the analyses because their performance on the value-learning task over the two days was below 70% correct and learning of the value/colour contingencies could not be assumed. Informed consent was obtained from all participants, and all procedures were approved by the University of Birmingham ethics committee. Based on a study by Gil-Gomez de Liaño et al. (2010), who reported an effect size of $\eta^2 = .39$ for a two-way interaction between WM-group (target-match or distractor-match) and Stroop congruency, and a power = 0.80 (two-tailed) the calculated sample size should be at least 18. A final sample of 24 was chosen to match Anderson et al. (2011). The same criteria were also used in Experiment 2.

Apparatus

A Stone PC-1210 running Matlab 2013b (The MathWorks, Inc) software with the Psychophysics toolbox was used to present the stimuli on 68 cm LCD monitor with a screen

resolution of 1920 x 1080 and a refresh rate of 60 Hz. Participants were seated approximately 70 cm from the screen in a room with ambient lighting. Responses were entered using a standard keyboard.

Stimuli

In both the value-learning and the test task, all stimuli were presented on a black background. The fixation cross subtended $0.5^\circ \times 0.5^\circ$ and was presented in white. In both tasks, the search display comprised 6 shapes ($2.3^\circ \times 2.3^\circ$) equally placed around an imaginary circle with a radius of 5° centered on fixation. Inside each circle was white line that was approximately 2° long and 0.1° wide. In the test task, the colour-WM array consisted of a 3 x 3 pattern of colours (red, green, blue, orange, yellow, pink, purple, white, and grey) subtending $5.6^\circ \times 5.6^\circ$. The shape-WM array consisted of an enclosed random 4-sided gray shape with a maximum area equal to that of the Colour-WM pattern. All WM arrays were centered on fixation.

Procedure

Each participant was tested over two consecutive days with the following routine. Each day participants first completed the value-learning task followed by a test task. Half of the participants completed the colour-WM task on Day 1 (colour-first) and the shape-WM task on Day 2; remaining participants performed the tasks in the alternate order (shape-first).

Value-Learning Task. See Figure 4.1a. Following a fixation cross that was presented for a randomly chosen interval of 400, 500, or 600 ms, the search display appeared for a maximum of 800 ms or until response. Then a blank screen (500 ms) followed by the reward display (1000 ms) appeared before the screen went blank (for 500 ms) and the next trial began.

The search display consisted of 5 distractor circles, each presented in a different colour (orange, yellow, pink, purple, and white). On each trial, either a red or a green circle was also presented, and this was always the target. Inside all distractor circles was a line segment oriented 45° randomly to the left or right, inside the target circle was either a vertical or a horizontal line segment. The locations of all the circles were chosen at random. Participants pressed either '1' or '2' with the index and middle fingers on their right-hand if the target line was vertical or horizontal, respectively, "as quickly as possible while minimizing errors". If the participant was correct, the reward display informed the participant how much cash they had earned on that trial (1 pence or 5 pence) and the total accumulated cash. If they were incorrect or too slow, the reward display informed them of this instead.

On Day 1, there were 240 trials with a self-paced break half-way through where the participant could see how much money they had accrued. On Day 2, there was one block of 120 trials. On both days, the target colour (high reward and low reward) and target line orientation (vertical and horizontal) were fully crossed and trials with every possible combination occurred equally often. Trial order was pseudorandom. The target location was random across the six possible locations on every trial. For half of participants, on 80% of trials a red circle predicted a high reward (5 pence) and a green circle predicted a low reward (1 pence); on the remaining 20% of trials for each colour the contingencies were reversed. These colour/reward associations were reversed for the other half of participants. The colour/reward associations were also counterbalanced within each WM task order group. Colour/reward associations remained consistent across both days for each participant. Before the experimental trials on Day 1, participants completed 50 practice trials in which rewards were replaced by a correct message on the reward display. There was no practice on day 2.

Test Task. See Figure 4.1b. The trial structure followed a 2-trial sequence configuration. Following a fixation cross presented for a randomly varying interval of 400, 500, or 600 ms, a WM array appeared (500 ms). Then two visual search trials began. Each started with a fixation cross for a randomly varying interval of 400, 500, or 600 ms. Then the search display appeared for a maximum of 2000 ms on the first visual search trial, and a maximum of 1500 ms on the second. After the maximum time had elapsed or a response was made the feedback screen appeared (1000 ms). Immediately after the feedback screen appeared on the second trial in the sequence, a WM test array appeared until a response was made or 1500 ms had elapsed. Finally, the screen went blank for 1000 ms before the next 2-trial sequence began.

Participants were informed to remember the WM array. The search display comprised five circular outlines (distractors) and one diamond outline (target), each presented in a different colour. The target was randomly presented in one of the distractor colours from the value-learning task and four of the distractor circles had colours matching the remaining distractor colours from the value-learning task. The final distractor colour was always presented in the high reward colour, low reward colour, or no-value colour (blue). The locations of all stimuli were chosen at random. A line segment randomly oriented 45° to the left or to the right was placed in each distractor circle. Inside the target diamond was either a horizontal or vertical line segment. Participants pressed the '1' or the '2' key with the index and middle fingers of their right-hand if the target line was vertical or horizontal, respectively, "as quickly as possible while minimizing errors". After every visual search trial, the feedback display informed the participant as to whether their performance was "correct", "wrong", or "too slow". The WM test array could either be the same as the WM array or different. On change trial sequences, for the colour-WM task four out of the five colours remained in their

original locations and the other 5 switched. For the shape-WM task change trials, 3 out of the 4 points and the x-axis position of the final point remained the same but the y-axis position of the 4th point could be 100 pixels (0.8°) above or below the original y-axis position. Participants were instructed to press the 'space-bar' with their left-hand if the WM test array had changed and withhold responding if it had not.

For each WM task, there were 360 trials with a self-paced break every 72 trials. The first trial (of the 2-trial sequence) distractor value (high reward, low reward, and no reward), first trial target line orientation (vertical and horizontal), second trial distractor value, and second trial target line orientation were all fully crossed. On half of the 2-trial sequences the WM test array had changed; on the rest, it was the same. On both days, before the experimental trials, participants completed 10 practice 2-trial sequences using the same WM task as they would on the experimental trials that day.

Data Analysis

Value-Learning Task. The first trial of every block was removed from the analysis. RT and accuracy on remaining trials were analysed with a 2 x 2 repeated-measures analysis of variance (ANOVA) with Day (1 vs. 2) and Target Value (low reward vs. high reward) as factors.

Test Task. For both RT and accuracy analyses, trials from the first 2-trial sequence and those with RT faster than 250 ms were removed from the analysis. Remaining trials were analysed with a 2 x 2 repeated-measures ANOVA with WM Task (colour-WM vs. shape-WM) and Distractor Value (no reward vs. high reward) as factors. Accuracy on the WM task (colour-based vs. shape-based) was analysed in a paired-samples, 2-tailed *t*-test. Follow-up planned

pairwise comparisons were corrected for multiple comparisons using the False Discovery Rate procedure (Benjamini & Hochberg, 1995). Alpha levels were set at .05 throughout.

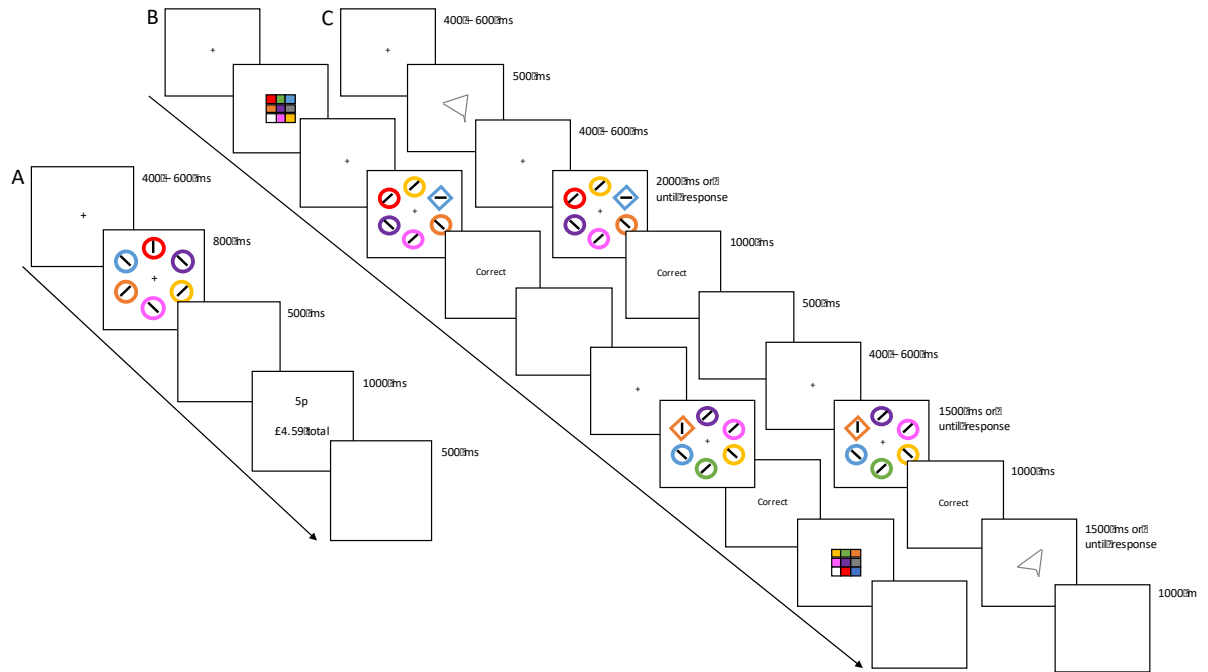


Figure 4.1. A. Example trial during the Value-learning task. Participants reported the orientation of the off-diagonal line segment (horizontal or vertical). The target was always within either a red or a green circle. One of the target colours predicted the receipt of a high reward (5p) and the other a low reward (1p) on 80% of trials and the reverse on 20% of trials. B. Example of a 2-trial sequence during the Test task in Experiment 1 in the colour working memory condition. C. Example of a 2-trial sequence during the Test task in the shape working memory condition. Participants first encoded the WM array, then performed two visual search trials, before performing a change-detection task with the WM test array (B and C are examples of WM change trial sequences). In the visual search task, the target was inside the shape singleton and one of the distractors was presented in the high-, low-, or a no-value colour. No further rewards were available. The test task in Experiment 2 was the same as in Experiment 1, but without the WM components of the trial.

Results and Discussion

Value-Learning Task. See Table 4.1 for RT data from the value-learning task. RT were faster on day 2 than Day 1 by 23 ms ($F(1, 23) = 21.334, p < .001, \eta^2 = .481$) and accuracy was higher on Day 2 than day 1 by 10% ($F(1, 23) = 87.396, p < .001, \eta^2 = .792$). RT were also faster when the target had a high compared to a low value by 9 ms ($F(1, 23) = 4.786, p < .05, \eta^2 = .172$), although accuracy for the two values was comparable ($F(1, 23) = 2.508, p = .127, \eta^2 =$

= .098). The two-way interaction was not significant for RT ($F(1, 23) = .551, p = .465, \eta^2 = .023$) or accuracy ($F(1, 23) = .821, p = .374, \eta^2 = .374$)

Table 4.1. Mean reaction times in milliseconds (with standard error in parenthesis) on the Value-Learning task in Experiment 1 (depending on Day) and in Experiment 2.

	Low-value	High-value
Experiment 1		
Day one	571 (8)	563 (8)
Day two	551 (11)	540 (10)
Overall	561 (9)	552 (9)
Experiment 2		
Overall	537 (10)	531 (9)

Note. There was only 1 day of testing in Experiment 2.

Test Task. See Table 4.2 for RT data from the test task. RT were comparable for visual search in both WM conditions ($F(1, 23) = .632, p = .431, \eta^2 = .027$) and regardless of WM task RT were marginally faster with a no value compared to a high value distractor ($F(1, 23) = 4.042, p = .056, \eta^2 = .149$). Crucially, the two-way interaction was also significant ($F(1, 23) = 5.622, p < .05, \eta^2 = .196$).

With a shape-based WM load typical value driven attentional capture was observed (Anderson et al., 2013; Anderson, Laurent, & Yantis, 2011a; Anderson et al., 2011b; Anderson & Yantis, 2012). RTs were slower when a high value distractor was in the search array compared to when a no value distractor was present ($t(23) = 2.598, p < .05$). However, value driven attentional capture was eliminated when participants held a colour information in WM ($t(23) = .907, p = .374$). Underlining the difference between the two WM conditions, VDAC (high value – no value) was significantly larger in the shape compared to the colour WM condition ($t(23) = 2.363, p < .05$). See figure 4.2 for VDAC in both WM conditions.

Table 4.2. Mean reaction times in milliseconds (with standard error in parenthesis) for each value distractor across both working memory (WM) conditions.

	No-value	Low-value	High-value
Colour WM	735 (26)	742 (26)	740 (26)
Shape WM	710 (21)	718 (21)	727 (23)

Accuracy on the search task did not depend on the WM task ($F(1, 23) = 1.379, p = .252, \eta^2 = .057$) or the distractor value ($F(1, 23) = .640, p = .432, \eta^2 = .027$) and the two-way interaction was also not-significant ($F(1, 23) = .164, p = .689, \eta^2 = .007$). Importantly, accuracy on the WM tasks was comparable (84% on both, $t(23) = .028, p = .978$), therefore WM task difficulty can be ruled out as an explanation for the lack of value driven attentional capture in the colour-based WM condition.

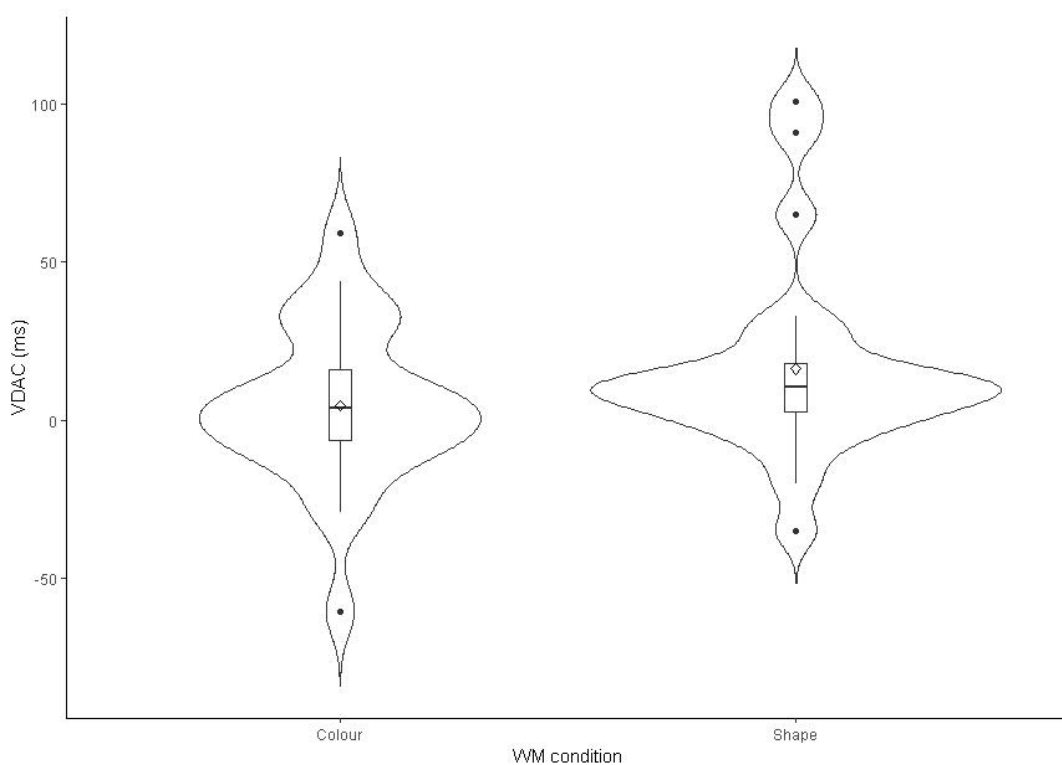


Figure 4.2. Mean value driven attentional capture effect (VDAC), calculated as High-value – No-value distractor conditions, for both the colour and the shape working memory (WM) conditions.

The finding that VDAC is eliminated when the contents of WM are in the same feature domain as the distractor feature that is associated with value (e.g., colour) are consistent with the previous findings of Kim et al. (2005). However, the current experiment expands on Kim et al. (2005) by demonstrating a feature-specific (e.g., colour vs. shape) influence of the WM load rather than a modality-specific (e.g., verbal vs. spatial) effect.

Importantly, the mere presence of a demanding secondary task was not sufficient to reduce VDAC, as evidenced by the typical VDAC observed with a concurrent shape-based WM task. Therefore, the results are inconsistent with Cognitive Load theory (Lavie, 2005), and accounts of super-distraction that suggest the underlying cognitive mechanism is involuntary attentional capture based on increased salience (Awh et al., 2012). Specifically, if this were the case, then VDAC should have been increased with a concurrent WM load because the load limits the executive resources available to suppress salient distractors (Lavie, 2005). Instead, the results favour an interpretation of super-distraction that suggests learned value-driven biases modulate (unconscious) strategic control (Shenhav et al., 2013). In particular, because colour processing during the maintenance of a colour-based WM load would interfere with the WM representation (Ahmad et al., 2017), the colours in the concurrent attention task must be ignored to reduce the conflict. When the WM load was shape-based, processing the value-associated distractors did not conflict with WM maintenance, so they were freely processed. Therefore, in Experiment 1 the current goals of the observer were found to interact with the strength of the learned value-driven bias.

Experiment 2

In Experiment 1, value-associated distractors were likely ignored because the sensory inputs would have potentially conflicted with maintenance of the memory representations for the colour-based WM task. In a typical VDAC experiment, processing the value-associated distractors also creates conflict with task-relevant processing within the visual search task; evidenced by the RT slowing with high value-associated distractors compared to neutral distractors (Anderson et al., 2011). However, strategic control does not seem to be immediately sensitive to this conflict, otherwise VDAC would not occur.

Nonetheless, there is some evidence that the attentional system adapts to this conflict after repeated exposures to the value-associated stimuli in extinction, i.e., when the reward is no longer forthcoming. Specifically, VDAC is known to be eliminated after as few as 60 extinction trials (Roper et al., 2014)³. If the cognitive mechanism responsible for super-distraction is strategic, then it should be sensitive to the conflict from inappropriate attentional capture by the value-associated distractors. This should be evident in behavioural adjustments on a trial-by-trial basis within the visual search task.

It is well known that trial-by-trial conflict driven adjustments in attentional control occur, such as negative priming (Tipper, 1985) and conflict adaptation (CA) effects (Gratton et al., 1992). For example, when stimuli conflict with target processing these stimuli are ignored on the subsequent trial. However, when stimuli facilitate target processing they are attended to on the next trial (Botvinick et al., 2001; Gratton et al., 1992). Such sequential trial effects have also been shown to be influenced by rewards (Della Libera & Chelazzi, 2006, 2009; Hickey

³ Of course, an alternative possibility is that extinction occurs because the stimuli lose their motivational salience through prediction error signaling (Schultz, 2000).

et al., 2010a, b; van Steenbergen et al., 2009). However, in these studies, rewards were dependent on performance and thus likely reinforced the behaviour on the prior trial.

Here, sequential trial effects were investigated in VDAC to examine strategic adjustments in control in response to the value-associated distractors. To do so, the classic VDAC paradigm was replicated (Anderson et al., 2011). The aim was to examine whether a value-associated distractor on the prior trial influences VDAC on the current trial. It was predicted that when the value-associated distractor is absent on the prior trial, typical VDAC should be observed on the subsequent trial because no conflict was experienced. However, following a high value-associated distractor trial, VDAC should be eliminated. Specifically, the conflict with target selection from the value-associated distractors should be strategically overcome on the subsequent trial by ignoring these distractors.

Method

Participants

Twenty-four (2 males; 22 right-handed; mean age = 19.38 years [S.D. = 2.2, range = 18 - 29]) naïve participants from the University of Birmingham took part in exchange for course credits or cash (£5, plus up to an additional £5 earned on the value-learning task).

Apparatus

Same as Experiment 1.

Stimuli

There was no WM arrays. All search display information in both the Value-learning task and the Test task are the same as in Experiment 1.

Procedure

The experiment took place over a single session.

Value-Learning Task. The same as Experiment 1.

Test Task. The visual search trials were the same as in Experiment 1, but with the following exceptions. The maximum presentation time of the search display was always 1200 ms. The search display either comprised five circular distractor and one diamond target outlines or five diamond distractor and one circular target outlines. The shape singleton always denoted the location of the target. There were 324 trials, with a self-paced break every 108 trials. The current trial distractor value (high-reward, low-reward, and no-reward), the target line orientation (vertical and horizontal), and the singleton type (circle and diamond) were all fully crossed. The location of the singleton was random on every trial. Participants first completed 20 practice trials that were the same as the experimental trials; except all practice trials were no-reward trials.

Data Analysis

Value-Learning Task. The first trial of every block was removed from the analysis. RT and accuracy on remaining trials were analysed with 2-tailed *t*-tests comparing high versus low value trials.

Test Task. For both RT and accuracy analyses, the first 2 trials and those with RT faster than 250 ms were removed from the analysis. Remaining trials were analysed with a 2 x 2 repeated-measures ANOVA with Previous Trial Distractor Value (No-value vs. High-value) and Current Trial Distractor Value (No-value vs. High-value) as factors. Follow-up planned pairwise comparisons were corrected for multiple comparisons using the False Discovery Rate procedure (Benjamini & Hochberg, 1995). Alpha levels were set at .05 throughout.

Results and Discussion

Value-Learning Task. See Table 4.1 for RT data from the value-learning task. RT were marginally faster when the target had a high compared to a low value by 6 ms ($t(23) = 1.774$, $p = .089$). Accuracy did not differ depending on the value of the target ($t(23) = .847$, $p = .405$).

Table 4.3. Mean reaction times in milliseconds (with standard error in parenthesis) for each value distractor when preceded by No-value and High-value distractor trials.

Previous trial distractor value	Current trial distractor value		
	No-value	Low-value	High-value
No-value	635 (14)	651 (14)	657 (15)
Low-value	649 (14)	650 (16)	642 (12)
High-value	640 (12)	642 (15)	631 (13)

Test Task. See Table 4.3 for RT data from the test task. RT were marginally faster when the previous trial distractor was associated with a high-value compared to no-value by 11 ms ($F(1, 23) = 4.054$, $p = .056$, $\eta^2 = .150$). The results failed to replicate Anderson et al. (2011) as no effect of distractor value was found on the current trial ($F(1, 23) = 1.211$, $p = .282$, $\eta^2 = .050$). Importantly, the two-way interaction between previous trial distractor value and current trial distractor value was significant ($F(1, 23) = 8.637$, $p < .01$, $\eta^2 = .274$).

When the distractor on the previous trial was associated with no-value, typical VDAC was observed (Anderson et al., 2011). When preceded by a no-value distractor trial, RT were significantly slower when the distractor value on the current trial was associated with a high-value compared to no-value ($t(23) = 2.726$, $p < .05$). This effect was eliminated when preceded by a high-value distractor trial ($t(23) = 1.175$, $p = .252$). Importantly, the VDAC (high-value – no-value) was significantly larger when the distractor on the previous trial was associated with no-value versus a high-value ($t(23) = 2.947$, $p < .05$). See Figure 4.3 for VDAC as a function of the previous trial.

Accuracy on the search task was consistent with previously reported current trial VDAC. Accuracy was lower when the distractor on the current trial was associated with a high-value (85%) compared to a low-value (89%) ($F(1, 23) = 4.518, p < .05, \eta^2 = .164$). The main effect of previous trial was not significant ($F(1, 23) = .392, p = .538, \eta^2 = .017$, nor was the interaction between previous and current trial distractor value ($F(1, 23) = .809, p = .378, \eta^2$).

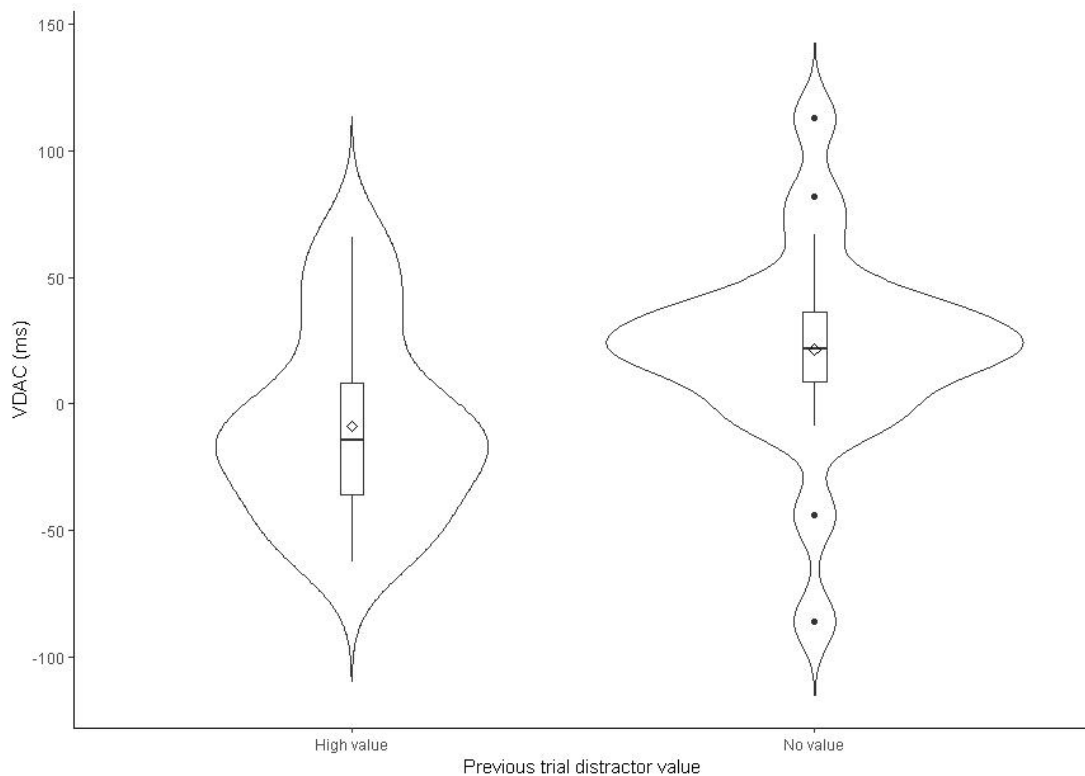


Figure 4.3. Mean value driven attentional capture effect (VDAC), calculated as High-value – No-value distractor conditions, when the distractor on the previous trial was associated with no-value and high-value.

This experiment provides evidence that the degree to which value-associated stimuli are attended is dependent on the predicted utility of those stimuli. This predicted utility was shown to be dependent on immediately prior experiences. Specifically, when attending to the value-associated distractors caused conflict with target selection, they were ignored on the subsequent trial. This further suggests that value-driven attentional biases are governed by strategic control. However, an alternative interpretation, consistent with repetition priming

(Mayr et al., 2003), suggests that RT should be faster on two consecutive high value distractor trials compared to a sequence that switches to a no-value distractor trial because the perceptual similarity between trials facilitates stimulus processing. Arguing against this interpretation, such repetition priming effects were not observed for two consecutive no-value or low-value trials in the current data. Therefore, I can rule out this possibility in explaining the sequential modulations in super-distraction observed here.

Despite these clear conflict-driven sequential effects, it should be noted that the current experiment failed to replicate the typical current trial VDAC effect (Anderson et al., 2011). One possibility for the null finding, which is consistent with the conflict driven interpretation of the sequential trial effects, is that the ratio of no-value to value trials was different here compared to the ratio used in the original VDAC experiment. Here, each distractor trial was equally likely. However, typically, no-value trials are more likely; appearing on 50% of trials. The remaining 50% of trials are split evenly between the low and high value distractor conditions (Anderson et al., 2011). With fewer no conflict (i.e., no-value) trials, the utility of the high value-associated distractor is relatively increased because it is less likely to be preceded by a trial with a high value-associated distractor. Accordingly, the overall magnitude of VDAC would be increased. This would be consistent with sequential trial effects in CA whereby distractor interference increases when the proportion of no conflict trials also increases (Lowe & Mitterer, 1982). Future research should examine this possibility.

However, without demonstrating the sequential trial effects when typical VDAC is also observed it is difficult to generalize the current findings to previous observations. To this end, I contacted another lab that had also ran a study using an Anderson et al. (2011) style paradigm and reported typical VDAC (Milner, personal communication). Their first experiment

was a replication of Anderson et al. (2011) but the target in both the training and the test task was defined by colour. They observed typical VDAC ($F(2, 44) = 9.190, p < .001, \eta^2 = .295$). Importantly, the analysis of the sequential trial effects was consistent with the current experiment. After a high-value distractor (15 ms) trial, VDAC was reduced compared to after a no-value distractor (35 ms) trial ($F(4, 88) = 7.205, p < .001, \eta^2 = .247$). This provides important evidence for sequential trial effects even when typical VDAC is observed.

In a second experiment ran by this group (Milner, personal communication), they replicated the design of Anderson et al. (2011) except they removed the no-value distractor condition. Here, VDAC was computed as the difference between high and low value-associated distractor trials (high-value – low-value). Again, after a high value-associated distractor (-4 ms) trial VDAC was eliminated, and was significantly reduced compared to after a low value-associated distractor (17 ms) trial ($F(1, 21) = 8.447, p < .01, \eta^2 = .287$). Interestingly, in this latter experiment there was no current trial VDAC ($F < 1$), which is consistent with other experiments comparing high vs low value-associated distractors (e.g., Sha & Jiang, 2016). Therefore, the strategically driven sequential trial effects reported here may help to interpret similar null findings.

General Discussion

In two experiments, super-distraction was shown to be dependent on the degree to which attending to value-associated stimuli conflicted with task-relevant processing. In Experiment 1, value-associated distractors were constantly ignored when processing the reward-predicting feature would have disrupted WM maintenance of similar items in a

secondary task. The same suppression was not observed when the relevant feature in the WM task differed from the reward-predicting feature. In Experiment 2, the likelihood that value-associated distractors were attended fluctuated on a trial-by-trial basis depending on their utility on the prior trial. In both Experiments, it was the cost associated with processing the reward-associated feature that determined super-distraction, which suggests a strategic bias in value-driven attentional capture.

Given that in both experiments, and across all conditions the initial reward learning was identical, these findings show that selection history is not sufficient to produce value effects on attention. Instead, the current experiments demonstrate that when a value-laden stimulus is encountered, sensitivity to the stimulus is determined by current strategic control. This is consistent with models of cognitive control that emphasize conflict monitoring (Botvinick et al., 2001) and the integration of conflict signals into the allocation of cognitive resources (Shenhav et al., 2013, 2016). The current data extends these models, suggesting that value signals potentially act on similar mechanisms as conflict signals in determining control. The two types of signal are effectively in competition in determining how control is allocated to stimuli. Whereas conflict signals typically instigate a tightening of attentional control consistent with current goals (Botvinick et al., 2001), value-signals appear to initiate a competing goal. This competing goal is the re-activation of a learned response to the stimulus (Anderson, 2015; Braver, 2012). One factor that determines whether this value-driven goal affects behaviour is the predicted benefit (i.e., the learned reward); when this is high it is more likely to bias cognition (e.g., Anderson et al., 2011). However, the current series of experiments further suggests that this competing goal only 'wins' the competition for control when the conflict it creates with task-relevant processing is weak. When processing the value-

associated stimulus is deemed highly costly to current goals it is ignored (e.g., Shenhav et al., 2013).

In conclusion, the experiments reported here have demonstrated that the allocation of attention to reward-predicting stimuli is not automatic and instead may be the result of an online computation of the costs-benefits associated with different cognitive strategies (Shenhav et al., 2013).

Chapter 5. Adolescent Incentive Cue-related Signal Suppression: An EEG Study

Abstract

Stimuli signalling the opportunity to gain reward are known to bias cognition in adolescents more than in adults. Although previous studies have examined value-driven attentional capture in teenager, here I examine how electrophysiological responses to incentive cues differ between adolescents and adults. EEG/ERP activity was recorded as adolescents (~17 years) and adults (~29 years) viewed a motivationally salient (reward-associated) or no-reward incentive cue and then did a simple visual search task involving two letters each in a different colour. Cue shape informed the participant about the reward magnitude for correct search performance; this required letter identification (colour was irrelevant). Importantly, in a previous conditioning task, cue shape also predicted target colour. Although irrelevant for the current task, the colour associated with the cue was either congruent or incongruent with the target colour. In adolescents, when cues signalled high reward, colour congruency between cue associations and target determined response times, an effect not seen in adults, but not when the cue signalled no reward. ERP activity suggested that adolescents reactively suppressed the no-reward cue (cue elicited Pd), which inhibited the learned colour-association. In adults, no behavioural or ERP effects were found. However, pre-stimulus alpha activity prior to the onset of the incentive array was increased in adults compared to adolescents. Together, these data suggest that adults proactively initiate task-related strategic control, whereas adolescents reactively initiate control consistent with that instantiated by the most rewarding motivational state (i.e., goal).

Adolescence is a time when morbidity rates soar relative to both older and younger age-groups (Dahl, 2004). Often this is ascribed to an increase in impulsive and risky behaviours considered to be the result of extensive neurobiological and psychological change occurring during this epoch of life. Typically, the increased impulsivity associated with teenagers is thought to relate to discrepancies in the maturation of cognitive control – the ability to regulate cognitive resources to coordinate actions in accordance with internal goals - and reward mediated neural circuitries (Casey, Jones, et al., 2008; Crone & Dahl, 2012; Steinberg et al., 2008). Specifically, neuroanatomical studies in adolescents have revealed that synaptic density in reward processing regions follows a parabolic trajectory, peaking at around 14 years of age. In contrast, cognitive control regions develop linearly throughout adolescence only reaching full maturity in early adulthood at around 25 years of age, consistent with the strengthening of long-range connectivity and greater neural specialization (Giedd et al., 1999; Gogtay & Giedd, 2004; Luna et al., 2015).

Recent electrophysiological work has reported that immature cognitive control in adolescents is the result of inappropriate allocation of control that relies on reactive compared to proactive mechanisms (Andrews-Hanna et al., 2011; Braver et al., 2007; Braver, 2012). Proactive control reflects preparatory activation of control related to behavioural goals, whereas reactive control is instantiated post-stimulus onset in response to goals activated by stimuli. When proactive control is strong, the competition from reactive goals is only weakly represented and unlikely to control cognition (Braver, 2012). Conversely, reactive control is relatively more competitive for cognitive resources when proactive control is weak (Shenhav et al., 2013). Although adolescents demonstrate a propensity for the reactive allocation of control, they do not completely lack the ability to initiate control proactively (Andrews-Hanna

et al., 2010; Romer et al., 2017). Nevertheless, even by late adolescence (~17 years) preparatory response related activity, indexed by the contingent negative variation of the ERP, is attenuated compared to adults, but subsequent P3b activity during response execution is relatively increased compared to adults (Killikelly & Szűcs, 2011). Together, this evidence along with supporting neuroimaging research (Andrews-Hanna et al., 2011) suggests that adolescents are not inclined to prepare sustained cognition in preparation for later responses (Luna et al., 2015). Instead, using reactive control, they rely on post hoc cognitive strategies that are activated post-stimulus onset (Andrews-Hanna et al., 2011; Braver et al., 2007; Braver, 2012; Killikelly & Szűcs, 2013; Solomon et al., 2014). The reduced tendency for adolescents to initiate control proactively is likely to contribute heavily to the increased risk-taking in adolescents.

In conjunction with immature proactive cognitive control, adolescents experience heightened sensitivity to value associated-stimuli, due to heightened incentive salience (e.g., Chapter 3, Robinson & Berridge, 1993; Roper et al., 2011). Hyper-activity in reward related processing regions may increase the relative weight of value associated stimuli compared to perceptually similar but motivationally neutral stimuli making suppression of these stimulus-linked motivations more difficult (Spears, 2004; Steinberg et al., 2008; Chapter 3). There is a large bank of fMRI research showing heightened striatal reward related activity in response to reward contingent stimuli in adolescents compared to adults (Crone & Dahl, 2012; Galvan et al., 2006; Geier et al., 2010; Padmanabhan et al., 2011; van Leijenhorst et al., 2010). Adolescents tend to show increased striatal activity in risk-taking studies both in anticipation and receipt of rewards (van Leijenhorst et al, 2010; Galvan et al., 2006; Ernst et al., 2005; Padmanabhan et al., 2011; Braams et al., 2014; Crone et al., 2016, although see Bjork et al.,

2004, 2010). Behaviourally, a similar propensity for adolescents to be overly biased by reward related cues has been shown, even when attending to them may be detrimental to current task demands (Geier & Luna, 2009; Roper et al., 2014). The strength of this evidence has led researchers to assume that adolescents are excessively driven by rewards without consideration of costs, leading to an increase in risk-taking (Crone et al., 2016).

To examine how irrelevant, reward-associated stimuli gain control over behaviour, adolescents (14 – 17 years) and adults (25 – 35 years) first took part in a value-learning task wherein white abstract symbols became instrumentally associated with a specific colour and a monetary value (win or no-value) outcome. These same colour-value associated symbols were then used as incentive cues in a subsequent 2-item target location task. Specifically, the white cue's associated value predicted the monetary outcome for correct performance on the search task. Although the cue's associated colour was irrelevant, the search array always had one item (target or distractor) in the cue-associated colour. The task was to locate a predefined target letter regardless of its colour. On half of trials the target's colour was the same as that predicted by the incentive cue, as learnt in the value-learning task; on remaining trials the incentive cue predicted the distractor's colour. This created a potential competition between the irrelevant colour and letter processing.

Effective proactive control should emphasize task-relevant processing (letter-processing), irrespective of the meaning of the incentive cue. When proactive control is strong there should be no influence of the cue-colour association, and no colour congruency effect. Conversely, when control is more likely to be allocated reactively the cue-colour association should be more competitive with task-relevant behaviours, making a colour congruency effect

more likely. However, when the cue-colour association was not rewarded during learning the competition should be resolved in favour of the task-relevant processing strategy.

To investigate strategic differences between adolescents and adults in the allocation of control, ERPs were measured during the letter-target detection task (but not the value-learning task). Of particular interest was neural signatures of attentional control in response to the incentive cues, i.e., when the symbols predicting reward (and formerly predicting colour) were presented. Previous research has shown that the N2pc and the distractor positivity (Pd) can both be used to index attentional control dynamics in response to incentive cues (Sawaki et al., 2015). The N2pc is thought to reflect the deployment of covert visuospatial attention (Luck, 2005; Luck & Hillyard, 1994b, 1994a); it is observed as relatively more negative voltage at contralateral than ipsilateral scalp sites, relative to the location of the attended stimulus (Luck, 2005). The Pd is associated with the active suppression of stimuli (Hickey et al., 2009; Luck, 2005; Sawaki, Geng, & Luck, 2012; Sawaki et al., 2015); it is seen as a more positive voltage at contralateral than ipsilateral scalp sites, to the visual field of the suppressed stimulus (Luck, 2005). Both components onset around 150 – 350 ms post stimulus at parietal-occipital electrode sites (Luck, 2005; Sawaki et al., 2015; Hickey, et al., 2010a). Recent reports have demonstrated the N2pc in children and adolescents (Couperus & Quirk, 2015; Shimi, Nobre, & Scerif, 2015; Wang et al., 2017), which suggests that electrophysiological markers of attentional capture are comparable to those found in adults. Evidence for the Pd in age-groups younger than adults though is lacking. Here, the adolescents might not show a Pd because suppression mechanisms are not yet developed but finding a Pd in adolescents would provide a means of investigating the application of suppression in future research.

In addition to analysing active suppression of incentive cues after stimulus presentation, posterior alpha power in the EEG prior to the onset of the incentive array was also examined. Increased pre-stimulus alpha activity is thought to indicate a reduced readiness to attend to external stimuli (Mazaheri, Nieuwenhuis, Van Dijk, & Jensen, 2009; Sawaki et al., 2015). Indeed, posterior alpha power is thought to be a marker of preparatory suppression modulated by top-down areas (Van Dijk, Schoffelen, Oostenveld, & Jensen, 2008).

The primary aim was to investigate active suppression (Pd) as an index of reactive inhibitory mechanisms in response to reward-predicting and neutral incentive cues. It was predicted adolescents would rely on post-hoc strategic control to maintain task-relevant behavioural goals (letter processing) and suppress the re-activation of the goal instantiated by the incentive cue when it is not associated with reward, reflected in a Pd. However, because the goal re-instantiated by a reward-predicting cue is more motivationally intense, it should be more difficult to reactively inhibit, so no active suppression (Pd) was expected. Rather, a N2pc to the reward-predicting cue was predicted because adolescents' hyper-sensitivity to rewards. In adults, a different pattern was expected. It was reasoned that if adults were more likely to utilize preparatory inhibition that effectively ignores the incentive cue, they might show increased alpha prior to their onset coupled with active suppression of the cues (a Pd), regardless of cue value.

Experiment 1

Method

Participants

Sixteen adolescents (5 males, mean age = 16.6 years [range: 14 – 17, SD = 0.8]) and sixteen adults (9 males, mean age = 28.5 years [range: 23 – 38, SD = 4.4]) from the West Midlands, UK area took part in the experiment in exchange for £20. The adolescents were recruited from advertisements in local secondary schools and through the university webpages. Adults were recruited from online advertisements (GumTree and Call For Participants). Couperus and Quirk (2015) reported an $\eta^2 = .386$ for the analysis of N2pc in children, based on a power = 0.8 (two-tailed) a sample size of 16 was calculated to be sufficient. This sample size is consistent with previous ERP studies with adolescents, such as Killikelly & Szűcs (2013) wherein there were 15 adolescents and 15 adults.

All participants had self-reported normal or corrected-to-normal vision, no history of neurological illness, and were naïve to both Japanese hiragana characters and the purpose of the experiment. In fact, no participant had participated in any previous psychology experiment at this or any other institution. Participants also completed the Munsell D-15 test for colour-blindness; all were successful. Informed consent was obtained not only from all participants but, in the case of the adolescents, also from their parents/guardians.

Stimuli/Apparatus

The stimuli were presented on a gray ([128, 128, 128]) background of a 68 cm LCD monitor with a screen resolution of 1920 x 1080 and a refresh rate of 60 Hz. Viewing distance was approximately 70 cm. Stimuli were programmed in Matlab (MathWorks Ltd.) using

Psychtoolbox. Responses were given using a standard keyboard. Eight Japanese symbols (PJ Hiragana font) subtending approximately $1.9^\circ \times 1.4^\circ$, always presented in white [255, 255, 255], served as relevant incentive and control (irrelevant) stimuli. The incentive array used in the value-learning task and the letter-detection task comprised two Hiragana, presented 2.5° to the left and right of fixation from the Hiragana edge. The colour choice array in the value-learning task comprised two filled circles subtending approximately 2° in diameter. The circles appeared 2.5° from fixation to the left and right along the horizontal meridian. One was always presented in orange [119, 84, 0] and the other in purple [99, 84, 99]. In the letter detection task, targets were always 'p' or 'd' and distractors were always 'q' or 'b'; each letter measured approximately $2^\circ \times 1.5^\circ$ and was presented in either orange or purple (as in the value-learning task). Letters were also presented in pairs along the vertical meridian, 2.5° above or below centre. Rewards (Arial font) were always presented at fixation.

Procedure

Value-Learning Task. See Figure 5.1a. Each trial began with a fixation cross that remained on screen throughout the task but was presented alone for 1000 ms between trials. Next, two white Hiragana symbols appeared until the symbol designated as 'relevant' was selected. Then a colour choice array comprised of two circles appeared until response. This sequence was followed by the fixation (1000 ms), and finally by a reward feedback screen that indicated the amount of points earned (if correct) or lost (if incorrect) on that trial (200 ms).

For each participant, four Hiragana symbols were designated as 'relevant' cues and four as 'irrelevant'. A 'relevant' cue was always presented alongside an 'irrelevant' item; each was equally likely to appear on the left or the right. Of the four 'relevant' symbols, half were assigned a point value of 0 (no-reward) and half a value of 500 (win). One symbol with each

value indicated that the correct colour choice for the subsequent screen was orange and its value-mate indicated that purple was the correct choice. Irrelevant symbols had no meanings. When the Hiragana symbols were presented at the start of each trial participants were instructed to select the 'relevant' symbol by pressing the 'left' or 'right' arrow key with their index finger or ring finger, respectively. If the 'irrelevant' symbol was chosen, the word 'INCORRECT' appeared and the trial ended. If the 'relevant' symbol was chosen, the trial progressed to the colour choice array. Now the task was to choose the colour associated with the 'relevant' symbol on that trial by using the middle finger to depress the 'up' or 'down' arrow key to select the circle on the top or bottom, respectively. The correct choice was equally likely to appear above or below fixation. If correct, the participant received the amount of points associated with the 'relevant' symbol for that trial; if incorrect, 500 points were deducted from their overall tally. Accumulated points were constantly presented at the bottom of the screen and updated after every trial. Participants were informed that points could later be exchanged for cash.

In total there were 256 trials, with each 'relevant' symbol appearing on a quarter of trials, pseudo-randomly ordered. Each 'irrelevant' symbol also appeared on a quarter of trials, equally often with each 'relevant' symbol. The assignment of Hiragana to relevance, and relevant symbols to value/colour were chosen randomly for each participant. There was a break every 64 trials, where the participants could see how much cash had been earned thus far.

Letter-Target Detection Task. See Figure 5.1b. Each trial began with a fixation cross presented alone for a jittered interval between 1000 – 1400 ms, which remained onscreen throughout the trial. Next, the incentive array was presented for 200 ms. Following another

jittered interval (between 800 – 1200 ms), the target-letter detection display was presented for 200 ms, followed by a fixation alone for 1000 ms, and finally the amount of points earned on that trial (200 ms).

The incentive array consisted of a 'relevant' and an 'irrelevant' symbol appearing to the left and right of fixation, the location of each was equally likely to be the left or the right. The 'relevant' cue informed the participant how many points they could earn for being correct on that trial, based on the reward-assignment from the value-learning task. The colour assigned to the 'relevant' symbol during learning was no longer informative and was equally likely to be congruent with the colour of the target letter as incongruent. Although only one 'relevant' symbol was meaningful for the trial both were presented to ensure that lateralized ERP responses were not confounded by low-level physical stimulus confounds. For the target-letter detection task, participants had to locate one of two predefined target letters ('p' or 'd') presented alongside a distractor letter ('q' or 'b'). On each trial there was always one, but only one, target letter presented in either the top or bottom location; the other location had a distractor letter. Participants pressed the '/' key with their left index finger or the 'z' key with their right index finger if a target letter was presented at the top or bottom, respectively. One of the letters was always presented in purple and the other in orange, although this was not informative for the letter-target detection task. If correct the participant received the amount of points associated with the 'relevant' symbol on that trial, if incorrect 500 points were deducted.

There were a total of 1024 trials in total. Half of trials had a win-associated incentive array; on remaining trials the incentive array indicated that no-reward was on offer for that trial (0 points could be earned if correct). On half of trials for each incentive array the colour

associated with the 'relevant' cue was congruent with the colour of the target letter meaning that a colour search would have resulted in the correct answer. On remaining trials for each incentive array the associated colour was incongruent with that of the target letter, meaning that searching for colour would give the wrong response. The target letter was equally likely to be either a 'p' or a 'd' on each trial, as the distractor letter was equally likely to be a 'q' or a 'b' (target and distractor letters being fully crossed). There were 128 trials per block. Each break between blocks was for a minimum of 15 seconds, apart from the fourth break that was a minimum of 1 minute. Participants could start the next block as soon as they liked after the minimum interval. During breaks participants could see how much extra cash they had earned so far.

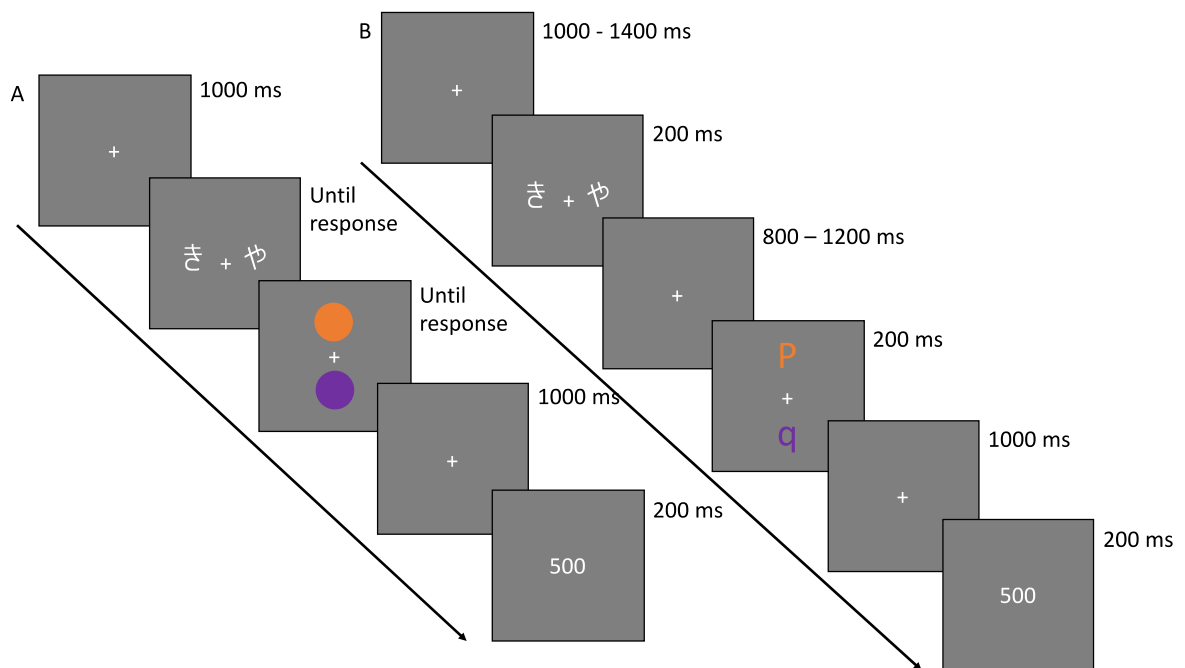


Figure 5.1. Schematic of a value-learning task trial (A), and a letter-target detection task trial (B). In the value-learning task, participants had to first decide which symbol was the 'relevant' symbol, then decide which colour was associated with this relevant symbol. If they chose the wrong symbol the trial would terminate with a message reading "Incorrect". In the current example, if the symbol on the left predicted purple in the value-learning task, attending to the colour in the letter-target detection task would slow responses because it is incongruent with the colour of the target (in this case P).

Recording and Analysis

With few exceptions the recording and analysis were consistent with a previous reported study also measuring the N2pc and Pd in response to incentive cues, but in adults (Sawaki et al., 2015). EEG was only recorded during the letter-detection task. The EEG was recorded using active Ag-AgCl electrodes (BioSemi) from 32 scalp sites (FP1, FP2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, and Iz) and the left and right mastoids according to the modified 10-20 system (American Electroencephalographic Society, 1994). For the detection of eye movements and blinks, the EOG was recorded from electrodes placed above and below the right eye and at the outer canthi of each eye. The EEG and EOG were low-pass filtered with a fifth-order sinc filter (half-power cutoff at 208 Hz) and digitized at 1024 Hz.

All ERP data analyses were conducted using the EEGLAB (Delorme & Makeig, 2004) and ERPLAB toolboxes (Lopez-Calderon & Luck, 2014) in Matlab (The MathWorks, Inc). The EEG signals were offline referenced to the average of the left and right mastoids. The EEG was bandpass filtered offline using a Butterworth infinite impulse response filter with half-power cutoffs at 0.05 and 30 Hz and a roll-off of 12 dB/octave. The data was then down-sampled to 256 Hz. To minimize sensory confounds EEG signals were collapsed across the possible locations of the relevant Hiragana stimuli (left or right) and the two Hiragana stimuli used for each reward possibility during the incentive array.

Trials containing noisy channels or segments (eye blinks, movement, muscle tensing, etc...) were removed via visual inspection and artefact rejection. Trials were removed if the EEG exceeded ± 100 μV in any channel or if a step function applied to the horizontal EOG exceeded 25 μV (Sawaki et al., 2015; Luck, 2005) between 100 ms before and 700 ms post

stimulus onset. Trials were also excluded if the vertical EOG exceeded $\pm 80 \mu\text{V}$ between 100 ms prior to and 200 ms post stimulus onset, this ensured that the eyes were not closed when the stimuli were presented.

Averaged ERP waveforms were computed encompassing 100 ms before the onset of the incentive array to 500 ms post stimulus onset. As is conventional, N2pc and Pd components were measured as the difference wave between the contralateral hemisphere minus the ipsilateral hemisphere, relative to the stimulus (Luck, 2005; Sawaki et al., 2015). The contralateral waveform for the 'relevant' stimulus was the average of the right hemisphere electrodes when the 'relevant' stimulus was in the left visual field, and the left hemisphere electrodes, when the 'relevant' stimulus was in the right visual field; the ipsilateral waveform for the 'relevant' stimulus was the average of the right hemisphere electrodes when the 'relevant' stimulus was in the right visual field, and the left hemisphere electrodes when the 'relevant' stimulus was in the left visual field. The amplitude for both the N2pc and the Pd were measured as the mean voltage during predefined time windows, baseline corrected to the 100 ms pre-stimulus baseline period recorded at posterior electrode sites where the N2pc and Pd were largest (Luck, 2005). The analysis was first conducted collapsing over multiple parietal-occipital electrode sites (PO3/PO4, PO7/PO8, P5/P6, and P7/P8) where the N2pc and Pd are typically observed, across the posterior of the scalp (e.g., Bacigalupo & Luck, 2015), and then the analysis was repeated focusing only on the PO7/PO8 electrode sites where the components have previously been found to be largest when investigating attention to incentive cues (Sawaki et al., 2015). The same time windows were measured as used by Sawaki et al. (2015) when determining the N2pc and Pd to incentive cues

in young adults. These were 250 – 300 ms post stimulus onset for the N2pc and 325 – 375 ms post stimulus onset for the Pd.

Prior to the calculation of time frequency representations (TFRs) independent component analysis (ICA) was used to estimate eye-blinks from the pre-stimulus period relative to the incentive array. Eye-blink related ICA components were identified using EyeCatch (Bigdely-Shamlo, Kreutz-Delgado, Kothe, & Makeig, 2013) and then removed. Consistent with the analysis of TFRs in Sawaki et al. (2015), the EEG was convolved with a Hanning-tapered seven-cycle Morlet wavelet and TFRs of power between 2 – 20 Hz were computed. To analyse power differences in the alpha band, the power was calculated for individuals from -2000 to 2000 ms relative to the onset of the incentive array, then averaged for each age-group. To examine age-related differences in pre-stimulus alpha activity (10-14 Hz, Sawaki et al., 2015), the power of alpha band frequencies across channels and time were analysed. Unpaired parametric statistical comparisons were conducted with alpha levels set at .01.

Behavioural Data Analysis

Value-Learning Task. Accuracy (percent correct) during the symbol selection stage and the colour selection stage were analysed separately in a 2 x 2 analysis of variance (ANOVA). The within-subject factor was cue-reward (reward vs. no-reward) and the between-subject factor was age-group (adolescents vs. adults).

Letter-Target Detection Task. Incorrect trials and the first trial of every block were excluded before participant condition means were averaged for the RT analysis. All remaining data were analysed with a 2 x 2 x 2 repeated-measures ANOVA with the within-subject factors of incentive value (reward vs. no-reward) and colour congruency (congruent vs. incongruent)

and the between-subject factor of age-group (adolescents vs. adults). Follow-up planned pairwise comparisons were corrected for multiple comparisons using the False Discovery procedure (Benjamini & Hochberg, 1995). Alpha levels were set at 0.05.

Table 5.1. Mean percent correct (standard error in parenthesis) for each age-group, decision stage and reward condition in the Value-Learning Task.

	Adolescents	Undergraduates	Adults
Shape-selection stage			
Reward	93 (1)	94 (2)	96 (1)
No-reward	89 (2)	91 (3)	96 (1)
Colour-selection stage			
Reward	84 (2)	88 (3)	89 (2)
No-reward	83 (3)	83 (3)	85 (2)

Results

Value-Learning Task. Performance measures are shown in Table 5.1. At the shape selection stage, although adults were overall more accurate by 5% at selecting the ‘relevant’ symbol than adolescents ($F(1, 30) = 8.212, p < .01, \eta^2 = .215$), accuracy was unaffected by cue-reward ($F(1, 30) = 2.524, p = .123, \eta^2 = .078$), and the interaction between cue-reward and age-group was also not significant ($F(1, 30) = 3.054, p = .091, \eta^2 = .092$). When analysing performance from only the final block, adults (99.7%) were again marginally more accurate than adolescents (98.05%) at selecting the ‘relevant’ symbol ($F(1, 30) = 3.433, p = .074, \eta^2 = .103$), suggesting that adults may have been better able to discriminate the meaningful from the irrelevant Hiragana symbols. However, given that performance in the final block is approaching ceiling for both age-groups, both groups appear to know which symbols were ‘relevant’. Similar to the analysis of overall accuracy, in the final block there was also no effect

on accuracy of the cue-reward ($F(1, 30) = 1.686, p = .204, \eta^2 = .053$), and no interaction between age-group and cue-reward ($F(1, 30) = 1.218, p = .279, \eta^2 = .039$).

At the colour selection stage, accuracy was unaffected by cue-reward ($F(1, 30) = 1.173, p = .287, \eta^2 = .038$) and age-group ($F(1, 30) = 1.202, p = .282, \eta^2 = .039$). The interaction between cue-reward and age-group was also non-significant ($F(1, 30) = .061, p = .806, \eta^2 = .002$). Together, these data from the value-learning task suggest that although adults may have been marginally better at discriminating the ‘relevant’ symbol, this was not differently affected by cue-reward. In addition, the ability to associate colour with Hiragana symbol was not different between age-groups.

Table 5.2. Mean RT (ms) and accuracy (standard error in parenthesis) for each age-group, congruency, and reward condition in the Letter-Target Detection Task.

	Adolescents	Undergraduates	Adults
RT			
Reward			
Congruent	429 (19)	479 (24)	482 (16)
Incongruent	443 (19)	501 (17)	475 (15)
No-reward			
Congruent	435 (18)	515 (26)	482 (15)
Incongruent	438 (18)	506 (20)	485 (15)
Accuracy			
Reward			
Congruent	84 (2)	95 (1)	94 (1)
Incongruent	86 (3)	87 (4)	93 (2)
No-reward			
Congruent	86 (3)	94 (1)	93 (1)
Incongruent	87 (2)	93 (2)	93 (1)

Notes. The undergraduate sample were from Experiment 2 and EEG was not recorded.

Letter-Target Detection Task.

Behavioural Data

Table 5.2 shows the behavioural data. Adolescents were marginally faster than adults at selecting the target letter ($F(1, 30) = 3.528, p = .08, \eta^2 = .105$). The two-way interaction

between age-group and congruency was significant ($F(1, 30) = 4.519, p < .05, \eta^2 = .131$). Crucially, the three-way interaction between age-group, congruency, and value was also significant ($F(1, 30) = 6.894, p < .05, \eta^2 = .186$). No other effects reached significance (all $ps > .17$).

To further explore the three-way interaction, separate 2 x 2 ANOVAs were conducted for each age-group. In adults, RT were unaffected by congruency ($F(1, 15) = .275, p = .608, \eta^2 = 0.18$), cue-reward ($F(1, 15) = 1.387, p = .257, \eta^2 = .085$), and the interaction between cue-reward and congruency was not significant ($F(1, 15) = 2.465, p = .137, \eta^2 = .141$). In adolescents, RT were faster when the colour of the target letter was congruent versus incongruent with the colour associated with the incentive cue ($F(1, 15) = 6.331, p < .05, \eta^2 = .297$). Importantly, the two-way interaction between cue-reward and incentive value was also significant ($F(1, 15) = 5.746, p < .05, \eta^2 = .277$). Specifically, after a reward incentive cue, RT were slowed by 14 ms when the incentive cue predicted the incongruent compared to the congruent colour ($t(15) = 4.020, p < .005$). However, after a no-reward incentive cue, RTs on congruent versus incongruent trials were not different ($t(15) = .899, p = .383$). In addition, the congruency effect (incongruent – congruent, see Figure 5.2) was larger after a reward (14 ms) than a no-reward (3 ms) incentive cue ($t(15) = 2.397, p < .05$). Finally, the congruency effect after a reward incentive cue was significantly ($t(30) = 3.615, p < .005$) larger in adolescents (14 ms) than in adults (-7 ms).

Adults were more accurate than adolescents ($F(1, 30) = 8.630, p < .01, \eta^2 = .223$). The two-way interactions between cue-reward and age-group ($F(1, 30) = 5.711, p < .05, \eta^2 = .160$) and between congruency and age-group ($F(1, 30) = 4.541, p < .05, \eta^2 = .131$) were significant. No other effects reached significance (all $ps > .2$). Although adolescents were

overall faster and less accurate compared to adults, speed-accuracy trade-offs do not appear to explain the value x colour congruency effects observed in the adolescent RT. In particular, when considering accuracy, the three-way interaction was not significant ($F(1, 30) = 1.680, p = .205, \eta^2 = .053$), and neither was the two-way interaction between congruency and cue-reward ($F(1, 30) = .044, p = .836, \eta^2 = .001$).

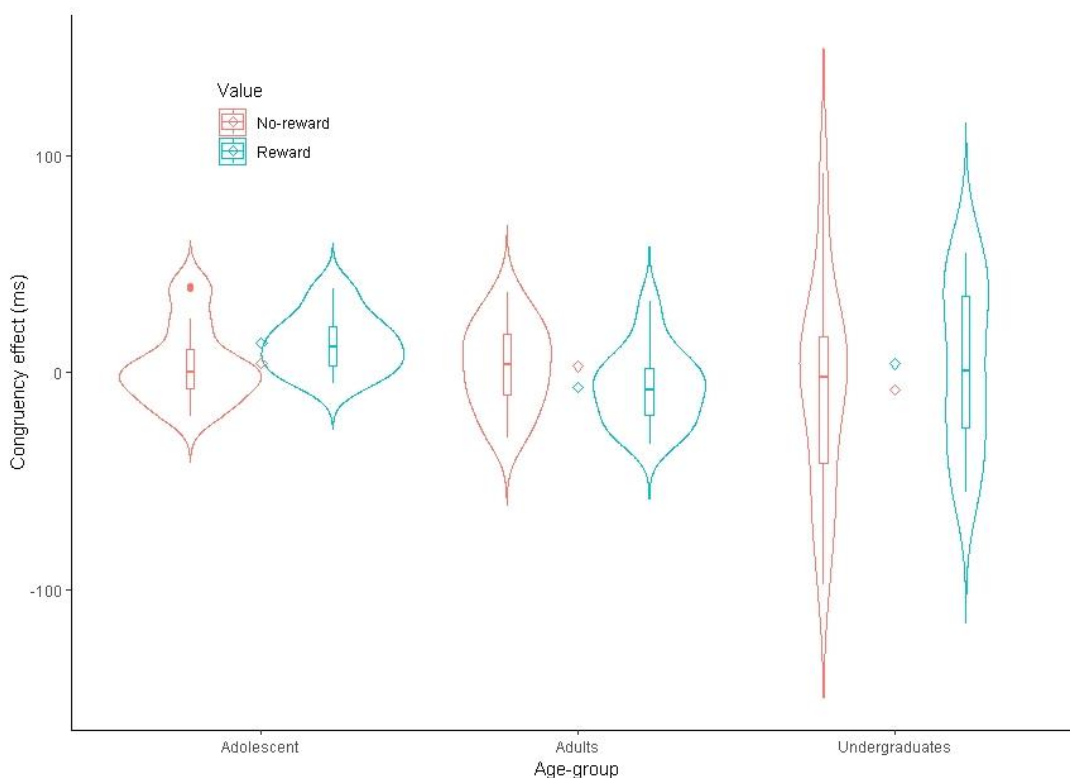


Figure 5.2. Response time congruency effects (incongruent – congruent) for reward and no-reward trials across all age-groups (Experiment 1: adolescents [mean age = 16.6 years] and adults [mean age = 28.5 years], Experiment 2: Undergraduates [mean age = 20.9 years]).

Incentive Array ERPs – The Pd

Figure 5.3 shows the ERP waveforms time-locked to the onset of the incentive arrays as collapsed across parietal-occipital electrode sites (PO3/PO4, PO7/PO8, P5/P6, and P7/P8, Bacigalupo & Luck, 2015), contralateral and ipsilateral to the ‘relevant’ cue. In adolescents, a significant Pd (a contralateral positivity) was observed only for an incentive cue that predicted no-reward, indicating that this was actively suppressed. Adolescents did not show a Pd for the

reward predicting incentive cue. Interestingly, in both adults and adolescents, the N2pc was not significant for either the no-reward or the reward symbol.

When measuring from all posterior electrode sites (Bacigalupo & Luck, 2015) the 2 (age-group) x 2 (incentive cue value) ANOVA on mean voltage, at the predefined time window of 325-375 ms (Sawaki et al., 2015) showed a significantly larger Pd when the incentive cue predicted no-reward ($F(1, 30) = 5.199, p < .05, \eta^2 = .148$). The Pd was also larger in the adolescents than the adults ($F(1, 30) = 4.816, p < .05, \eta^2 = .138$). Importantly, the 2-way interaction was also significant ($F(1, 30) = 4.665, p < .05, \eta^2 = .135$). In the adolescents, the mean voltage was significantly different from zero in a one-sample t test of the contralateral – ipsilateral difference wave for the Pd component when the incentive cue predicted no-reward ($t(15) = 2.382, p < .05$) but not different from zero for the reward condition ($t(15) = .124, p = .903$). Moreover, for adolescents, the Pd was statistically larger in the no-reward than the reward condition ($t(15) = 2.568, p < .05$). In adults, no Pd signal was present on either reward or no-reward condition.

A similar pattern was also found at the PO7/PO8 electrode site. The two-way interaction was significant ($F(1, 30) = 8.305, p < .01, \eta^2 = .217$). Again only in adolescents was the mean voltage greater than zero in the no-reward ($t(15) = 2.739, p < .05$), but not the reward ($t(15) = .285, p = .485$) condition. The Pd was also greater in response to a no-reward compared to a reward incentive cue ($t(15) = 3.060, p < .01$) at PO7/PO8.

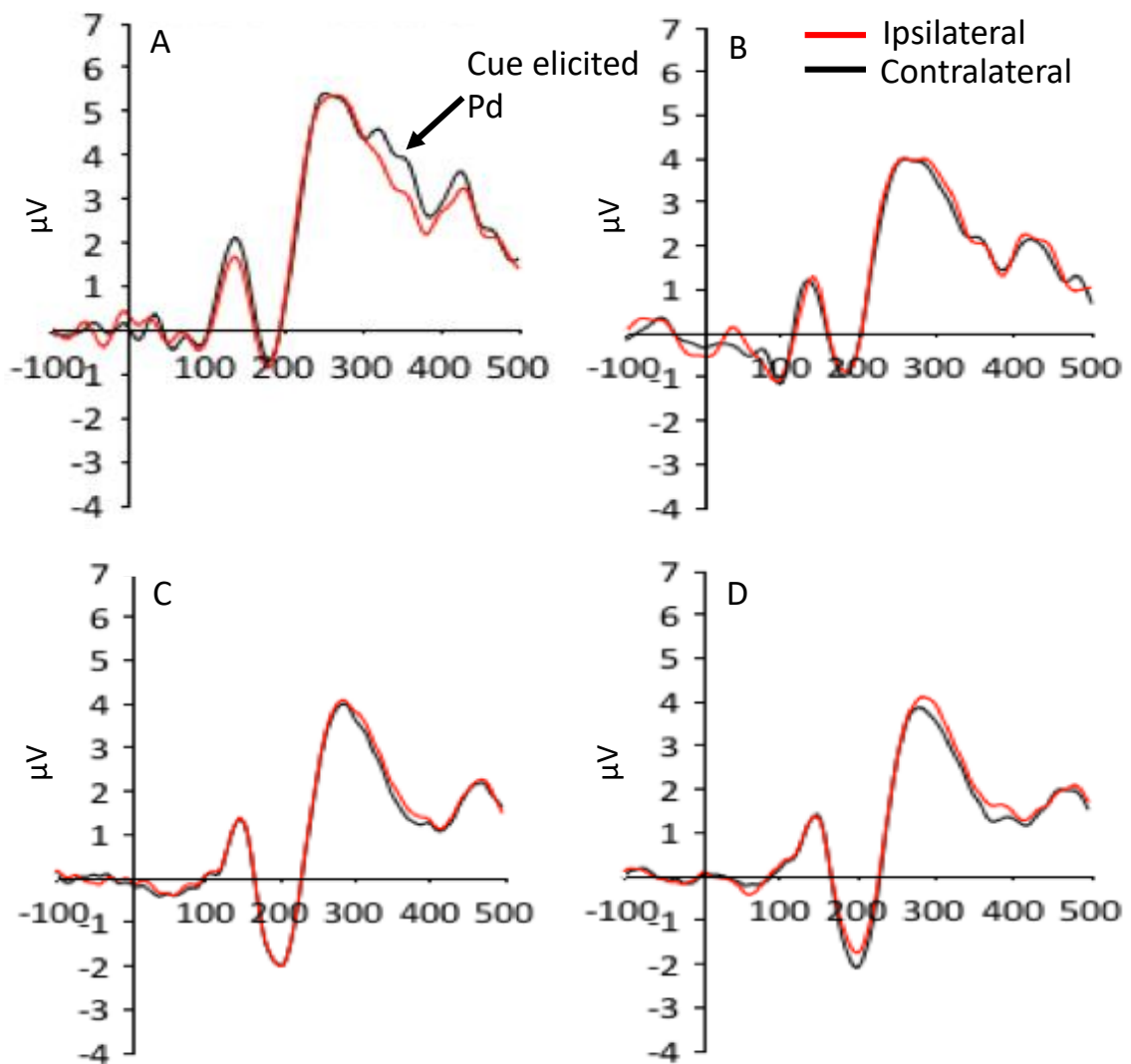


Figure 5.3. ERPs elicited by the incentive cues over lateral parietal/occipital electrodes (P5/P6, P7/P8, PO3/PO4, and PO7/PO8). Grand-averaged waveforms for no-reward and reward cues at contralateral and ipsilateral electrode sites relative to the 'relevant' symbol. On the top row are the ERPs elicited by adolescents to the no-reward (A) and the reward (B) cues. The bottom row are the ERPs elicited by adults to the no-reward (C) and the reward (D) cues. Positive is plotted up.

Pre-Incentive Array TFRs

Figure 5.4 shows the TFRs of the data prior to the onset of the incentive cue arrays. Statistical comparisons revealed significantly greater alpha power (10 – 14 Hz) in a cluster of electrodes (O2 and PO8) in the right posterior region in adults compared to adolescents during the pre-stimulus period, from 800 ms prior to the onset of the incentive array until the onset

($p < .01$). This pre-stimulus difference between adolescents and adults is consistent with both age-groups preparing differently for the incentive array⁴.

⁴ The same analysis was also repeated comparing pre-stimulus alpha (10 – 14 Hz) activity in adolescents and adults in the interval preceding the letter search array (-800 – 0 ms). No differences were observed at any electrode sites (all $ps > .1$). Therefore, the pre-stimulus alpha difference observed prior to the incentive array is unlikely to be an age-related difference related to skull thickness (Minhas, Bikson, Woods, & Kessler, 2012), because the same increased pre-stimulus alpha power difference was not observed in this second analysis.

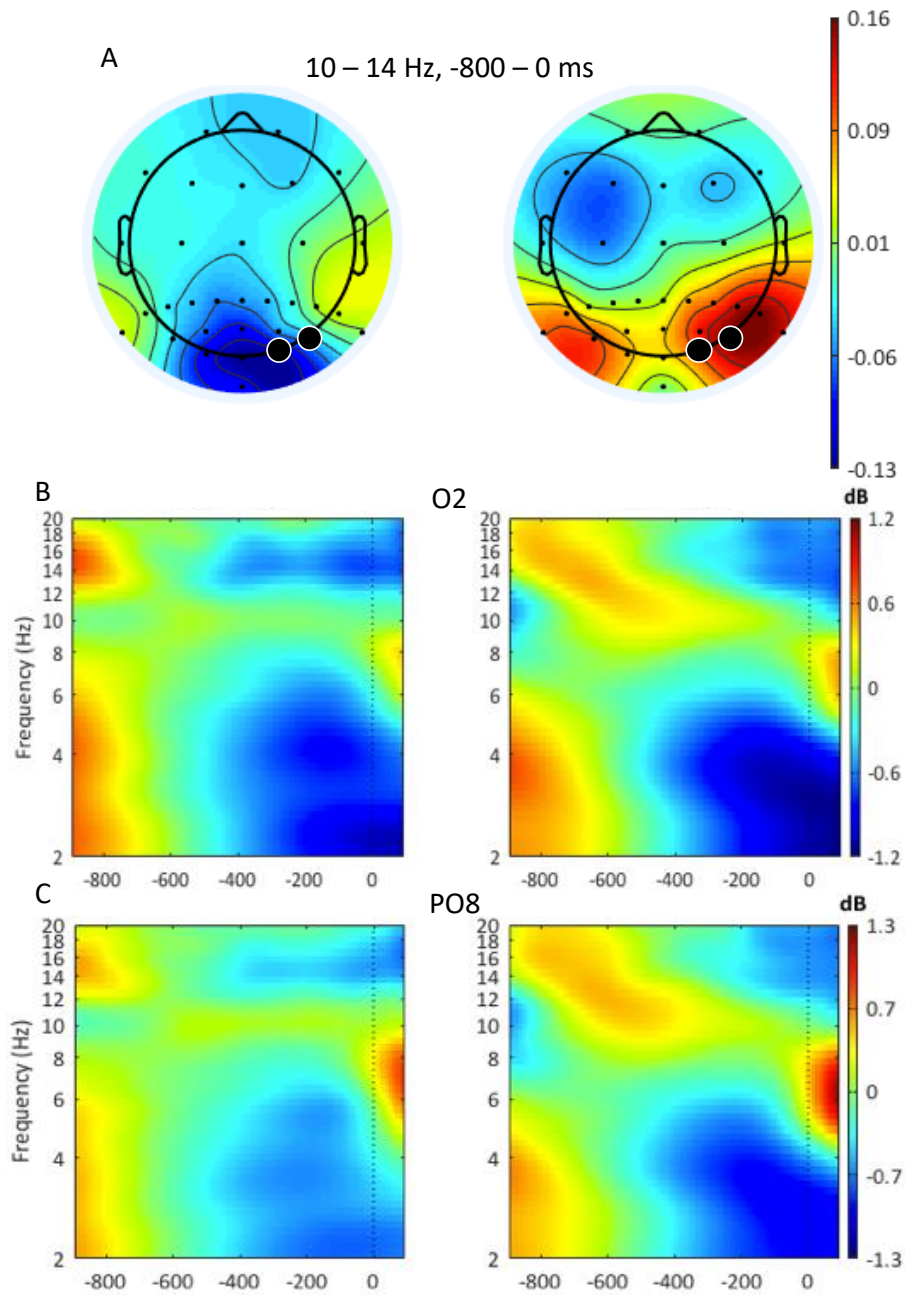


Figure 5.4. TFR results during the pre-stimulus period prior to the incentive array during the Letter detection task. Figures on the left are for the adolescents, on the right are for the adults. (A) Grand-averaged topographic plots of the TFR power averaged over 10 – 14 Hz between -800 – 0 ms prior to the incentive array. Circles with white outlines mark the locations (O2 & PO8) with significantly different ($p < .01$) activity between the adolescents and adults. (B & C) Grand-averaged power of neural oscillations in the EEG as a function of oscillation frequency and time prior to the incentive array at electrode sites O2 (B) and PO8 (C).

Experiment 2

In Experiment 2, a group of participants that are more typically used in studies examining the influence of motivationally salient stimuli on cognition were used; namely, undergraduate students. The aim was to investigate whether behavioural performance in undergraduates is more akin to adolescents or adults. Neural maturation is believed to continue into the mid-20s. Therefore, it could be argued that typical undergraduate students fall into a distinct category of ‘very’ late adolescence, but they are not yet fully mature adults. If this were the case, then performance should be influenced by the colour predicted by the incentive cue, as it was in adolescents.

Method

Participants

Nineteen new undergraduate participants (4 males, mean age = 20.9 years [range: 18 – 31, SD = 2.9]) were recruited from the University of Birmingham. All participants had normal or correct-to-normal vision, no history of neurological illness, and were naïve to both Japanese Hiragana characters and the purpose of the experiment. Participants also completed the Munsell D-15 test for colour-blindness; all were successful. Informed consent was obtained from all participants. Two participants were removed because their accuracy on the value-learning task was at chance. A further participant was removed because their performance on the letter-target detection task was at chance. All analyses reported in the results section were conducted on the remaining 16 participants.

Stimuli/Apparatus

The same as in Experiment 1.

Procedure

Value-Learning Task. The procedure was the same as Experiment 1, except there were fewer trials. In total there were 192 trials, with each 'relevant' symbol appearing on a quarter of trials, pseudo-randomly ordered. Each 'irrelevant' symbol also appeared on a quarter of trials, equally with each 'relevant' symbol. There was a break every 32 trials, where the participants could see how much cash they had earned so far.

Letter-Target Detection Task. The same as Experiment 1, except there was no EEG recording.

Data Analysis

Behavioural data in both parts of the experiment were treated the same as in Experiment 1, but analyses were run without the between-subject factor of age-group.

Results

Value-Learning Task.

At the shape selection stage, RT were faster on reward than no-reward trials ($F(1, 15) = 5.526, p < .05, \eta^2 = .269$). However, accuracy was unaffected by the cue-reward value ($F(1, 15) = 2.019, p = .176, \eta^2 = .119$). At the colour selection stage, RT was unaffected the cue-reward value ($F(1, 15) = .996, p = .335, \eta^2 = .064$). Accuracy, though, was better for the reward associated than no-reward associated colours ($F(1, 15) = 4.776, p < .05, \eta^2 = .242$). Importantly, though by the final block of trials accuracy was similar when selecting the colour for both cue-reward values ($F(1, 15) = 1.614, p = .223, \eta^2 = .097$), suggest that all cue/colour associations had been equally well learned.

Letter-Target Detection Task.

RTs (see Table 5.1) were faster when the incentive cue predicted a reward versus no reward ($F(1, 15) = 7.302, p < .05, \eta^2 = .327$). There was no main effect of congruency ($F(1, 15) = .206, p = .657, \eta^2 = .014$). However, the two-way interaction between incentive cue value and congruency was significant ($F(1, 15) = 4.753, p < .05, \eta^2 = .241$). As in the adolescents, the congruency effect in the undergraduates was significantly ($t(15) = 2.193, p < .05$) larger when the incentive cue predicted a reward (22 ms) compared to no-reward (-9 ms).

Accuracy mirrored RT. The two-way interaction was significant ($F(1, 15) = 5.223, p < .05, \eta^2 = .258$). When the incentive cue predicted a reward, accuracy was reduced when the colour-association was incongruent compared to congruent ($t(15) = 2.435, p < .05$), but not when it predicted no reward ($t(15) = .718, p = .484$).

General Discussion

In the current study, participants first learnt to associate novel cues with both a value (reward or no-reward) and a colour (purple or orange). These cues were then used as incentive cues in a subsequent letter detection task where participants had to locate a predefined target letter. The colour predicted by the cue could either be congruent or incongruent with the colour of the target letter. The colour prediction was, therefore, task-irrelevant. However, adolescents still demonstrated a bias for colour processing. Behaviourally, adolescents showed a colour congruency effect based on the colour predicted by the incentive cue, but only when this contingency was reward-associated in the learning task. When the incentive cue predicted no reward, no colour congruency effect was observed. The lack of a colour

congruency was also accompanied by a Pd signal to the no reward cue, indicating active suppression. Adults showed no such Pd or colour congruency for either cue, instead there was an indication that pre-stimulus alpha activity was increased in adults compared to adolescents in the interval prior to the incentive cues. This may be indicative of preparatory inhibition.

The behavioural data is consistent with the extant literature that rewards bias cognition in adolescents more so than in adults. For examples, Roper et al. (2014) showed that attentional control in adolescents is more sensitive than in adults to previously rewarding stimuli. Moreover, they found that value driven attentional capture persisted longer in adolescents than adults. Both those results (Roper et al., 2014) and the current data could be explained by slower extinction of stimulus-response associations in adolescents than in adults. However, in the current study there was no significant differences in performance between the age-groups by the end of the learning task. If the symbol-colour-value associations were equally well learned between groups and across stimulus values, then there is no reason to believe that extinction rates should differ. Furthermore, consistent with previous literature (Reimers & Maylor, 2005) the colour congruency effect observed in the adolescents in response to the reward incentive cue is not because of task-switching difficulties between the value-learning task and the letter detection task. Specifically, the lack of a colour congruency effect for the no reward incentive cue in adolescents suggests that they switched to letter processing for the letter-detection task.

The data are consistent with recent models of cognitive control that incorporate prior reward learning into the current allocation of control (Braver, 2012; Kool et al., 2017; Shenhav et al., 2013, 2016). These models may be useful when interpreting the current behavioural and EEG data, and more widely when considering adolescent risk-taking. Specifically, such

views suggest that behavioural goals can be activated both by external stimuli, based on prior associative learning, and internally, consistent with task-relevant requirements. It has been proposed that the competition between these sources for the allocation of cognitive resources is determined by the computation of an internal cost-benefit analysis that takes into account the predicted benefits (e.g., rewards) and costs (e.g., effort required) of each goal. The most potentially beneficial goal relative to the others 'wins' control over high level cognition. The current data can be easily interpreted within this framework.

Here, the two potential goals in the current letter detection task are, 'attend letter', which is the task-relevant goal, and 'attend colour', which is re-activated from learning by the presentation of the incentive cues. For the 'attend letter' state, the costs are related to potential opportunity costs (Kurzban et al., 2014; Shenhav et al., 2017), i.e., on congruent trials, if the strategy was to 'attend colour' the task would have been easier. The predicted benefits are task-related, i.e., correct performance on the task, which has an intrinsic value and also avoids a loss. For the 'attend colour' state, the costs are related to the conflict that needs to be resolved when the colour is incongruent (Botvinick et al., 2001). The benefits are that colour processing is easier (and faster) than letter processing by virtue of the hierarchical nature of the visual processing stream. Here, in adolescents and undergraduates, the 'attend colour' goal 'won' the competition for cognitive control, but only when the predicted benefit was heightened (i.e., reward incentive cue), because of the learned reward association with colour processing. Without this additional predicted benefit conditioned during the learning task, the intensity of the 'attend colour' goal is not strong enough to overcome the task-relevant 'attend letter' goal.

The current results also extend this framework. Specifically, the processing of external stimuli that trigger competing, but less successful goals must be suppressed, so that the strongest state can take control. Consistent with this notion is the signal suppression hypothesis (Sawaki & Luck, 2010) that suggests that a distractor stimulus with an attentional priority (e.g., perceptual salience) must be suppressed to halt further processing of that stimulus, if task-relevant stimuli are to be successfully attended. In the current study, this is evidenced by the Pd to a no-reward incentive cue, which inhibits the 'attend colour' goal resulting in the congruency effect being eliminated.

This is the first observation of a Pd marker of active suppression in adolescents. The presence of the Pd in adolescents is consistent with previous work that showed an N2pc response in both children and adolescents (Couperus & Quirk, 2015; Shimi et al., 2015; Wang et al., 2017). Both the N2pc and Pd have similar topographies, but with opposite polarities, and are thought to rely on similar underlying neural mechanisms (Sawaki & Luck, 2014). The knowledge that markers of active suppression can also be observed in adolescents offers a potentially interesting avenue for future research into the development of attentional suppression mechanisms.

Interestingly, despite previous studies showing an N2pc in adolescents (Couperus & Quirk, 2015; Shimi et al., 2015; Wang et al., 2017), here, no evidence of an N2pc to the incentive cues was found here. Although the no-reward cue required active suppression, the reward cue did not capture attention but still biased cognition and behaviour. The lack of a perceptual response to the reward cue suggests that although adolescents are hyper-sensitive to goals that have been conditioned with rewards, the cues themselves do not garner increased salience. The lack of an N2pc response further suggests that selective attentional

resources were not required to identify the relevant symbol from the incentive array, which is consistent with previous research showing an attenuated N2pc when target search is easy (Luck, 1995).

The pattern of data in adults was quite different to the adolescents. Not only did they show no behavioural colour-related processing, they also did not demonstrate active suppression or attentional selection ERP responses to the incentive array. However, pre-stimulus alpha activity prior to the incentive array was increased in adults compared to adolescents. Previous work has shown that increases in pre-stimulus alpha power are associated with reduced visual discrimination abilities (van Dijk et al., 2008), and have been linked to inhibitory processes (Mazaheri et al., 2009). In the current study, the increased posterior alpha in adults compared to adolescents possibly reflects a reduced readiness to process the incentive cues in adults. In other words, strategically or passively, adults may have proactively disengaged from the incentive array. Conversely the decreased alpha activity in adolescents compared to adults may have reflected an increased readiness for processing the incentive array. The current data cannot disentangle the two possibilities. However, consistent with prior research (Andrews-Hanna et al., 2011; Killikelly & Szűcs, 2013), it is apparent that proactive control is utilized differently in the two age-groups.

This EEG responses to the incentive cues in the current study are at odds with a previous experiment. In that study, adults demonstrated a Pd to a high value incentive cue (Sawaki et al., 2015). It was suggested that the active suppression to the incentive array allowed the participants to optimize attentional resources for the subsequent search task. Indeed, subsequent alpha suppression was also found prior to the search task following a high incentive cue. A couple of key differences between this previous study and the current

experiment may go some way to explain the different pattern of results. First, the age-groups used in the two experiments were different. Whereas the sample used by Sawaki et al. (2015) was typical of an undergraduate sample (18 – 30 years), in the current study EEG responses were obtained from a younger group (14 – 17 years) and an older group (23 – 38 years). This may have contributed to the different patterns of active suppression observed in both studies. However, this explanation is perhaps unlikely given that in Experiment 2 the behavioural results observed in the current undergraduate sample appear to mirror those of the adolescents and contradict what would be expected if the reward incentive cue was actively suppressed. A more likely explanation is that although the incentive array in both studies notified the participant of the reward available on each trial, in the current study the symbol also had a colour association that was potentially disruptive to performance. This may have discouraged adults from processing the incentive array; thus, active suppression was not required, and anticipatory inhibition was applied.

Despite the evidence in favour of adolescents and adults utilizing proactive control differently towards the incentive array in the current study, it should be noted that the time-frequency analysis was not optimal and therefore the results should be treated with caution. First, as absolute pre-stimulus alpha power was compared across two different populations the results are confounded by any potential differences in alpha power recorded at the scalp level. For example, differences previously observed in the skull size, shape and thickness through development, as shown in rats (Gefen, Gefen, Zhu, Raghupathi, & Marguiles, 2004) and humans (Susanne, Guidotti, & Hauspie, 1985), may have contributed to the alpha power differences observed here. Rather than taking a measure of absolute pre-stimulus alpha it would have been more appropriate to compare changes in alpha power from a baseline to

the pre-stimulus period between the two age-groups (e.g., Sawaki et al., 2015). Such an analysis would have also allowed for a stronger conclusion to be made about the direction of the possible difference observed between adults and adolescents. Despite alpha power being increased in adults compared to adolescents, it is unclear whether this represents an increase in alpha power in adults, a reduction in alpha power in adolescents, or both. Comparing changes in alpha power within groups would have better characterised the underlying direction of the effect. A second issue with the time-frequency analysis is that despite the primary frequency of interest being alpha band activity the current analysis offers the best frequency resolution at lower frequencies (2 Hz – 8 Hz). Instead, it would have been more appropriate to use linearly spaced frequency bins (e.g., Sawaki et al., 2015) to better understand the specific frequency of interest. Similarly, as I was not interested in high frequency activity, rather than using a seven-cycle Morlet wavelet, a lower number of cycles (three – five) may have been desirable to increase the temporal resolution and more appropriately analyse the alpha band activity. Given, the apparent issues with the time-frequency analysis these results offer only tentative evidence in favour of a difference in the way proactive control was utilized between adolescents and adults.

Finally, the observation that behavioural performance in a typical sample of undergraduates is more akin to that found in adolescents than adults also has potential wider implications for research investigating reward-driven effects in attentional control. Convenience typically dictates that the majority of research is conducted with undergraduates, but results are generalized to a wider population of ‘adults’. In future, it is worth bearing in mind the potential neural immaturity of undergraduate populations. This is especially important when investigating reward-effects because adolescence is known to be

a time when rewards have maximal impact on behaviour, so generalizations to the wider population may not always be appropriate. Future research should investigate potential differences in underlying neural activity in response to rewards between undergraduate and 'fully mature' adult samples.

In sum, adolescents are more inclined to reactively re-active learned reward-associated goals even when doing so is potentially harmful to current task performance. This is consistent with adolescents inflating the perceived benefits of previously rewarding behavioural goals, as was also found in Chapter 3. The current study also expands this notion by showing that stimuli instigating behavioural goals that are not chosen are actively suppressed in a reactive fashion by adolescents.

Chapter 6. Can Value-associated Stimuli Influence Ensemble Perception?

Abstract

Even with very brief exposure to multiple object arrays, observers seem able to use summary statistics of display properties to make generalized judgments of object attributes. Such ensemble perception is thought to aid visual cognition of complex scenes by overcoming tight capacity limitations through extraction of 'gist'. However, even when a scene is rich with perceptual consistencies, some stimuli within it may have greater motivational salience than others. Previous work from our lab has shown that value-associated stimuli are processed faster and maintained in WM better than neutral stimuli, suggesting that such stimuli may bias ensemble perception. To investigate participants were asked to adjust a response circle to match the average size of 12 heterogeneously sized circles viewed simultaneously for 200 ms (test array). In an initial value-learning phase, all circles had the same colour; responses were rewarded in a performance contingent manner with either a high or a low reward depending on array colour. In the second phase, test arrays comprised circles of three different colours and again the participant had to adjust a response circle to match the average size of the just viewed test array circles. No rewards were provided. On different trials, the smallest or largest four circles were presented in the previously high reward-associated colour. In the first experiment, average size estimates were biased towards the mean size of circles with the high reward-associated colour, especially when they comprised the largest circles. To investigate whether this effect occurred late in processing, the experiment was repeated, this time inserting a pattern mask immediately after the test array in test phase trials only. In addition to value-biasing being eliminated, test phase (but not value learning phase) performance accuracy was significantly better than in the first experiment. The results demonstrate that previously rewarding stimuli bias the extraction of summary statistics and I suggest that such biases result from slow recurrent processes.

The world is rich with visual redundancy; objects with shared features, such as leaves on a tree, could be represented more efficiently in the brain as a single entity or *ensemble* rather than each item being represented individually. Such an approach to scene processing would aid visual cognition by overcoming the tight capacity limitations of high-level visual perception, attention, and working memory (Cohen, Dennett, & Kanwisher, 2016). Indeed, substantial evidence of ensemble-oriented processing has recently been accumulated. For example, low level features such as the orientation of visual gratings (Dakin & Watt, 1997; Haberman, Brady, & Alvarez, 2015), colour (Haberman et al., 2015), the speed and direction of motion (Alvarez & Oliva, 2008; Sweeny, Haroz, & Whitney, 2012), and the size of circles (Ariely, 2001; Chong & Treisman, 2003, 2005) are just a few domains where ensemble perception has been shown. Nevertheless, little is known about how different types of saliency (physical or motivational) within scenes influence the coding of ensembles.

Typically, when investigating ensemble perception, the observer views an array of items and is instructed to judge the mean of a feature, e.g. size, shared by these items. Ariely (2001) was the first to demonstrate that the visual system could compress complex scenes into a summary of the scenes statistical properties (e.g., average size of all items). In this study, observers were presented with a brief (500 ms) array of up to 16 heterogeneously sized circles; immediately thereafter they judged whether a probe circle was larger or smaller than the average size of the original array. Mean size was estimated remarkably precisely; discriminations were accurate when the probe was around 4% different than the actual average size. However, the same participants were unable to correctly identify whether a probe item was actually a member of the original set. This series of experiments demonstrates that even with set sizes well beyond what is considered the capacity (around 4 items) for

selective attention (Pylyshyn & Storm, 1988) and working memory (Luck & Vogel, 1997), the visual system is proficient at creating representations of stimulus features that are informed by the entire set, but without explicit knowledge of individual items.

In fact, ensemble perception is largely unaffected by increases in set size that are well beyond the limits of attention and working memory (Chong & Treisman, 2003, 2005), indeed performance may actually improve with larger set sizes (Ariely, 2001; Robitaille & Harris, 2011). In addition, ensemble estimates can be performed with stimulus durations of 50 ms (Chong & Treisman, 2003) or 200 ms with masked displays (Whiting & Oriet, 2011), below the time necessary for sufficient shifts in attention (Egeth & Yantis, 1997). It therefore appears that ensemble statistics are independent of single object representations (Cohen et al., 2016), with evidence suggesting that ensemble representations can become consciously available without explicitly encoding individual items (Corbett & Oriet, 2011). Such studies support the view ensemble coding is automatic and uses a parallel mode of processing (Chong & Treisman, 2005).

Despite individual identities being supposedly lost, participants are capable of creating ensemble estimates for only a subset of items in a display. Brady & Alvarez (2011) used a working memory task wherein participants viewed an array of nine circles. Importantly, three circles were blue, three were red, and three were green. Participants were told to remember the sizes of all the red and blue circles but ignore the green circles. Following a brief delay (1 s), a probe circle then appeared in the location of one of the blue or red circles and participants had to adjust its size to match the original circle. Participants responses were found to be biased towards the mean size of all the circles in the probed circle's colour. However, in a subsequent experiment, when participants were not told to segregate the display based on

colour, responses were not biased by the mean size of the circles in the probed circle's colour (Brady & Alvarez, 2011).

Therefore, despite much evidence suggesting that representations of individual items are somehow lost during ensemble perception, there is some indication that individual items can be segregated based on task-relevant stimulus features before ensemble measures are formed. However, Brady and Alvarez (2011) demonstrated that the representation of a single entity is biased by the average of similar items. It still remains unclear whether individual items that are characterized by task-irrelevant features may bias ensemble judgments about entire displays. Specifically, in all previous such studies all items presented in the arrays have been equal in terms of salience, selection history, and reward properties. Here, I was interested in the influence of two types of saliency on ensemble judgments; the first was physical salience, determined by size, the second was motivational salience, determined by prior reward learning.

Physically salient stimuli garner preferential visual processing in a bottom-up fashion (Theeuwes, 1991). Size contrast is one determinant of physical salience, with larger items receiving visual priority (Proulx & Egeth, 2008). Similarly, many previous studies have shown that stimuli once associated with a large reward but that no longer result in the receipt of the reward are nevertheless prioritized for visual processing, resulting in faster recognition (O'Brien & Raymond, 2012) even when attention is limited (Raymond & O'Brien, 2009; O'Brien & Raymond, 2012). Although these findings suggest that both the physical saliency and the motivational saliency of specific stimuli might bias ensemble perception, high level representation of individual stimuli it is not thought necessary for ensemble perception (Corbett & Oriet, 2011), arguing against this possibility.

To investigate, participants performed two ensemble judgment tasks wherein they were required to adjust the size of a probe circle to match the average size of 12 different-sized circles presented briefly in a circular fashion around a central fixation point. In the first phase, all the circles were presented in the same colour. Participants were rewarded with a low (maximum 10 points) or a high (maximum 1000 points) reward for their responses depending on circle colour. Points were later exchanged for cash. Following this colour-reward learning phase, participants repeated the ensemble size task; however, now the test array comprised circles of three different colours and no rewards were forthcoming. Importantly, the four largest circles (large set), the four mid-sized circles (medium set), or the four smallest circles (small set) could be presented in the high value-associated colour. A control condition was also included wherein no circles had the high value-associated colour; instead all sets had novel colours.

The influence of large items should be evident across ensemble estimates. It was predicted that participants would overestimate the average size of the arrays, during both the colour-reward learning task and the second task that was performed in extinction. The effect of motivational salience was expected to be more nuanced and specific to the extinction task. Average size estimates were expected to follow the average size of the subset of circles presented in the high value-associated colour compared to the control condition. A second experiment investigated whether the mechanism by which saliency biases ensemble judgments is consistent with early selection or late, recurrent processes. To do so, a pattern mask was presented between the test array and the probe to inhibit late processing.

Experiment 1

Method

Participants

23 participants (4 males, between the ages of 18 – 35 years [Mean = 22.0 years, SD = 4.42 years]) from the University of Birmingham took part in exchange for course credits or were compensated £6 (plus the extra cash earned on the value-learning task). All participants had normal or corrected to normal vision and were naïve to the purpose of the experiment. Participants also completed the Munsell D-15 colour blindness test; all were successful. Informed consent was obtained from all participants. Alvarez and Brady (2011) tested 20 participants and obtained an effect size of Cohen's $d = 1.82$. To calculate the sample size, I assumed a more conservative Cohen's $d = 1.4$, a power = 0.80 and a two-tailed test. The result was a sample size of 19.

Apparatus

Value-Learning & Extinction Task. Stimulus presentation and data recording were controlled by a Macintosh computer and were programmed in Matlab (The MathWorks, Inc) using the Psychophysics Toolbox. Responses were recording using a standard keyboard and mouse. Stimuli were presented in RGB colour space on a black background ([0, 0, 0]) of a 68 cm LCD monitor [name manufacturer and model) with a screen resolution of 1920 x 1080 and a refresh rate of 60 Hz. Viewing distance was approximately 60 cm.

Stimuli

Value-Learning & Extinction Task. There were two primary displays presented on all trials: a test array and a response circle. Test arrays comprised 12 colour-filled circles with

diameters that could range between 10 and 160 pixels. The diameters of the circles on each trial were drawn from a log-normal distribution (natural logarithm) with a standard deviation of 35 pixels; there were 25 actual mean diameter sizes possible, equally spaced between 49 – 121 pixels. Each possible mean diameter was presented equally for all conditions. In each condition the average correct mean diameter was 85 pixels (an area of 5675 pixels²). The centre of each circle was placed along the circumference of an invisible circle that was centered on fixation and had a radius of 8°. Circle positions were chosen randomly with the constraint that no circle overlapped. In the value-learning task, all test array circles had the same colour (drawn in RGB colour space); in the extinction task, three different colours were used (with 4 circles in each colour). Colours used in experimental trials were purple [148, 131, 165], red [230, 93, 85], and orange [182, 133, 58]. Three different colours were used for control trials, pink [226, 90, 121], brown [215, 115, 58], and green [110, 151, 125]). The response display comprised a single circle presented at fixation, it matched the colour of the test array on that trial in the value-learning task, and was grey ([127, 127, 127]) in the extinction task. On initial presentation, its diameter was randomly chosen (between 10 and 160 pixels) but could never be within 20 pixels of the actual mean size.

Procedure

Value-Learning Task. See Figure 6.1. Following a fixation cross (1000 ms), the test array was presented for 200 ms immediately followed by the response circle (until response), and finally the amount of points earned on that trial (1000 ms). There were two colours that the circles could be presented in on every trial. One colour denoted a potential high reward trial (maximum reward of 1000 points), the other a low reward trial (maximum reward of 10 points). Each test array contained 12 circles. Participants were instructed to estimate the

average size of all of the circles in the test array. To indicate their response the participants adjusted the size of a central response circle by moving the mouse to the left (to shrink it) or right (to enlarge it) until it matched the perceived average circle size, pressing the left mouse button to submit the response (cf. Brady & Alvarez, 2011). The response circle size adjusted linearly in response to movements of the mouse. If response was within 5% (smaller or larger) of the actual average size, the maximum number of points for that trial was presented; otherwise the percentage error (larger or smaller) was deducted from the maximum amount of points for that trial (rounded to the nearest 10%) and presented as feedback. A running total of the points earned was presented at the bottom of the screen throughout the session and was updated after each trial.

There were 200 trials in total with high and low reward trials presented equally often in a pseudo random manner. Participants completed four blocks of 50 trials. During inter-block breaks, participants were presented with the number of points earned so far and how much cash this translated into (20000 points = £1). At the end of the value-learning task, participants were given the cash that they had earned. For the first five trials of every block the participant was given the choice of which colour test array they would like on the next trial. Participants were explicitly told to pick the colour that would give them the highest number of points. This gave us an explicit measure of whether participants had learned the reward contingencies. To ensure that participants had equal exposure to both colours, five extra trials were randomly placed in the subsequent block composed of the alternate colour to that which the participant chose on the choice trials.

Extinction Task. See Figure 6.1. All stimulus timings were the same as in the value-learning task, although there was no feedback stage. Participants were explicitly told that no

further points would be awarded for performance on this task. On each trial the test array consisted of 12 circles, and as before the task was judge the average size of all the circles. Unlike the value-learning task, the response circle was always grey, and the colour of the test circles differed from one another. Here, the four largest circles (Large Set) were presented in one colour, the four mid-sized circles (Medium Set) in another colour, and the four smallest circles (Small Set) in a third colour. On every trial the average size of circles in the Medium Set was equal to the average size of all circles in that array. On each trial, one set was presented in the previously high-reward colour, one in the previously-low reward colour, and one in a novel colour (the unused colour from the value-learning task, see *Stimuli* section). There were four possible colour x set experimental conditions. Of primary interest are the high-value biasing conditions. In these, the high-value colour was used for the Large or Small set, the low-value colour was used for the Medium set, and the remaining set (Small or Large, respectively) had the novel (no-reward) colour. The high-value colour was also used for the Medium set; in this condition the low-value colour was used for the Small or Large set and the novel colour made up the remaining set. A fourth control condition used three different novel colours for each set of circles. Each of these colours was pseudo randomly assigned to set so that each was used for the Large, Medium, or Small sets equally often.

There were 500 trials in total, with 100 trials of each experimental and control condition, the order of which was pseudo random. There were 10 blocks of 50 trials.

Data Analysis

Value-Learning & Extinction Task. Three participants failed to choose the correct colour on the choice trials on more than 13% of trials, indicating weak or absent colour-value learning. One further participant was removed because their average response was over 2.5

SD greater than the group mean. Their data was excluded from further analyses. For both the value-learning task and the extinction task, the first two trials of every block were removed before the mean response circle area (pixels²) of the response circle for each condition was then calculated. The mean percent increase from the actual average size was then calculated. For the value-learning task, paired-sample *t*-tests were used to compare high vs. low reward trials on measures of percent increase and response times (RT). For the extinction task, the effect of the high-biasing conditions was analysed in a one-way analyses of variance (ANOVA) on the percent increase. The ANOVA used biasing set (Small, Medium or Large) as a within-subjects factor. Follow-up planned pairwise comparisons were corrected for multiple comparisons by means of the False Discovery Rate procedure (Benjamini & Hochberg, 1995). Alpha levels were set at 0.05.

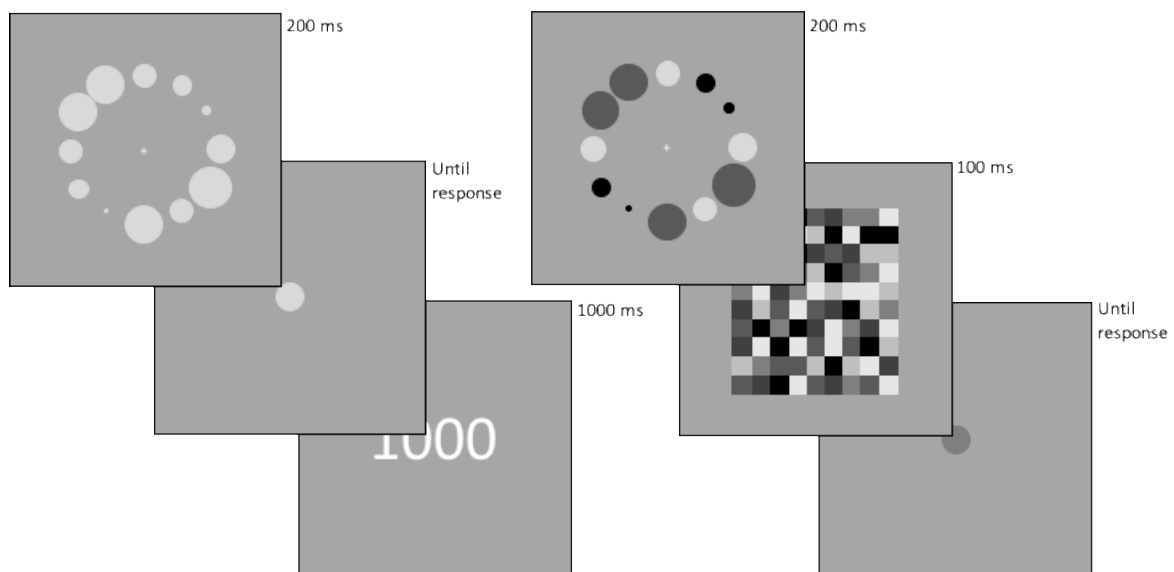


Figure 6.1. Left) The value-learning task trial structure in both Experiment 1 and 2. Right) The extinction task structure in Experiment 2. In Experiment 1 there was no mask presented between the test array and the response circle in the extinction task.

Results and Discussion

Value-Learning Task. See Table 6.1 for mean RT and mean circle areas. Performance was more effortful for high rewards as revealed by longer RT for the high (2681 ms) versus low (2474) reward condition ($t(18) = 2.820, p < .05$), but there was no difference in percent increase from the actual average size ($t(18) = 1.607, p = .125$).

Table 6.1. Mean RTs (ms) and percent increase in the estimates of circle size in the value-learning task for low-value and high-value circles in Experiment 1 and 2.

Trial type	Experiment 1 (No-mask)		Experiment 2 (Mask)	
	RT	Percent increase	RT	Percent increase
Low-value	2474 (28)	38 (1.4)	2999 (42)	32 (1.0)
High-value	2631 (28)	42 (1.4)	3229 (42)	33 (1.0)

Note. Within-subject standard error (Cousineau, 2005) in parenthesis.

Extinction Task. See Figure 6.2 for percent increase in all conditions from both experiments. Participants overestimated the average circle size; percent increase was greater than zero in the control condition (33%, $t(18) = 4.966, p < .001$).

For the high value-biasing conditions, the set with the high value colour had a significant influence on performance ($F(2, 36) = 4.472, p < .05, \eta^2 = .199$). When the high value colour was used for the Small set, percent increase (29%) was significantly smaller than when this colour was used for the Large set (33%, $t(18) = 3.217, p < .01$). When this colour was used for the Medium set, percent increase was marginally smaller than when used for the Large set ($t(18) = 1.762, p = .095$).

Comparisons of the percent increase in the different high value-biasing conditions compared to the control condition suggest that the influence of value was driven by the Small set reducing the percent increase in average circle size estimates. Percent increase was

significantly smaller than in the control condition when the high value colour was used for the Small set ($t(18) = 2.511, p < .05$), but not the Medium or Large set (both $ps > .19$).

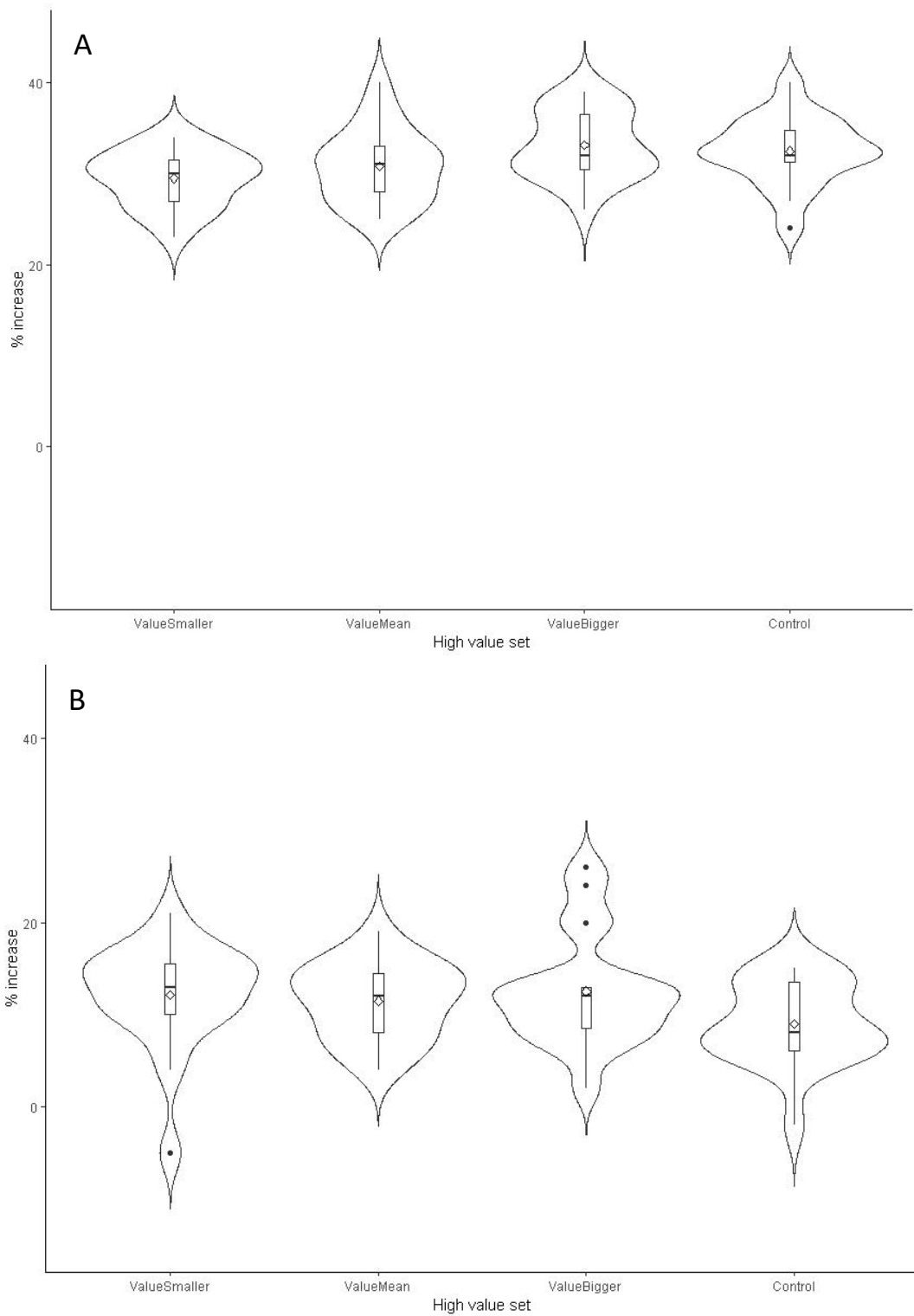


Figure 6.2. Percent increases in the judgments of average circle size from the actual average size depending on the high value-biasing condition in the Extinction task. A) Experiment 1. B) Experiment 2.

Experiment 1 provides novel evidence for a bias in ensemble perception from both physical and motivational salience. Specifically, average circle size judgments were consistently overestimated. However, when the smallest circles in the display were in the high value-associated colour this overestimation was slightly reduced. It remains unclear at what stage of ensemble processing the physical and motivational salience were having an influence. It is possible that the salient stimuli captured attention during the initial encoding of the stimuli influencing the formation of the ensemble estimate, in line with previous research showing that high value-associated task-relevant stimuli are processed faster (O'Brien & Raymond, 2011) than low value task-relevant stimuli. However, it may also be possible that salience has no influence during the initial ensemble formation but nevertheless facilitates entry of these items into WM (Raymond & O'Brien, 2009) or facilitate their maintenance in WM (Pedale & Santangelo, 2015; Raymond & O'Brien, 2009; Thomas, FitzGibbon, & Raymond, 2016) and thereby influence recurrent processing that may be used when ensemble estimates are computed. The second experiment examined these two possibilities.

Experiment 2

In Experiment 2, a pattern mask was introduced immediately following the presentation of the initial ensemble test array. If in Experiment 1, physical and motivational salience influenced the formation of the ensemble judgment then again it should be found to be overestimated with an influence of the high-reward coloured circles. However, if rewards operated through a recurrent feedback mechanism then the masking of the test array should block this operation, eliminating high-reward effects.

Method

Participants

23 participants (3 males, between the ages of 18 – 21 years [Mean = 19.35 years, SD = 0.81 years]) from the University of Birmingham took part in exchange for course credits or were compensated £6 (plus the extra cash earned on the value-learning task). All participants had normal or correct to normal vision and were naïve to the purpose of the experiment. Participants also completed the Munsell D-15 colour blindness test; all were successful. Informed consent was obtained from all participants.

Apparatus

Value-Learning & Extinction Task. Same as Experiment 1.

Stimuli

Value-Learning & Extinction Task. In Experiment 2 a mask was used in the Extinction task, but all other stimuli were the same as in Experiment 1. The mask was a grid, subtending approximately $9.5^\circ \times 9.5^\circ$, comprised of randomly coloured squares, each subtending approximately $0.5^\circ \times 0.5^\circ$. Each square was presented in one of the six possible colours from the Extinction task.

Procedure

Value-Learning Task. Same as Experiment 1.

Extinction Task. All information was the same as in Experiment 1, with one exception. Immediately following the test array, the mask was presented for 100 ms, which was immediately followed by the response circle.

Data Analysis

Value-Learning & Extinction Task. Four participants failed to choose the correct colour on the choice trials on more than 13% of trials, indicating weak or absent colour-value learning. Their data was excluded from further analyses. All other information was the same as in Experiment 1.

Results and Discussion

Value-Learning Task. As in Experiment 1, RT were longer for high rewards as revealed by longer RT for the high (3229 ms) versus low (2999 ms) reward condition ($t(18) = 2.738, p < .05$), but there was no difference in percent increase ($t(18) = .659, p = .518$).

Extinction Task. In contrast to Experiment, the presentation of the pattern mask after the test array eliminated the overestimation in average circle size estimates. Percent increase was not significantly greater than zero in the control condition (9%, $t(18) = 1.593, p = .129$). In addition, the percent increase in the control condition was significantly smaller in Experiment 2 than in Experiment 1 ($t(36) = 2.771, p < .01$)⁵. There was also no effect of the high-value biasing conditions ($F(2, 36) = .142, p = .868$).

The presentation of a mask after the initial test array not only substantially reduced the tendency to overestimate the average circle size but also eliminated any influence of value. These data from Experiment 2 suggest that the initial formation of an ensemble

⁵ Percent increase was not different between the experiments during the value-learning task ($t(36) = .741, p = .463$).

judgment is highly representative of the actual visual array. However, these judgments are then heavily biased by recurrent processing of salient stimuli.

General Discussion

The first experiment reported here shows that ensemble perception of mean circle size can be biased towards the mean size of a subset of the display. Specifically, when a subset of an array of circles was previously predictive of a large monetary reward, ensemble estimates were biased towards the mean size of that subset. In addition, regardless of value, estimates were also found to be heavily biased by the largest circles in the display. The second experiment showed that these effects of both motivational salience and physical salience are abolished when a coloured pattern mask is applied immediately after display presentation. The latter findings suggest that the underlying mechanism for the value-associated bias seen in the former experiment most likely stems from recurrent processing of higher order brain areas on lower level sensory areas.

The finding that value-associated stimuli disproportionately influence ensemble size estimates suggests that the neural mechanisms responsible for ensemble perception are sensitive to motivational cues. This finding is perhaps unsurprising given that reward-associations have previously been shown to have a positive influence on visual processing of task relevant information. For example, masked recognition tasks show that high-value associated stimuli are processed faster than similar low-value associated stimuli (O'Brien & Raymond, 2012). Moreover, these items are also more likely to access conscious processing when attention resources are limited (Raymond & O'Brien, 2009) and are maintained better

in working memory (Thomas et al., 2016). Other works shows that reward associations also influence distractor processing, causing irrelevant items to capture attention during visual search (Anderson et al., 2011), Generally, reward-associated stimuli are assumed to be given priority in visual processing because of learned incentive salience (Robinson & Berridge, 1993). Here, it was demonstrated that even when making general judgments about entire displays reward-associated stimuli remain prioritized.

The current results are contrary to previous conclusions that ensemble estimates are performed independently of individual item coding (Ariely, 2001; Corbett & Oriet, 2011; Whitney et al., 2014). The results, though, are consistent with Brady and Alvarez (2011) who showed that individual item representations can be biased by the average of a subset of items in an array. However, the current study extends these findings. First, here, the average of a subset of items was found to bias global ensemble judgments, rather than judgments about individual items. Second, Alvarez and Brady (2011) only found separate ensembles to be formed when the segregating feature was task-relevant, whereas here, the feature was task-irrelevant (colour).

I believe the current data suggest a unifying framework that accounts for the contradictory evidence on the role of individual object processing in ensemble perception. Specifically, Experiment 2 suggests that ensemble coding can proceed automatically (Treisman, 2006) in a very precise manner, within 200 ms, and without the need for high-level coding of individual items. Later processing of a subset of items then interacts with the initial formation of the ensemble, in a recurrent manner, as seen in Experiment 1. The selection of this subset is driven by the (physically or motivationally) salient items in the display, likely related to selective attention mechanisms prioritizing these items for working memory

maintenance (Thomas et al., 2016; Vogel, Woodman, & Luck, 2005). Together, these data show that ensemble estimates of low-level visual features are initially very precise but are subject to later interference from both physically and motivationally salient items in the display.

Chapter 7. General Discussion

A core aim of this thesis was to develop and test a motivation-based as opposed to a perception-based explanation for reward association effects on visual attention. Even when irrelevant to current goals and perceptually conspicuous, value-associated stimuli capture attention (Anderson et al., 2011). Such super-distraction effects do not fit with classic models of top-down and bottom-up attentional control (Awh et al., 2012; Failing & Theeuwes, 2017). Recent conceptualizations of value-driven biases in attention suggest that learned value boosts the perceptual representational strength of value-associated stimuli on attentional priority maps (Anderson et al., 2011, 2014; Awh et al., 2012; Della Libera & Chelazzi, 2006; Failing & Theeuwes, 2017; Kiss, Driver, & Eimer, 2009). In this view, this representational boost allows value-associated stimuli to be perceptually competitive for attention with task-relevant stimuli. However, an alternative proposal that is grounded in the cognitive control literature suggests that value-associated stimuli compete to alter current goals. This motivational competition is resolved by a rapid computation of the predicted costs and benefits (motivational intensity) of achieving each goal (Shenhav et al., 2013). Motivational states can be instantiated by external stimuli, such as value-associated stimuli, based on prior experience. They can, of course, also be instigated internally in a 'top-down' manner based on task-relevant demands. The benefits associated with each state are determined by payoffs predicted by previous experience. The costs are internally computed based on the potential negative outcomes of each state and the cognitive effort required. For example, conflict with task-relevant processing is one such cost (Botvinick et al., 2001). In this thesis, I have demonstrated that this motivational competition may likely be at the core of super-distraction effects. Next, I will summarize the evidence in favour of this conclusion.

Summary of the studies

In all but two experiments in this thesis, I utilized a two-phase experimental procedure. First, stimuli were associated with a value. In Chapters 2 and 3, stimuli were associated with loss, neutral and gain values. In Chapters 4 – 6, losses were excluded, and the value could be neutral, low-reward or high-reward. Then, in the second phase, these same stimuli were used as either distractors (Chapters 2 – 4) or incentive cues (Chapter 5) in attention tasks, or targets (Chapter 6) in an ensemble perceptual judgment task. Taking a developmental approach, in Chapters 3 and 5, value-driven biases in cognitive control were examined in late adolescents (14 – 17 years old).

In Chapter 2, the aim was to contrast the different predictions made depending on whether motivational or perceptual competition is used to explain super-distraction effects. To investigate, I used a simple colour-flanker task; crucially, flankers could be motivationally or perceptually salient. Of interest was whether sequential trial effects (conflict adaptation, CA) would differ depending on the motivational versus perceptual salience of the flankers. Effects attributable to motivational salience only occurred following conflict trials (colour-incongruent flankers); whereas effects attributable to perceptual salience only occurred after no-conflict trials (colour-congruent flankers). Importantly, this demonstrated that value-based super-distraction effects are inconsistent with classic perceptual competition accounts. Perceptual salience appeared to boost distractor representations when attention was unconstrained. Motivational salience counteracted the conflict driven adjustments in cognitive control that are typical in CA. These experiments are consistent with motivational salience competing to alter cognitive control settings.

In Chapter 2 (experiment 4) and Chapter 4 (experiment 1), the basic two-phase experiment was elaborated to involve a secondary WM task during the second phase. Whilst maintaining information in WM, the presentation of perceptually similar stimuli is known to distort WM representations (Ahmad et al., 2017). Consistent with this finding, studies have also shown that observers are more likely to ignore stimuli in a secondary attention task that match the contents of WM (Kim et al., 2005). In Chapter 2, the concurrent WM task and the target in the flanker task required colour processing, whereas distractor value-associations in the flanker task were defined by shape. Super-distraction (following conflict) in the flanker task was shown to be increased with a concurrent colour-based WM load compared to without a WM load. In Chapter 4, the shape-colour contingencies were reversed. Here, the attention task was a partial replication of the visual search paradigm developed by Anderson et al. (2011). Distractor value-associations were defined by colour during search for a unique shape. Alongside the search task, participants held either a colour- or shape-based WM load. This time, super-distraction was increased when the WM load being maintained was shape-based compared to colour-based. Motivation based competition explains these results as follows. By introducing a WM task that relies on the same or similar processing networks as those required for identifying the target in the attention task, the cognitive cost of processing the target is increased, thus markedly reducing motivational intensity for target processing. Importantly, the concurrent WM does not affect motivational intensity to engage with the value-associated items in the test array. Thus, the relative difference in motivational intensity to engage with targets versus distractors is shifted in favour of distractors and super-distraction is more evident. These studies again suggest that estimates of motivational intensity are relative to those of other active states.

As a further test of these ideas within the value-driven attentional capture paradigm, In Chapter 4 (experiment 2), using a direct replication of Anderson et al. (2011), I examined sequential trial effects, so that the role of conflict could be investigated. In this experiment, following a trial with a high value-associated distractor, which presumably interfered with target processing, value driven attentional capture was reduced on the subsequent trial. This demonstrates that when value-associated motivational states are experienced as costly to performance, they are less likely to bias cognition.

Such sequential trial effects also concern a larger issue in the study of attentional control. Specifically, in a host of attentional paradigms sequential trial effects have been observed (e.g., Gratton et al., 1992; Tipper, 1995; Lowe & Mitterer, 1982; Della Libera & Chelazzi, 2006; Hickey et al., 2010), yet they are often overlooked in the literature. Attentional processing on a single trial is not an isolated event. The data from Chapter 4 further demonstrated that sequential effect may even mask differences between conditions. Although top-down attentional control may be set based on task-demands, such settings are constantly being updated, even on a trial-to-trial basis.

In Chapters 3 and 5, super-distraction effects were investigated in adolescents (14 – 17 years). In Chapter 3, adolescents performed the same colour-flanker task used in Chapter 2 (Experiment 3 & 4). Whereas, adults showed no super-distraction when the value was only weakly associated with the stimulus in the flanker task, adolescents showed strong super-distraction effects (following conflict trials). This was despite both groups being equally reactive to conflict signals, i.e., both groups demonstrated CA when flankers were associated with a neutral outcome. This study suggests that developmental stage is an important factor in the internal predictions of payoffs for value-associated motivational states. Specifically, in

this experiment, adolescents appeared to inflate the rewarding properties of value-associated states but estimates of costs (conflict) were similar to those in adults.

Similarly, in Chapter 5, adolescents were again unable to ignore value-associated motivational states. In this study, during learning, a symbol presented prior to an array of colours informed the participant which colour should be chosen and whether they would be rewarded for choosing the correct colour. In a subsequent attention task, the same symbols were used as incentive cues, but the colour association was now irrelevant. Instead, search was for a target letter. Crucially, on half of trials the distractor was in the previously associated colour; on remaining trials the target was in the associated colour. There was evidence that adolescents altered their strategic control to search for colour, but only when the cue also predicted a reward. ERP evidence further suggested that adolescents actively suppressed a neutral cue, evidenced by a Pd signature (Hickey et al., 2009) in the ERP, but not the reward cue. This further suggests that when two competing motivational states are active, one must be suppressed.

To the best of my knowledge, a Pd signature has not previously been observed in adolescents. Therefore, the Pd found here could have wider implications for studying the development of active suppression mechanisms in adolescents.

These chapters also show the utility of a taking a developmental approach in the study of motivation. Although my studies are not the first to examine the effects of rewards on attention in adolescents, Chapter 3, and to a lesser extent Chapter 5, are among the few experiments (see Roper et al., 2014) that have studied value-driven motivation independently of top-down attention (Maunsell, 2004) in this age group. Nearly all previous reward and attention studies in adolescents confounded motivation with attention by making rewards

contingent on attention to a stimulus or location (c.f. Geier & Luna, 2009). In this thesis, I have shown that when motivation and attention are dissociated, adolescents can offer a window into the mechanisms underlying motivational competition.

Link to other theories of super-distraction

The motivational competition framework is compatible with other recent accounts of super-distraction, although the emphasis here is shifted to competition between motivational states rather than perceptual competition. For example, consistent with selection history accounts (Awh et al., 2012; Failing & Theeuwes, 2017), a key to motivational competition is the idea that the goal during prior learning is re-activated when the value-associated stimulus is re-encountered. The selection history of value-associated stimuli, therefore, forms the basis of the motivational competition. However, the new framework offers a more mechanistic appraisal of the conditions under which the learned goals will be re-instantiated, which is lacking in selection history accounts. Similarly, super-distraction has also been discussed in terms of habitual control (Anderson, 2016, Anderson et al., 2016; Anderson et al., 2017), whereby the response is automatically re-activated on perception of the stimulus. One possibility is that because of their automatic nature, habitual behaviours generally 'win' the competition for cognitive control because they do not require cognitive resources to initiate and complete (Schneider & Shiffrin, 1977). In effect, they are a 'low-cost' form of information processing. Whether this is the case for value-associated stimuli is an open question, but the evidence presented in this thesis suggests that value-associated motivational states are certainly not always perceived as 'low-cost'. More broadly, to comprehensively integrate

habitual control into the motivational competition framework more focused research into the question is required.

Future considerations

The studies in this thesis have added to a growing literature on motivated cognition but they also raise some interesting questions for follow-up experiments. First, a key tenet of the proposed motivational competition framework is the concept of a cost-benefit trade-off for each motivational state that determines how cognitive control is utilised (Shenhav et al., 2013). However, although the neural correlates of the costs that lead to adjustments in control are quite well delineated, the rapid incorporation of benefits into computations of motivational intensity are less well understood.

Conflict as a cost leading to adjustments in top-down control is well established (Botvinick et al., 2001). There is imaging evidence that conflict is registered in the dACC and prefrontal regions regulate control based on this conflict (MacDonald et al., 2000). Many ERP components have also been discovered that have a neural source in the dACC that are responsive to conflict, errors and performance feedback, such as the N2, ERN, CRN, and FRN, respectively. Cognitive effort is another source of costs (Shenhav et al., 2013; Botvinick & Braver, 2015); again, evidence suggests that the ACC is rapidly responsive to the amount of cognitive effort required (Botvinick & Braver, 2015).

In this thesis, I have suggested that value-associations act as a potential benefit in the rapid computations of motivational intensity. This is consistent with the vast neuroimaging work that the brain processes value codes in the midbrain (Anderson et al., 2016; Anderson et al., 2017; Schultz, 2000), OFC (Saez et al., 2017), and DLPFC (Marcos et al., 2018) regions.

However, the motivational competition theory suggests that these value codes can lead to rapid adjustments in cognitive control. For example, in Chapter 2 the behavioural responses to the value-associated distractors were evident after only around 600 ms from onset of the stimuli. A future line of research may be to investigate neural responses originating from the ACC in response to value-associated stimuli. Similar ERP responses as those found for predicted costs may also be evident for estimates of predicted benefit. These responses may be linked to midbrain dopaminergic activity that signal the presence of reward-associated stimuli (Anderson et al., 2016; Anderson et al., 2017), and should be predictive of behavioural change in response to value-associated distractors.

A second potential line of future investigation could further explore the developmental course of motivational competition. Although the two adolescent studies reported here demonstrated clear differences in motivated cognition between adolescents and adults, the adolescents tested were from a narrow developmental window, namely late adolescence (14 – 17 years). It is unknown how much the ideas expressed in this thesis would relate to younger adolescents and children. For example, previously it has been shown that younger compared to older adolescents under-recruit the ACC during tasks requiring performance monitoring (Ladouceur et al., 2010). Given that the ACC is thought to be central in determining how cognitive control is allocated (Shenhav et al., 2013), does this lead to more irrational biases in decision making in younger adolescents compared to adults and even late adolescents?

Related to investigating the developmental course of motivated cognition, Chapter 5 demonstrated that late adolescents (14 – 17 years) and adults (24+ years) show markedly different response tendencies to value-associated stimuli, but in a third sample of typical undergraduates participants, performance was remarkably similar to that found in

adolescents. Given the ongoing neural maturation throughout adolescence and into earlier adulthood (Giedd et al., 1999) that often manifests itself as a heightened sensitivity to rewards (Geier & Luna, 2009), generalization of motivation effects from undergraduates to wider 'adult' populations may not always be appropriate. In addition, the use of undergraduate samples may also make comparisons between studies problematic. For example, a study conducted on first year students (~18 years old) may not yield comparable results to a study performed with a group of neurally more mature third year students (~21 years old) or 'fully' mature, at least in terms of neural maturation (Giedd et al., 1999), graduate students (~25 years old). A further goal of future research could be to characterize the changes in super-distraction through this important period of development (i.e., 18 – 25 years) to better understand the current literature.

A third area for future work to investigate is the influence of different types of reward. In this thesis, monetary feedback was used as the measure of reward. However, it is not clear whether all participants value money equally. Indeed, this may be particularly true when investigating developmental differences. For example, adolescents may be more motivated by the relatively small monetary incentives used in experimental paradigms. To this end, future studies should seek to better equate the incentives between different experimental groups. In addition, future research should also investigate the roles of different types of incentives, such as social rewards, as well as the influence of negative outcomes on motivated cognition.

Finally, in the current thesis, the sample sizes were small, which may limit the generalizability of the findings. In particular, although the power to observe the experimental effects in the current experiments was high, this may have been artificial. In all the reported

experiments, participants were removed from the analyses if their accuracy in the value-learning task did not meet strict criteria for assessing whether they had learned the stimulus-reward contingencies. By applying these criteria, it is possible that two types of participant were removed from the analyses, 1) those that did not understand the instructions, and 2) those that were not sensitive to rewards, which may have hindered their learning. By potentially removing participants that were insensitive to rewards, the interpretations of the results may be limited to a specific reward-sensitive group of people. To overcome this limitation, future studies should increase the sample sizes and investigate how individual differences to reward sensitivity impact motivated cognition.

Wider implications

The proposed motivational competition framework has wide reaching implications for the understanding of a broad range of experimental findings and potentially in understanding the mechanisms underlying addiction and other mental health issues. For example, individuals with depression may under-estimate the perceived benefits of stimulus-driven motivational states, leaving them unmotivated, whereas addicts may inflate the perceived benefits, making them oversensitive to addiction related motivational states. How the motivational competition framework applies to different mental health disorders is a further possible line of future research.

In conclusion, in this thesis, I have built on the work of Shenhav, Botvinick, Braver and colleagues to develop a cognitive model of motivated cognition that can quickly incorporate relevant experience into a simple cost-benefit analysis that determines goal-directed behaviour. This work addresses an age-old question raised by Renaissance

philosophers Dante Alighieri and Jean Buridan; how can motivation dictate competitive decision making? I believe that the proposed framework suggests a plausible and mechanistic model that allows humans to make quick decisions that are grounded in experience and contextual knowledge.

Chapter 8. List of References

Aarts, H., & Dijksterhuis, A. (2000). Habits as knowledge structure: Automaticity in goal-directed behavior. *Journal of Personality and Social Psychology*, *78*(1), 53–63.

Ahmad, J., Swan, G., Bowman, H., Wyble, B., Nobre, A. C., Shapiro, K. L., & McNab, F. (2017). Competitive interactions affect working memory performance for both simultaneous and sequential stimulus presentation. *Scientific Reports*, *7*(1), 1–16.

<http://doi.org/10.1038/s41598-017-05011-x>

Ahmed, L., & de Fockert, J. W. (2012). Focusing on Attention: The Effects of Working Memory Capacity and Load on Selective Attention. *PLoS ONE*, *7*(8).

<http://doi.org/10.1371/journal.pone.0043101>

Alvarez, G. A., & Oliva, A. (2008). The representation of simple ensemble visual features outside the focus of attention. *Psychological Science*, *19*(4), 392–398.

<http://doi.org/10.1111/j.1467-9280.2008.02098.x>.The

Amiez, C., Joseph, J. P., & Procyk, E. (2006). Reward encoding in the monkey anterior cingulate cortex. *Cerebral Cortex*, *16*(7), 1040–1055.

<http://doi.org/10.1093/cercor/bhj046>

Anderson, B. A. (2015a). Value-driven attentional capture is modulated by spatial context. *Visual Cognition*, *23*(1), 67–81. <http://doi.org/10.1038/nmeth.2839>.A

Anderson, B. A. (2015b). Value-driven attentional priority is context specific. *Psychonomic Bulletin & Review*, *22*(3), 750–756. <http://doi.org/10.3758/s13423-014-0724-0>

Anderson, B. A. (2016). The attention habit: How reward learning shapes attentional selection. *Annals of the New York Academy of Sciences*, *1369*(1), 24–39.

<http://doi.org/10.1111/nyas.12957>

Anderson, B. A., Chiu, M., DiBartolo, M. M., & Leal, S. L. (2017). On the distinction between value-driven attention and selection history: Evidence from individuals with depressive symptoms. *Psychonomic Bulletin and Review*, *24*(5), 1636–1642.

<http://doi.org/10.3758/s13423-017-1240-9>

Anderson, B. A., Faulkner, M. L., Rilee, J. J., Yantis, S., & Marvel, C. L. (2013). Attentional bias for non-drug reward is magnified in addiction. *Experimental and Clinical Psychopharmacology*, *21*(6), 499–506. <http://doi.org/10.1002/ar.20849.3D>

Anderson, B. A., Folk, C. L., Garrison, R., & Rogers, L. (2016). Mechanisms of Habitual Approach. *Journal of Experimental Psychology: General*, *145*(6), 796–805.

<http://doi.org/10.1037/xge0000169>

Anderson, B. A., & Halpern, M. (2017). On the value-dependence of value-driven attentional capture. *Attention, Perception, & Psychophysics*, *79*(4), 1001–1011.

<http://doi.org/10.3758/s13414-017-1289-6>

Anderson, B. A., Kronemer, S. I., Rilee, J. J., Sacktor, N., & Marvel, C. L. (2016). Reward, attention, and HIV-related risk in HIV+ individuals. *Neurobiology of Disease*, *92*(B), 157–165.

Anderson, B. A., Kuwabara, H., Wong, D. F., Gean, E. G., Rahmim, A., Brašić, J. R., ... Yantis, S. (2016). The role of dopamine in value-based attentional orienting. *Current Biology*, *26*(4), 550–555. <http://doi.org/10.1016/j.cub.2015.12.062>

Anderson, B. A., Kuwabara, H., Wong, D. F., Roberts, J., Rahmim, A., Brašić, J. R., & Courtney, S. M. (2017). Linking dopaminergic reward signals to the development of attentional bias: A positron emission tomographic study. *NeuroImage*, *157*, 27–33.

- <http://doi.org/10.1016/j.neuroimage.2017.05.062>
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011a). Learned value magnifies salience-based attentional capture. *PLoS ONE*, *6*(11). <http://doi.org/10.1371/journal.pone.0027926>
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011b). Value-driven attentional capture. *Proceedings of the National Academy of Sciences*, *108*(25), 10367–10371. <http://doi.org/10.1073/pnas.1104047108>
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2014). Value-driven attentional priority signals in human basal ganglia and visual cortex. *Brain Research*, *1587*(1), 88–96. <http://doi.org/10.1016/j.brainres.2014.08.062>
- Anderson, B. A., Leal, S. L., Hall, M. G., Yassa, M. A., & Yantis, S. (2014). The attribution of value-based attentional priority in individuals with depressive symptoms. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(4), 1221–1227. <http://doi.org/10.3758/s13415-014-0301-z>
- Anderson, B. A., & Yantis, S. (2012). Value-driven attentional and oculomotor capture during goal-directed, unconstrained viewing. *Attention, Perception, & Psychophysics*, *74*(8), 1644–1653. <http://doi.org/10.3758/s13414-012-0348-2>
- Anderson, B. A., & Yantis, S. (2013). Persistence of value-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(1), 6–9. <http://doi.org/10.1109/TMI.2012.2196707>. Separate
- Anderson, R. I., Bush, P. C., & Spear, L. P. (2013). Environmental manipulations alter age differences in attribution of incentive salience to reward-paired cues. *Behavioural Brain Research*, *257*, 83–9. <http://doi.org/10.1016/j.bbr.2013.09.021>
- Andrews-Hanna, J. R., Mackiewicz Seghete, K. L., Claus, E. D., Burgess, G. C., Ruzic, L., &

- Banich, M. T. (2011). Cognitive control in adolescence: neural underpinnings and relation to self-report behaviors. *PLoS One*, *6*(6), e21598.
<http://doi.org/10.1371/journal.pone.0021598>
- Ansorge, U., Kiss, M., Worschech, F., & Eimer, M. (2011). The initial stage of visual selection is controlled by top-down task set: New ERP evidence. *Attention, Perception, & Psychophysics*, *73*(1), 113–122. <http://doi.org/10.3758/s13414-010-0008-3>
- Ariely, D. (2001). Seeing Sets : Representation by Statistical Properties. *Psychological Science*, *12*(2), 157–162.
- Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, *16*(8), 437–443.
<http://doi.org/10.1016/j.tics.2012.06.010>.Top-down
- Bacigalupo, F., & Luck, S. J. (2015). The allocation of attention and working memory in visual crowding. *Journal of Cognitive Neuroscience*, *27*(6), 1180–1193.
<http://doi.org/10.1162/jocn>
- Baddeley, A. (1986). *Working Memory*. Oxford: Clarendon Press.
- Balleine, B. W., & O'Doherty, J. P. (2010). Human and rodent homologies in action control: Corticostriatal determinants of goal-directed and habitual action. *Neuropsychopharmacology*, *35*(1), 48–69. <http://doi.org/10.1038/npp.2009.131>
- Barkley-Levenson, E., & Galván, A. (2014). Neural representation of expected value in the adolescent brain. *Proceedings of the National Academy of Sciences*, *111*(4), 1646–1651.
<http://doi.org/10.1073/pnas.1319762111>
- Bayer, M., Rossi, V., Vanlessen, N., Grass, A., Schacht, A., & Pourtois, G. (2017). Independent effects of motivation and spatial attention in the human visual cortex. *Social Cognitive*

- and Affective Neuroscience*, 12(1), 146–156. <http://doi.org/10.1093/scan/nsw162>
- Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, 49(10), 1154–1165. <http://doi.org/10.1016/j.visres.2008.07.012>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate : A Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series B*, 57(1), 289–300.
- Bergen, B., Medeiros-Ward, N., Wheeler, K., Drews, F., & Strayer, D. (2013). The crosstalk hypothesis: Why language interferes with driving. *Journal of Experimental Psychology: General*, 142(1), 119–130. <http://doi.org/10.1037/a0028428>
- Berridge, K. C. (2007). The debate over dopamine's role in reward: The case for incentive salience. *Psychopharmacology*, 191(3), 391–431. <http://doi.org/10.1007/s00213-006-0578-x>
- Bichot, N. P., Rossi, A. F., & Desimone, R. (2010). Parallel and Serial Neural Mechanisms for Visual Search in Macaque Area V4. *Science*, 529(2005), 529–535. <http://doi.org/10.1126/science.1109676>
- Bigdely-Shamlo, N., Kreutz-Delgado, K., Kothe, C., & Makeig, S. (2013). EyeCatch: Data-mining over half a million EEG independent components to construct a fully-automated eye-component detector. *Conf Proc IEEE Eng Med Biol Soc*, 2013, 5845–5848.
- Bjork, J. M., Knutson, B., Fong, G. W., Caggiano, D. M., Bennett, S. M., & Hommer, D. W. (2004). Incentive-Elicited Brain Activation in Adolescents: Similarities and Differences from Young Adults. *Journal of Neuroscience*, 24(8), 1793–1802. <http://doi.org/10.1523/JNEUROSCI.4862-03.2004>

- Bjork, J. M., Smith, A. R., Chen, G., & Hommer, D. W. (2010). Adolescents, adults and rewards: comparing motivational neurocircuitry recruitment using fMRI. *PLoS One*, *5*(7), e11440. <http://doi.org/10.1371/journal.pone.0011440>
- Botdorf, M., Rosenbaum, G. M., Patrianakos, J., Steinberg, L., & Chein, J. M. (2017). Adolescent risk-taking is predicted by individual differences in cognitive control over emotional, but not non-emotional, response conflict. *Cognition and Emotion*, *31*(5), 972–979. <http://doi.org/10.1080/02699931.2016.1168285>
- Botvinick, M., & Braver, T. (2015). Motivation and Cognitive Control: From Behavior to Neural Mechanism. *Annual Review of Psychology*, *66*(1), 83–113. <http://doi.org/10.1146/annurev-psych-010814-015044>
- Botvinick, M. M. (2007). Conflict monitoring and decision making: reconciling two perspectives on anterior cingulate function. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(4), 356–366. <http://doi.org/10.3758/CABN.7.4.356>
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review*, *108*(3), 624–652.
- Bourgeois, A., Chelazzi, L., & Vuilleumier, P. (2016). How motivation and reward learning modulate selective attention. *Progress in Brain Research*, *229*, 325–342. <http://doi.org/10.1016/bs.pbr.2016.06.004>
- Bourgeois, A., Neveu, R., Bayle, D. J., & Vuilleumier, P. (2015). How does reward compete with goal-directed and stimulus-driven shifts of attention? *Cognition and Emotion*, *31*(1), 109–118. <http://doi.org/10.1080/02699931.2015.1085366>
- Braams, B. R., van Duijvenvoorde, A. C. K., Peper, J. S., & Crone, E. A. (2015). Longitudinal Changes in Adolescent Risk-Taking: A Comprehensive Study of Neural Responses to

- Rewards, Pubertal Development, and Risk-Taking Behavior. *Journal of Neuroscience*, 35(18), 7226–7238. <http://doi.org/10.1523/JNEUROSCI.4764-14.2015>
- Brady, T. F., & Alvarez, G. A. (2011). Hierarchical encoding in visual working memory: Ensemble statistics bias memory for individual items. *Psychological Science*, 22(3), 384–392. <http://doi.org/10.1177/0956797610397956>
- Braet, C., & Crombez, G. (2003). Cognitive Interference Due to Food Cues in Childhood Obesity. *Journal of Clinical Child & Adolescent Psychology*, 32(1), 32–39. http://doi.org/http://dx.doi.org/10.1207/S15374424JCCP3201_04
- Braver, T. S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, 16(2), 106–13. <http://doi.org/10.1016/j.tics.2011.12.010>
- Braver, T. S., Gray, J., & Burgess, G. C. (2007). Explaining the many varieties of working memory variation: Dual mechanisms of cognitive control. In A. Conway, J. C., K. M., M. A., & T. J. (Eds.), *Variation in working memory* (pp. 76–109). Oxford: Oxford University Press.
- Braver, T. S., Krug, M. K., Chiew, K. S., Kool, W., Westbrook, A. J., Clement, N. J., ... Custers, R. (2014). Mechanisms of motivation-cognition interaction: Challenges and opportunities. *Cognitive, Affective, & Behavioral Neuroscience*, 14(2), 443–472. <http://doi.org/10.3758/s13415-014-0300-0.Mechanisms>
- Braver, T. S., Paxton, J. L., Locke, H. S., & Barch, D. M. (2009). Flexible neural mechanisms of cognitive control within human prefrontal cortex. *Proceedings of the National Academy of Sciences*, 106(18), 7351–6. <http://doi.org/10.1073/pnas.0808187106>
- Brown, J. W., & Braver, T. S. (2005). Learned predictions of error likelihood in the anterior cingulate cortex. *Science*, 307(5712), 1118–1121.

- <http://doi.org/10.1126/science.1105783>
- Bucker, B., Belopolsky, A. V., & Theeuwes, J. (2015). Distractors that signal reward attract the eyes. *Visual Cognition*, *23*(1–2), 1–24. <http://doi.org/10.1080/13506285.2014.980483>
- Bucker, B., Silvis, J. D., Donk, M., & Theeuwes, J. (2015). Reward modulates oculomotor competition between differently valued stimuli. *Vision Research*, *108*, 103–112. <http://doi.org/10.1016/j.visres.2015.01.020>
- Buschman, T. J., & Kastner, S. (2015). From Behavior to Neural Dynamics: An Integrated Theory of Attention. *Neuron*, *88*(1), 127–144. <http://doi.org/10.1016/j.neuron.2015.09.017>
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, *4*(6), 215–222. [http://doi.org/10.1016/S1364-6613\(00\)01483-2](http://doi.org/10.1016/S1364-6613(00)01483-2)
- Bush, G., Vogt, B. A., Holmes, J., Dale, A. M., Greve, D., Jenike, M. A., & Rosen, B. R. (2002). Dorsal anterior cingulate cortex: A role in reward-based decision making. *Proceedings of the National Academy of Sciences*, *99*(1), 523–528. <http://doi.org/10.1073/pnas.012470999>
- Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D. C., & Cohen, J. D. (1998). Anterior Cingulate Cortex, Error Detection, and the Online Monitoring of Performance. *Science*, *280*(5364), 747–749. <http://doi.org/10.1126/science.280.5364.747>
- Carver, C. S., & White, T. L. (1994). Behavior inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology*, *67*, 319–333. <http://doi.org/10.1037/0022-3514.67.2.319>

- Casey, B. J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review*, 28(1), 62–77. <http://doi.org/10.1016/j.dr.2007.08.003>
- Casey, B. J., Jones, R. M., & Hare, T. A. (2008). The adolescent brain. *Annals of the New York Academy of Sciences*, 1124, 111–126. <http://doi.org/10.1002/ar.20849.3D>
- Chambers, R. ., Taylor, J. R., & Potenza, M. N. (2003). Reviews and Overviews Developmental Neurocircuitry of Motivation in Adolescence : A Critical Period of Addiction Vulnerability. *American Journal Of Psychiatry*, 160, 1041–1052.
- Chelazzi, L., E to inova, J., Calletti, R., Lo Gerfo, E., Sani, I., Della Libera, C., & Santandrea, E. (2014). Altering Spatial Priority Maps via Reward-Based Learning. *Journal of Neuroscience*, 34(25), 8594–8604. <http://doi.org/10.1523/JNEUROSCI.0277-14.2014>
- Chelazzi, L., Perlato, A., Santandrea, E., & Della Libera, C. (2013). Rewards teach visual selective attention. *Vision Research*, 85, 58–62.
<http://doi.org/10.1016/j.visres.2012.12.005>
- Chong, S. C., & Treisman, A. M. (2003). Representation of statistical properties. *Vision Research*, 43(4), 393–404. [http://doi.org/10.1016/S0042-6989\(02\)00596-5](http://doi.org/10.1016/S0042-6989(02)00596-5)
- Chong, S. C., & Treisman, A. M. (2005). Statistical processing: Computing the average size in perceptual groups. *Vision Research*, 45(7), 891–900.
<http://doi.org/10.1016/j.visres.2004.10.004>
- Clayson, P. E., & Larson, M. J. (2011). Conflict adaptation and sequential trial effects: Support for the conflict monitoring theory. *Neuropsychologia*, 49(7), 1953–1961.
<http://doi.org/10.1016/j.neuropsychologia.2011.03.023>
- Cocker, P. J., Hosking, J. G., Benoit, J., & Winstanley, C. A. (2012). Sensitivity to cognitive effort mediates psychostimulant effects on a novel rodent cost/benefit decision-making

- task. *Neuropsychopharmacology*, 37(8), 1825–1837.
<http://doi.org/10.1038/npp.2012.30>
- Cohen, M. A., Dennett, D. C., & Kanwisher, N. (2016). What is the Bandwidth of Perceptual Experience? *Trends in Cognitive Sciences*, 20(5), 324–335.
<http://doi.org/10.1016/j.tics.2016.03.006>
- Connor, C. E., Egeth, H. E., & Yantis, S. (2004). Visual attention: Bottom-up versus top-down. *Current Biology*, 14(19), 850–852. <http://doi.org/10.1016/j.cub.2004.09.041>
- Cools, R. (2008). Role of Dopamine in the Motivational and Cognitive Control of Behavior. *The Neuroscientist*, 14(4), 381–395. <http://doi.org/10.1177/1073858408317009>
- Corbett, J. E., & Oriet, C. (2011). The whole is indeed more than the sum of its parts: Perceptual averaging in the absence of individual item representation. *Acta Psychologica*, 138(2), 289–301. <http://doi.org/10.1016/j.actpsy.2011.08.002>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–215.
<http://doi.org/10.1038/nrn755>
- Couperus, J. W., & Quirk, C. (2015). Visual search and the N2pc in children. *Attention, Perception, & Psychophysics*, 77(3), 768–776. <http://doi.org/10.3758/s13414-015-0833-5>
- Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social – affective engagement and goal flexibility. *Nature*, 13(9), 636–650.
<http://doi.org/10.1038/nrn3313>
- Croxson, P. L., Walton, M. E., O'Reilly, J. X., Behrens, T. E. J., & Rushworth, M. F. S. (2009). Effort-based cost-benefit valuation and the human brain. *Journal of Neuroscience*,

- 29(14), 4531–4541. <http://doi.org/10.1523/JNEUROSCI.4515-08.2009>
- Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, 7(9), 415–423.
[http://doi.org/10.1016/S1364-6613\(03\)00197-9](http://doi.org/10.1016/S1364-6613(03)00197-9)
- Dahl, R. E. (2004). Adolescent Brain Development: A Period of Vulnerability and Opportunities. *Annals of the New York Academy of Sciences*, 102(1), 1–22.
<http://doi.org/10.1196/annuals.1308.001>
- Dakin, S. C., & Watt, R. J. (1997). The computation of orientation statistics from visual texture. *Vision Research*, 37(22), 3181–3192. [http://doi.org/10.1016/S0042-6989\(97\)00133-8](http://doi.org/10.1016/S0042-6989(97)00133-8)
- de Fockert, J. W., Rees, G., Frith, C. D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science*, 291, 1803–1806.
<http://doi.org/10.1126/science.1056496>
- de Wit, S., Watson, P., Harsay, H. A., Cohen, M. X., van de Vijver, I., & Ridderinkhof, K. R. (2012). Corticostriatal connectivity underlies individual differences in the balance between habitual and goal-directed action control. *Journal of Neuroscience*, 32(35), 12066–12075. <http://doi.org/10.1523/JNEUROSCI.1088-12.2012>
- DeAngeli, N. E., Miller, S. B., Meyer, H. C., & Bucci, D. J. (2017). Increased sign-tracking behavior in adolescent rats. *Developmental Psychobiology*, 59(7), 840–847.
<http://doi.org/10.1002/dev.21548>
- Dehaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological Science*, 5(5), 303–305.
<http://doi.org/10.1111/j.1467-9280.1994.tb00630.x>

- Della Libera, C., & Chelazzi, L. (2006). Visual selective attention and the effects of monetary rewards. *Psychological Science*, *17*(3), 222–227. <http://doi.org/10.1111/j.1467-9280.2006.01689.x>
- Della Libera, C., & Chelazzi, L. (2009). Learning to attend and to ignore is a matter of gains and losses. *Psychological Science*, *20*(6), 778–784. <http://doi.org/10.1111/j.1467-9280.2009.02360.x>
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21. <http://doi.org/10.1016/j.jneumeth.2003.10.009>
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222. <http://doi.org/10.1146/annurev.ne.18.030195.001205>
- DiFeliceantonio, A. G., & Berridge, K. C. (2012). Which cue to “want”? Opioid stimulation of central amygdala makes goal-trackers show stronger goal-tracking, just as sign-trackers show stronger sign-tracking. *Behavioural Brain Research*, *230*(2), 399–408. <http://doi.org/10.3174/ajnr.A1256>
- Dijksterhuis, A., & Aarts, H. (2010). Goals, Attention, and (Un)Consciousness. *Annual Review of Psychology*, *61*(1), 467–490. <http://doi.org/10.1146/annurev.psych.093008.100445>
- Dreisbach, G., & Fischer, R. (2012). The role of affect and reward in the conflict-triggered adjustment of cognitive control. *Frontiers in Human Neuroscience*, *6*, 1–6. <http://doi.org/10.3389/fnhum.2012.00342>
- Dreisbach, G., & Fischer, R. (2015). Conflicts as aversive signals for control adaptation. *Current Directions in Psychological Science*, *24*(4), 255–260.

<http://doi.org/10.1177/0963721415569569>

- Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General*, 113(4), 501–17. <http://doi.org/10.1037/0096-3445.113.4.501>
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96(3), 433–458.
- Eder, A. B., Rothermund, K., De Houwer, J., & Hommel, B. (2015). Directive and incentive functions of affective action consequences: an ideomotor approach. *Psychological Research*, 79(4), 630–649. <http://doi.org/10.1007/s00426-014-0590-4>
- Egeth, H. E., & Yantis, S. (1997). Visual attention: control, representation, and time course. *Ann. Rev. Psychol.*, 48, 269–297.
- Egner, T., Ely, S., & Grinband, J. (2010). Going, going, gone: Characterizing the time-course of congruency sequence effects. *Frontiers in Psychology*, 1, 1–8.
<http://doi.org/10.3389/fpsyg.2010.00154>
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, 8(12), 1784–1790.
<http://doi.org/10.1038/nn1594>
- Eimer, M., & Kiss, M. (2008). Involuntary attentional capture is determined by task set : Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, 20(8), 1423–1433. <http://doi.org/10.1162/jocn.2008.20099>
- Engle, R. W. (2002). Working memory capacity as executive attention. *Current Directions in Psychological Science*, 11(1), 19–23. <http://doi.org/10.1111/1467-8721.00160>
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a

- target letter in a non-search task. *Perception & Psychophysics*, *16*(1), 143–149.
<http://doi.org/10.3758/BF03203267>
- Eriksen, C. W. (1995). The flankers task and response competition: A useful tool for investigating a variety of cognitive problems. *Visual Cognition*, *2*(2), 101–118.
- Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention: a zoom lens model. *Perception & Psychophysics*, *40*(4), 225–240.
- Ernst, M., Daniele, T., & Frantz, K. (2011). New perspectives on adolescent motivated behavior: Attention and conditioning. *Developmental Cognitive Neuroscience*, *1*(4), 377–389. <http://doi.org/10.1016/j.dcn.2011.07.013>
- Ernst, M., Nelson, E. E., McClure, E. B., Monk, C. S., Munson, S., Eshel, N., ... Pine, D. S. (2004). Choice selection and reward anticipation: an fMRI study. *Neuropsychologia*, *42*(12), 1585–97. <http://doi.org/10.1016/j.neuropsychologia.2004.05.011>
- Ernst, M., Pine, D. S., & Hardin, M. G. (2006). Triadic model of the neurobiology of motivated behavior in adolescence. *Psychological Medicine*, *36*(3), 299–312.
<http://doi.org/10.1017/S0033291705005891>.Triadic
- Failing, M. F., Nissens, T., Pearson, D., Le Pelley, M. E., & Theeuwes, J. (2015). Oculomotor capture by stimuli that signal the availability of reward. *Journal of Neurophysiology*, *114*(4), 2316–2327. <http://doi.org/10.1152/jn.00441.2015>
- Failing, M. F., & Theeuwes, J. (2014). Exogenous visual orienting by reward. *Journal of Vision*, *14*(5), 1–9. <http://doi.org/10.1167/14.5.6>
- Failing, M. F., & Theeuwes, J. (2017). Don't let it distract you: how information about the availability of reward affects attentional selection. *Attention, Perception, & Psychophysics*, *79*(8), 2275–2298. <http://doi.org/10.3758/s13414-017-1376-8>

- Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (2000). Effects of error in choice reaction time tasks on the ERP under focused and divided attention. In A. W. K. Gailard & A. Kok (Eds.), *Psychophysiological Brain Research* (pp. 192–195). Tilburg, The Netherlands: Tilburg University Press.
- Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences*, *10*(8), 382–390.
<http://doi.org/10.1016/j.tics.2006.06.011>
- Field, M., Mogg, K., Zetteler, J., & Bradley, B. P. (2004). Attentional biases for alcohol cues in heavy and light social drinkers: The roles of initial orienting and maintained attention. *Psychopharmacology*, *176*(1), 88–93. <http://doi.org/10.1007/s00213-004-1855-1>
- Flagel, S. B., Watson, S. J., Robinson, T. E., & Akil, H. (2007). Individual differences in the propensity to approach signals vs goals promote different adaptations in the dopamine system of rats. *Psychopharmacology*, *191*(3), 599–607. <http://doi.org/10.1007/s00213-006-0535-8>
- Flowers, J. H., & Wilcox, N. (1982). The effect of flanking context on visual classification: The joint contribution of interactions at different processing levels. *Perception & Psychophysics*, *32*(6), 581–591. <http://doi.org/10.3758/BF03204214>
- Folk, C. L., & Remington, R. W. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(3), 847–858.
<http://doi.org/10.1037/0096-1523.24.3.847>
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human*

- Perception and Performance*, 18(4), 1030–10.
- Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, 45(1), 152–170.
<http://doi.org/10.1111/j.1469-8986.2007.00602.x>
- Franconeri, S. L., & Simons, D. J. (2003). Moving and looming stimuli capture attention. *Perception & Psychophysics*, 65(7), 999–1010. <http://doi.org/10.3758/BF03194829>
- Fröber, K., Stürmer, B., Frömer, R., & Dreisbach, G. (2017). The role of affective evaluation in conflict adaptation: An LRP study. *Brain and Cognition*, 116, 9–16.
<http://doi.org/10.1016/j.bandc.2017.05.003>
- Funes, M. J., Lupiáñez, J., & Humphreys, G. W. (2010a). Analyzing the generality of conflict adaptation effects. *Journal of Experimental Psychology: Human Perception and Performance*, 36(1), 147–161. <http://doi.org/10.1037/a0017598>
- Funes, M. J., Lupiáñez, J., & Humphreys, G. W. (2010b). Sustained vs. transient cognitive control: evidence of a behavioral dissociation. *Cognition*, 114(3), 338–47.
<http://doi.org/10.1016/j.cognition.2009.10.007>
- Galvan, A. (2010). Adolescent development of the reward system. *Frontiers in Human Neuroscience*, 4, 1–9. <http://doi.org/10.3389/neuro.09.006.2010>
- Galván, A., & McGlennan, K. M. (2013). Enhanced striatal sensitivity to aversive reinforcement in adolescents versus adults. *Journal of Cognitive Neuroscience*, 25(2), 284–296.
- Gefen, A., Gefen, N., Zhu, Q., Raghupathi, R., & Marguiles, S.S. (2004). Age-dependent changes in material properties of the brain and braincase of the rat. *Journal of Neurotrauma*, 20, 1163–1177. <https://doi.org/10.1089/089771503770802853>

- Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, *4*(6), 385–390.
- Gehring, W. J., & Willoughby, A. R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, *295*(5563), 2279–2282.
<http://doi.org/10.1126/science.1066893>
- Geier, C. F., Terwilliger, R., Teslovich, T., Velanova, K., & Luna, B. (2010). Immaturities in reward processing and its influence on inhibitory control in adolescence. *Cerebral Cortex*, *20*(7), 1613–1629. <http://doi.org/10.1093/cercor/bhp225>
- Geier, C., & Luna, B. (2009). The maturation of incentive processing and cognitive control. *Pharmacology Biochemistry and Behavior*, *93*(3), 212–221.
<http://doi.org/10.1016/j.pbb.2009.01.021>
- Ghinescu, R., Schachtman, T. R., Ramsey, A. K., Gratton, G., & Fabiani, M. (2016). Conflict adaptation and cue competition during learning in an Eriksen flanker task. *PLoS ONE*, *11*(12), 1–19. <http://doi.org/10.1371/journal.pone.0167119>
- Giedd, J. N. (2004). Structural magnetic resonance imaging of the adolescent brain. *Annals of the New York Academy of Sciences*, *1021*, 77–85.
- Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., ... Rapoport, J. L. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, *2*(10), 861–863.
- Gil-Gómez de Liaño, B., Umiltà, C., Stablum, F., Tebaldi, F., & Cantagallo, A. (2010). Attentional distractor interference may be diminished by concurrent working memory load in normal participants and traumatic brain injury patients. *Brain and Cognition*, *74*(3), 298–305. <http://doi.org/10.1016/j.bandc.2010.08.009>

- Gogtay, N., & Giedd, J. N. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences, 101*(21), 8174–9. <http://doi.org/10.1073/pnas.0402680101>
- Gratton, G., Coles, M. G. H., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General, 121*(4), 480–506.
- Graybiel, A. M. (2008). Habits, Rituals, and the Evaluative Brain. *Annual Review of Neuroscience, 31*(1), 359–387.
<http://doi.org/10.1146/annurev.neuro.29.051605.112851>
- Greenwald, A. G. (1970). Sensory feedback mechanisms in performance control: With special reference to the ideomotor mechanism. *Psychological Review, 77*(2), 73–99.
- Gronau, N., Cohen, A., & Ben-Shakhar, G. (2003). Dissociations of personally significant and task-relevant distractors inside and outside the focus of attention: A combined behavioral and psychophysiological study. *Journal of Experimental Psychology: General, 132*(4), 512–529. <http://doi.org/10.1037/0096-3445.132.4.512>
- Grose-Fifer, J., Rodrigues, A., Hoover, S., & Zottoli, T. (2013). Attentional capture by emotional faces in adolescence. *Advances in Cognitive Psychology, 9*(2), 81–91.
<http://doi.org/10.5709/acp-0134-9>
- Haberman, J., Brady, T. F., & Alvarez, G. A. (2015). Individual differences in ensemble perception reveal multiple, independent levels of ensemble representation. *Journal of Experimental Psychology: General, 144*(2), 432–446.
<http://doi.org/10.1037/xge0000053>
- Hajcak, G., Moser, J. S., Yeung, N., & Simons, R. F. (2005). On the ERN and the significance of

- errors. *Psychophysiology*, 42(2), 151–160. <http://doi.org/10.1111/j.1469-8986.2005.00270.x>
- Hare, T. a, Camerer, C. F., & Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. *Science*, 324, 646–648.
- Hickey, C., Chelazzi, L., & Theeuwes, J. (2010a). Reward changes salience in human vision via the anterior cingulate. *Journal of Neuroscience*, 30(33), 11096–11103. <http://doi.org/10.1523/JNEUROSCI.1026-10.2010>
- Hickey, C., Chelazzi, L., & Theeuwes, J. (2010b). Reward guides vision when it's your thing: Trait reward-seeking in reward-mediated visual priming. *PLoS ONE*, 5(11), 1–5. <http://doi.org/10.1371/journal.pone.0014087>
- Hickey, C., Chelazzi, L., & Theeuwes, J. (2011). Reward has a residual impact on target selection in visual search, but not on the suppression of distractors. *Visual Cognition*, 19(1), 117–128. <http://doi.org/10.1080/13506285.2010.503946>
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21(4), 760–775. <http://doi.org/10.1162/jocn.2009.21039>
- Hickey, C., & Peelen, M. V. (2015). Neural mechanisms of incentive salience in naturalistic human vision. *Neuron*, 85(3), 512–518. <http://doi.org/10.1016/j.neuron.2014.12.049>
- Hickey, C., & Van Zoest, W. (2012). Reward creates oculomotor salience. *Current Biology*, 22(7), R219–R220. <http://doi.org/10.1016/j.cub.2012.02.007>
- Holroyd, C. B., & Yeung, N. (2012). Motivation of extended behaviors by anterior cingulate cortex. *Trends in Cognitive Sciences*, 16(2), 122–128. <http://doi.org/10.1016/j.tics.2011.12.008>

- Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event-coding (TEC): A framework for perception and action planning. *Behavioural and Brain Sciences*, *24*, 849–937. <http://doi.org/10.1017/S0140525X01000103>
- Hosking, J. G., Cocker, P. J., & Winstanley, C. A. (2014). Dissociable contributions of anterior cingulate cortex and basolateral amygdala on a rodent cost/benefit decision-making task of cognitive effort. *Neuropsychopharmacology*, *39*(7), 1558–1567. <http://doi.org/10.1038/npp.2014.27>
- Humphreys, G. W., & Sui, J. (2016). Attentional control and the self: The Self-Attention Network (SAN). *Cognitive Neuroscience*, *7*(1–4), 5–17. <http://doi.org/10.1080/17588928.2015.1044427>
- Hwang, K., Velanova, K., & Luna, B. (2010). Strengthening of top-down frontal cognitive control networks underlying the development of inhibitory control: A functional magnetic resonance imaging effective connectivity study. *Journal of Neuroscience*, *30*(46), 15535–15545. <http://doi.org/10.1523/JNEUROSCI.2825-10.2010>
- Inzlicht, M., Schmeichel, B. J., & Macrae, C. N. (2014). Why self-control seems (but may not be) limited. *Trends in Cognitive Sciences*, *18*(3), 127–133. <http://doi.org/10.1016/j.tics.2013.12.009>
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, *40*(10–12), 1489–1506. [http://doi.org/10.1016/S0042-6989\(99\)00163-7](http://doi.org/10.1016/S0042-6989(99)00163-7)
- Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics*, *43*(4), 346–354. <http://doi.org/10.3758/BF03208805>
- Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during

- intertemporal choice. *Nature Neuroscience*, *10*(12), 1625–1633.
<http://doi.org/10.1038/nn2007>.The
- Kadel, H., Feldmann-Wüstefeld, T., & Schubö, A. (2017). Selection history alters attentional filter settings persistently and beyond top-down control. *Psychophysiology*, *54*(5), 736–754. <http://doi.org/10.1111/psyp.12830>
- Kahneman, D., Treisman, A. M., & Gibbs, B. J. (1992). The reviewing of object files: Object-specific integration of information. *Cognitive Psychology*, *24*(2), 175–219.
[http://doi.org/10.1016/0010-0285\(92\)90007-O](http://doi.org/10.1016/0010-0285(92)90007-O)
- Kann, L., S.A., K., Williams, B. I., Ross, J. G., Lowry, R., Grunbaum, J. A., & Kolbe, L. J. (2013). Youth risk behavior surveillance: United States. *Morbidity and Mortality Weekly Report: Surveillance Summaries*, *63*(4), 1–32.
- Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia*, *39*(12), 1263–1276. [http://doi.org/10.1016/S0028-3932\(01\)00116-6](http://doi.org/10.1016/S0028-3932(01)00116-6)
- Kerns, J. G. (2006). Anterior cingulate and prefrontal cortex activity in an fMRI study of trial-to-trial adjustments on the Simon task. *NeuroImage*, *33*(1), 399–405.
<http://doi.org/10.1016/j.neuroimage.2006.06.012>
- Kerns, J. G., Cohen, J. D., MacDonald III, A. ., Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, *303*(5660), 1023–6. <http://doi.org/10.1126/science.1089910>
- Killikelly, C., & Szűcs, D. (2013). Delayed development of proactive response preparation in adolescents: ERP and EMG evidence. *Developmental Cognitive Neuroscience*, *3*, 33–43.
<http://doi.org/10.1016/j.dcn.2012.08.002>

- Kim, S.-Y., Kim, M.-S., & Chun, M. M. (2005). Concurrent working memory load can reduce distraction. *Proceedings of the National Academy of Sciences*, *102*(45), 16524–16529.
<http://doi.org/10.1073/pnas.0505454102>
- Kiss, M., Driver, J., & Eimer, M. (2009). Reward priority of visual target singletons modulates ERP signatures of attentional selection. *Psychological Science*, *20*(2), 245–251.
<http://doi.org/10.1111/j.1467-9280.2009.02281.x>.Reward
- Kiss, M., Raymond, J. E., Westoby, N., Nobre, A. C., & Eimer, M. (2008). Response inhibition is linked to emotional devaluation: Behavioural and electrophysiological evidence. *Frontiers in Human Neuroscience*, *2*, 1–9. <http://doi.org/10.3389/neuro.09.013.2008>
- Kiyonaga, A., Egnér, T., & Soto, D. (2012). Cognitive control over working memory biases of selection. *Psychonomic Bulletin and Review*, *19*(4), 639–46.
<http://doi.org/10.3758/s13423-012-0253-7>
- Kool, W., McGuire, J. T., Rosen, Z. B., & Botvinick, M. M. (2010). Decision making and the avoidance of cognitive demand. *Journal of Experimental Psychology: General*, *139*(4), 665–682. <http://doi.org/10.1037/a0020198>.Decision
- Kool, W., Shenhav, A., & Botvinick, M. M. (2017). Cognitive Control as Cost-Benefit Decision Making. In T. Egnér (Ed.), *The Wiley Handbook of Cognitive Control* (pp. 167–189). New Jersey: Wiley-Blackwell. <http://doi.org/10.1002/9781118920497.ch10>
- Kramer, A. F., De Sather, J. C. M. G., & Cassavaugh, N. D. (2005). Development of attentional and oculomotor control. *Developmental Psychology*, *41*(5), 760–772.
<http://doi.org/10.1037/0012-1649.41.5.760>
- Kurzban, R., Duckworth, A., Kable, J. W., & Myers, J. (2014). An opportunity cost model of subjective effort and task performance. *Behavioral and Brain Sciences*, *36*(6), 1–45.

<http://doi.org/10.1017/S0140525X12003196>.An

Ladouceur, C. D., Dahl, R. E., & Carter, C. S. (2007). Development of action monitoring through adolescence into adulthood: ERP and source localization. *Developmental Science*, *10*(6), 874–891. <http://doi.org/10.1111/j.1467-7687.2007.00639.x>

Lavie, N. (2005). Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, *9*(2), 75–82. <http://doi.org/10.1016/j.tics.2004.12.004>

Lavie, N., Hirst, A., De Fockert, J. W., & Viding, E. (2004). Load theory of selective attention and cognitive control. *Journal of Experimental Psychology: General*, *133*(3), 339–354. <http://doi.org/10.1037/0096-3445.133.3.339>

Le Pelley, M. E. (2004). The role of associative history in models of associative learning: A selective review and a hybrid model. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology*, *57*(3), 193–243. <http://doi.org/10.1080/02724990344000141>

Le Pelley, M. E., Mitchell, C. J., Beesley, T., George, D. N., & Wills, A. J. (2016). Attention and associative learning in humans : An integrative review. *Psychological Bulletin*, *142*(10), 1111–1140.

Le Pelley, M. E., Pearson, D., Griffiths, O., & Beesley, T. (2015). When goals conflict with values: Counterproductive attentional and oculomotor capture by reward-related stimuli. *Journal of Experimental Psychology: General*, *144*(1), 158–171. <http://doi.org/10.1037/xge0000037>

Leon, M. I., & Shadlen, M. N. (1999). Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron*, *24*(2), 415–425. [http://doi.org/10.1016/S0896-6273\(00\)80854-5](http://doi.org/10.1016/S0896-6273(00)80854-5)

- Levinson, D. B., Stoll, E. L., Kindy, S. D., Merry, H. L., & Davidson, R. J. (2014). A mind you can count on: Validating breath counting as a behavioral measure of mindfulness. *Frontiers in Psychology, 5*, 1–10. <http://doi.org/10.3389/fpsyg.2014.01202>
- Li, Y., Vanni-Mercier, G., Isnard, J., Mauguière, F., & Dreher, J. C. (2016). The neural dynamics of reward value and risk coding in the human orbitofrontal cortex. *Brain, 139*(4), 1295–1309. <http://doi.org/10.1093/brain/awv409>
- Ljungberg, T., Apicella, P., & Schultz, W. (1992). Responses of monkey dopamine neurons during learning of behavioral reactions. *Journal of Neurophysiology, 67*(1), 145–163. <http://doi.org/10.1016/j.tins.2007.03.003>
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience, 8*, 1–14. <http://doi.org/10.3389/fnhum.2014.00213>
- Lowe, D. G., & Mitterer, J. O. (1982). Selective and divided attention in a Stroop task. *Canadian Journal of Psychology, 36*(4), 684–700. <http://doi.org/10.1037/h0080661>
- Lubman, D. I., Peters, L. A., Mogg, K., Bradley, B. P., & Deakin, J. F. W. (2000). Attentional bias for drug cues in heroin dependence. *Psychological Medicine, 30*, 169–175. <http://doi.org/10.3724/SP.J.1042.2013.02174>
- Luciana, M., & Collins, P. F. (2012). Incentive motivation, cognitive control, and the adolescent brain: Is it time for a paradigm shift? *Child Development Perspectives, 6*(4), 392–399. <http://doi.org/10.1111/j.1750-8606.2012.00252.x>
- Luck, S. J. (1995). Multiple mechanisms of visual-spatial attention: recent evidence from human electrophysiology. *Behavioural Brain Research, 71*(1–2), 113–123. [http://doi.org/10.1016/0166-4328\(95\)00041-0](http://doi.org/10.1016/0166-4328(95)00041-0)

- Luck, S. J. (2005). *An Introduction to the Event-Related Potential Technique* (7th ed.). Cambridge: MIT Press.
- Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural Mechanisms of Spatial Selective Attention in Areas V1, V2, and V4 of Macaque Visual Cortex. *Journal of Neurophysiology*, *77*(1), 24–42.
- Luck, S. J., & Hillyard, S. A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291–308. <http://doi.org/10.1111/j.1469-8986.1994.tb02218.x>
- Luck, S. J., & Hillyard, S. A. (1994b). Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(5), 1000–1014. <http://doi.org/10.1037/0096-1523.20.5.1000>
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–284. <http://doi.org/10.1038/36846>
- Luna, B., Garver, K. E., Urban, T. A., Lazar, N. A., & Sweeney, J. A. (2004). Maturation of cognitive processes from late childhood to adulthood. *Child Development*, *75*(5), 1357–1372. <http://doi.org/10.1111/j.1467-8624.2004.00745.x>
- Luna, B., Marek, S., Larsen, B., Tervo-Clemmens, B., & Chahal, R. (2015). An Integrative Model of the Maturation of Cognitive Control. *Annual Review of Neuroscience*, *38*(1), 151–170. <http://doi.org/10.1146/annurev-neuro-071714-034054>
- Luna, B., Padmanabhan, A., & O’Hearn, K. (2010). What has fMRI told us about the Development of Cognitive Control through Adolescence? *Brain and Cognition*, *72*(1), 101–113. <http://doi.org/10.1016/j.bandc.2009.08.005>
- MacDonald III, A. ., Cohen, J. D., Stenger, V. ., & Carter, C. S. (2000). Dissociating the role of

- the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, 288, 1835–1839.
- MacLean, M. H., Diaz, G. K., & Giesbrecht, B. (2016). Irrelevant learned reward associations disrupt voluntary spatial attention. *Attention, Perception, & Psychophysics*, 78(7), 2241–2252. <http://doi.org/10.3758/s13414-016-1103-x>
- Maclean, M. H., & Giesbrecht, B. (2015). Neural evidence reveals the rapid effects of reward history on selective attention. *Brain Research*, 1606, 86–94. <http://doi.org/10.1016/j.brainres.2015.02.016>
- MacLean, M. H., & Giesbrecht, B. (2015). Irrelevant reward and selection histories have different influences on task-relevant attentional selection. *Attention, Perception, & Psychophysics*, 77(5), 1515–1528. <http://doi.org/10.3758/s13414-015-0851-3>
- Marcos, E., Nougaret, S., Tsujimoto, S., & Genovesio, A. (2018). Outcome modulation across tasks in the primate dorsolateral prefrontal cortex. *Neuroscience*, 371, 96–105. <http://doi.org/10.1016/j.neuroscience.2017.11.019>
- Mattler, U. (2003). Delayed flanker effects on lateralized readiness potentials. *Experimental Brain Research*, 151(2), 272–288. <http://doi.org/10.1007/s00221-003-1486-5>
- Maunsell, J. H. R. (2004). Neuronal representations of cognitive state: Reward or attention? *Trends in Cognitive Sciences*, 8(6), 261–265. <http://doi.org/10.1016/j.tics.2004.04.003>
- Mayr, U., Awh, E., & Laurey, P. (2003). Conflict adaptation effects in the absence of executive control. *Nature Neuroscience*, 6(5), 450–2. <http://doi.org/10.1038/nn1051>
- Mazaheri, A., Nieuwenhuis, I. L. C., Van Dijk, H., & Jensen, O. (2009). Prestimulus alpha and mu activity predicts failure to inhibit motor responses. *Human Brain Mapping*, 30(6), 1791–1800. <http://doi.org/10.1002/hbm.20763>

- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annu Rev Neurosci*, *24*, 167–202.
- Minhas, P., Bikson, M., Woods, A. J., & Kessler, S. K. (2012). Transcranial direct current stimulation in pediatric Brain: A computational modeling study. *Conf Proc IEEE Eng Med Biol Soc*, *2012*, 859–62. <http://doi.org/10.1109/EMBC.2012.6346067>
- Morey, C. C., & Cowan, N. (2004). When visual and verbal memories compete: Evidence of cross-domain limits in working memory. *Psychonomic Bulletin and Review*, *11*(2), 296–301. <http://doi.org/10.3758/BF03196573>
- Munneke, J., Belopolsky, A. V., & Theeuwes, J. (2016). Distractors associated with reward break through the focus of attention. *Attention, Perception, & Psychophysics*, *78*(7), 2213–2225. <http://doi.org/10.3758/s13414-016-1075-x>
- Munneke, J., Hoppenbrouwers, S. S., & Theeuwes, J. (2015). Reward can modulate attentional capture, independent of top-down set. *Attention, Perception, & Psychophysics*, *77*(8), 2540–2548. <http://doi.org/10.3758/s13414-015-0958-6>
- Muraven, M., & Baumeister, R. F. (2000). Self-regulation and depletion of limited resources: Does self-control resemble a muscle? *Psychological Bulletin*, *126*(2), 247–259. <http://doi.org/10.1037//0033-2909.126.2.247>
- Noël, X., Colmant, M., Van Der Linden, M., Bechara, A., Bullens, Q., Hanak, C., & Verbanck, P. (2006). Time course of attention for alcohol cues in abstinent alcoholic patients: The role of initial orienting. *Alcoholism: Clinical and Experimental Research*, *30*(11), 1871–1877. <http://doi.org/10.1111/j.1530-0277.2006.00224.x>
- O'Brien, J. L., & Raymond, J. E. (2012). Learned Predictiveness Speeds Visual Processing. *Psychological Science*, *23*(4), 359–363. <http://doi.org/10.1177/0956797611429800>

- Ogawa, T., & Komatsu, H. (2004). Target Selection in Area V4 during a Multidimensional Visual Search Task. *Journal of Neuroscience*, *24*(28), 6371–6382.
<http://doi.org/10.1523/JNEUROSCI.0569-04.2004>
- Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in visual working memory: When it guides attention and when it does not. *Trends in Cognitive Sciences*, *15*(7), 327–334. <http://doi.org/10.1016/j.tics.2011.05.004>
- Padilla, M. L., Pfefferbaum, A., Sullivan, E. V., Baker, F. C., & Colrain, I. M. (2014). Dissociation of preparatory attention and response monitoring maturation during adolescence. *Clinical Neurophysiology*, *125*(5), 962–970. <http://doi.org/10.1016/j.clinph.2013.10.012>
- Padmanabhan, A., Geier, C. F., Ordaz, S. J., Teslovich, T., & Luna, B. (2011). Developmental changes in brain function underlying the influence of reward processing on inhibitory control. *Developmental Cognitive Neuroscience*, *1*(4), 517–529.
<http://doi.org/10.1016/j.dcn.2011.06.004>
- Parkinson, J. A., Willoughby, P. J., Robbins, T. W., & Everitt, B. J. (2000). Disconnection of the anterior cingulate cortex and nucleus accumbens core impairs pavlovian approach behavior: Further evidence for limbic cortical-ventral striatopallidal systems. *Behavioral Neuroscience*, *114*(1), 42–63. <http://doi.org/10.1037//0735-7044.114.1.42>
- Pastötter, B., Dreisbach, G., & Bauml, K.-H. T. (2013). Dynamic adjustments in cognitive control: Oscillatory correlates of the conflict adaptation effect. *Journal of Cognitive Psychology*, *25*(12), 2167–2178. <http://doi.org/10.1162/jocn>
- Patton, J. H., Stanford, M. S., & Barratt, E. S. (1995). Factor structure of the barratt impulsiveness scale. *Journal of Clinical Psychology*, *51*(6), 769–774.
- Pearson, D., Donkin, C., Tran, S. C., Most, S. B., & Le Pelley, M. E. (2015). Cognitive control

- and counterproductive oculomotor capture by reward-related stimuli. *Visual Cognition*, 23(1), 1–26. <http://doi.org/10.1080/13506285.2014.994252>
- Pedale, T., & Santangelo, V. (2015). Perceptual salience affects the contents of working memory during free-recollection of objects from natural scenes. *Frontiers in Human Neuroscience*, 9, 1–8. <http://doi.org/10.3389/fnhum.2015.00060>
- Peirce, J. W. (2007). PsychoPy-Psychophysics software in Python. *Journal of Neuroscience Methods*, 162(1–2), 8–13. <http://doi.org/10.1016/j.jneumeth.2006.11.017>
- Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, 2, 1–8. <http://doi.org/10.3389/neuro.11.010.2008>
- Pfeifer, J. H., & Allen, N. B. (2012). Arrested development? Reconsidering dual-systems models of brain function in adolescence and disorders. *Trends in Cognitive Sciences*, 16(6), 322–329. <http://doi.org/10.1016/j.tics.2012.04.011>
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, 32(1), 3–25. <http://doi.org/10.1080/00335558008248231>
- Proulx, M. J., & Egeth, H. E. (2008). Biased competition and visual search: The role of luminance and size contrast. *Psychological Research*, 72(1), 106–113. <http://doi.org/10.1007/s00426-006-0077-z>
- Ptak, R. (2012). The frontoparietal attention network of the human brain: Action, saliency, and a priority map of the environment. *Neuroscientist*, 18(5), 502–515. <http://doi.org/10.1177/1073858411409051>
- Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: evidence of parallel tracking mechanisms. *Spatial Vision*, 3(3), 179–197.
- Qi, S., Zeng, Q., Ding, C., & Li, H. (2013). Neural correlates of reward-driven attentional

- capture in visual search. *Brain Research*, 1532, 32–43.
<http://doi.org/10.1016/j.brainres.2013.07.044>
- Raichle, M. E., Fiez, J. A., Videen, T. O., Macleod, A. K., Pardo, J. V., Fox, P. T., & Petersen, S. E. (1994). Practice-related changes in human brain functional anatomy during nonmotor learning. *Cerebral Cortex*, 4, 8–26.
- Raymond, J. E., & O'Brien, J. L. (2009). Selective visual attention and motivation: The consequences of value learning in an attentional blink task. *Psychological Science*, 20(8), 981–988. <http://doi.org/10.1111/j.1467-9280.2009.02391.x>
- Reimers, S., & Maylor, E. A. (2005). Task switching across the life span: Effects of age on general and specific switch costs. *Developmental Psychology*, 41(4), 661–671.
<http://doi.org/10.1037/0012-1649.41.4.661>
- Reynolds, J. H., & Desimone, R. (2003). Interacting roles of attention and visual salience in V4. *Neuron*, 37(5), 853–863. [http://doi.org/10.1016/S0896-6273\(03\)00097-7](http://doi.org/10.1016/S0896-6273(03)00097-7)
- Richter, C. G., Thompson, W. H., Bosman, C. A., & Fries, P. (2017). Top-down beta enhances bottom-up gamma. *The Journal of Neuroscience*, 37(28), 6698–6711.
<http://doi.org/10.1523/JNEUROSCI.3771-16.2017>
- Robinson, T. E., & Berridge, K. C. (1993). The neural basis of drug craving: An incentive-sensitization theory of addiction. *Brain Research Reviews*, 18(3), 247–291.
[http://doi.org/10.1016/0165-0173\(93\)90013-P](http://doi.org/10.1016/0165-0173(93)90013-P)
- Robitaille, N., & Harris, I. M. (2011). When more is less: Extraction of summary statistics benefits from larger sets. *Journal of Vision*, 11(12), 1–8.
<http://doi.org/10.1167/11.12.18.Introduction>
- Romer, D., Reyna, V. F., & Satterthwaite, T. D. (2017). Beyond stereotypes of adolescent risk

- taking: Placing the adolescent brain in developmental context. *Developmental Cognitive Neuroscience*, 27, 19–34. <http://doi.org/10.1016/j.dcn.2017.07.007>
- Roper, Z. J. J., Vecera, S. P., & Vaidya, J. G. (2014). Value-driven attentional capture in adolescence. *Psychological Science*, 25(11), 1987–1993. <http://doi.org/10.1177/0956797614545654>
- Rothermund, K., Wentura, D., & Bak, P. M. (2001). Automatic attention to stimuli signalling chances and dangers: Moderating effects of positive and negative goal and action contexts. *Cognition and Emotion*, 15(2), 231–248. <http://doi.org/10.1080/02699930126213>
- Rushworth, M. F. S., & Behrens, T. E. J. (2008). Choice, uncertainty and value in prefrontal and cingulate cortex. *Nature Neuroscience*, 11(4), 389–397. <http://doi.org/10.1038/nn2066>
- Rushworth, M. F. S., Walton, M. E., Kennerley, S. W., & Bannerman, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, 8(9), 410–417. <http://doi.org/10.1016/j.tics.2004.07.009>
- Rutherford, H. J. V., O'Brien, J. L., & Raymond, J. E. (2010). Value associations of irrelevant stimuli modify rapid visual orienting. *Psychonomic Bulletin and Review*, 17(4), 536–542. <http://doi.org/10.3758/PBR.17.4.536>
- Saez, R. A., Saez, A., Paton, J. J., Lau, B., & Salzman, C. D. (2017). Distinct roles for the amygdala and orbitofrontal cortex in representing the relative amount of expected reward. *Neuron*, 95(1), 70–77.e3. <http://doi.org/10.1016/j.neuron.2017.06.012>
- Sali, A. W., Anderson, B. A., & Yantis, S. (2014). The role of reward prediction in the control of attention. *Journal of Experimental Psychology: Human Perception and Performance*,

- 40(4), 1654–1664. <http://doi.org/10.1037/a0037267>
- Sawaki, R., Geng, J. J., & Luck, S. J. (2012). A common neural mechanism for preventing and terminating the allocation of attention. *Journal of Neuroscience*, *32*(31), 10725–10736. <http://doi.org/10.1523/JNEUROSCI.1864-12.2012.A>
- Sawaki, R., & Luck, S. J. (2010). Capture versus suppression of attention by salient singletons: Electrophysiological evidence for an automatic attend-to-me signal. *Attention, Perception, & Psychophysics*, *72*(6), 1455–1470. <http://doi.org/10.3758/APP.72.6.1455>
- Sawaki, R., & Luck, S. J. (2014). How the Brain Prevent and Terminates Shifts of Attention. In G. R. Mangun (Ed.), *Cognitive Electrophysiology of Attention: Signals of the Mind*. (pp. 16–29). San Diego: Elsevier.
- Sawaki, R., Luck, S. J., & Raymond, J. E. (2015). How attention changes in response to incentives. *Journal of Cognitive Neuroscience*, *27*(11), 2229–2239. <http://doi.org/10.1162/jocn>
- Schmidt, L. J., Belopolsky, A. V., & Theeuwes, J. (2015). Attentional capture by signals of threat. *Cognition and Emotion*, *29*(4), 687–694. <http://doi.org/10.1080/02699931.2014.924484>
- Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. Detection, search, and attention. *Psychological Review*, *84*(1), 1–66. <http://doi.org/10.1037/0033-295X.84.1.1>
- Schultz, W. (2000). Multiple reward signals in the brain. *Nature Reviews Neuroscience*, *1*(3), 199–207. <http://doi.org/10.1038/35044563>
- Schultz, W., Dayan, P., & Montague, P. R. (1997). Neural Substrate of Prediction and. *Science*, *275*(5306), 1593–1599. <http://doi.org/10.1126/science.275.5306.1593>

- Schweimer, J., & Hauber, W. (2006). Dopamine D1 receptors in the anterior cingulate cortex regulate effort-based decision making. *Learning & Memory*, 777–782.
<http://doi.org/10.1101/lm.409306>
- Seer, C., Lange, F., Loens, S., Wegner, F., Schrader, C., Dressler, D., ... Kopp, B. (2017). Dopaminergic modulation of performance monitoring in Parkinson's disease: An event-related potential study. *Scientific Reports*, 7(June 2016), 1–13.
<http://doi.org/10.1038/srep41222>
- Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in Cognitive Sciences*, 10(1), 38–45. <http://doi.org/10.1016/j.tics.2005.11.008>
- Sha, L. Z., & Jiang, Y. V. (2016). Components of reward-driven attentional capture. *Attention, Perception, & Psychophysics*, 78(2), 403–414. <http://doi.org/10.3758/s13414-015-1038-7>
- Shadmehr, R., Huang, H. J., & Ahmed, A. A. (2016). A Representation of Effort in Decision-Making and Motor Control. *Current Biology*, 26(14), 1929–1934.
<http://doi.org/10.1016/j.cub.2016.05.065>
- Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The expected value of control: An integrative theory of anterior cingulate cortex function. *Neuron*, 79(2), 217–240.
<http://doi.org/10.1016/j.neuron.2013.07.007>
- Shenhav, A., Musslick, S., Lieder, F., Kool, W., Griffiths, T. L., Cohen, J. D., & Botvinick, M. M. (2017). Toward a rational and mechanistic account of mental effort. *Annual Review of Neuroscience*, 40(1), 99–124. <http://doi.org/10.1146/annurev-neuro-072116-031526>
- Shenhav, A., Straccia, M. A., Cohen, J. D., & Botvinick, M. M. (2014). Anterior cingulate engagement in a foraging context reflects choice difficulty, not foraging value. *Nature*

- Neuroscience*, 17(9), 1249–1254. <http://doi.org/10.1016/j.coviro.2015.09.001>. Human Sheth, S. A., Mian, M. K., Patel, S. R., Asaad, W. F., Williams, Z. V., Dougherty, D. D., ... Eskandar, E. N. (2013). Human dorsal anterior cingulate cortex neurons mediate ongoing behavioral adaptation. *Nature*, 488(7410), 218–221. <http://doi.org/10.1038/nature11239>
- Shimi, A., Nobre, A. C., & Scerif, G. (2015). ERP markers of target selection discriminate children with high vs. low working memory capacity. *Frontiers in Systems Neuroscience*, 9, 153. <http://doi.org/10.3389/fnsys.2015.00153>
- Solomon, M., Yoon, J. H., Ragland, J. D., Niendam, T. A., Lesh, T. A., Fairbrother, W., & Carter, C. S. (2014). The development of the neural substrates of cognitive control in adolescents with autism spectrum disorders. *Biological Psychiatry*, 76(5), 412–421. <http://doi.org/10.1016/j.biopsych.2013.08.036>
- Somerville, L. H., Jones, R. M., & Casey, B. J. (2010). A time of change: Behavioral and neural correlates of adolescent sensitivity to appetitive and aversive environmental cues. *Brain and Cognition*, 72(1), 124–133. <http://doi.org/10.1016/j.bandc.2009.07.003>
- Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Reviews*, 24(4), 417–463. [http://doi.org/10.1016/S0149-7634\(00\)00014-2](http://doi.org/10.1016/S0149-7634(00)00014-2)
- Steinberg, L. (2010). A dual systems model of adolescent risk-taking. *Developmental Psychobiology*, 52(3), 216–224. <http://doi.org/10.1002/dev.20445>
- Steinberg, L., Albert, D., Cauffman, E., Banich, M., Graham, S., & Woolard, J. (2008). Age Differences in Sensation Seeking and Impulsivity as Indexed by Behavior and Self-Report: Evidence for a Dual Systems Model. *Developmental Psychology*, 44(6), 1764–

1778. <http://doi.org/10.1037/a0012955>
- Stormark, K. M., Field, N. P., Hugdahl, K., & Horowitz, M. (1997). Selective processing of visual alcohol cues in abstinent alcoholics: An approach-avoidance conflict? *Addictive Behaviors, 22*(4), 509–519. [http://doi.org/10.1016/S0306-4603\(96\)00051-2](http://doi.org/10.1016/S0306-4603(96)00051-2)
- Stürmer, B., Soetens, E., Leuthold, H., Schröter, H., & Sommer, W. (2002). Control over location-based response activation in the Simon task: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception and Performance, 28*(6), 1345–1363. <http://doi.org/10.1037//0096-1523.28.6.1345>
- Sui, J., He, X., & Humphreys, G. W. (2012). Perceptual effects of social salience: Evidence from self-prioritization effects on perceptual matching. *Journal of Experimental Psychology: Human Perception and Performance, 38*(5), 1105–1117. <http://doi.org/10.1037/a0029792>
- Susanne, C., Guidotti, A., & Hauspie, R. (1985). Age changes of skull dimensions. *Anthropologischer Anzeiger, 43*, 31-36.
- Sweeny, T. D., Haroz, S., & Whitney, D. (2012). Reference repulsion in the categorical perception of biological motion. *Vision Research, 64*, 26–34. <http://doi.org/10.1016/j.visres.2012.05.008>
- Telzer, E. H. (2016). Dopaminergic reward sensitivity can promote adolescent health: A new perspective on the mechanism of ventral striatum activation. *Developmental Cognitive Neuroscience, 17*, 57–67. <http://doi.org/10.1016/j.dcn.2015.10.010>
- Theeuwes, J. (1991). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Perception & Psychophysics, 49*(1), 83–90. <http://doi.org/10.3758/BF03211619>

- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & Psychophysics*, *51*(6), 599–606.
- Theeuwes, J., & Belopolsky, A. V. (2012). Reward grabs the eye: Oculomotor capture by rewarding stimuli. *Vision Research*, *74*, 80–85.
<http://doi.org/10.1016/j.visres.2012.07.024>
- Thomas, P. M. J., FitzGibbon, L., & Raymond, J. E. (2016). Value conditioning modulates visual working memory processes. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(1), 6–10. <http://doi.org/10.1037/xhp0000144>
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *Psychological Monographs: General and Applied*, *2*(4), 1–109.
- Tipper, S. P. (1985). The negative priming effect : Inhibitory priming by ignored objects The Negative Priming Effect : Inhibitory Priming by Ignored Objects. *The Quarterly Journal of Experimental Psychology*, *37*(A), 571–590. <http://doi.org/10.1080/14640748508400920>
- Tong, F., & Nakayama, K. (1999). Robust representations for faces: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(4), 1016–1035. <http://doi.org/10.1037//0096-1523.25.4.1016>
- Trapp, S., Shenhav, A., Bitzer, S., & Bar, M. (2015). Human preferences are biased towards associative information. *Cognition and Emotion*, *29*(6), 1054–1068.
<http://doi.org/10.1080/02699931.2014.966064>
- Treisman, A. M. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology: Human Perception and Performance*, *8*(2), 194–214. <http://doi.org/10.1037/0096-1523.8.2.194>
- Treisman, A. M. (2006). How the deployment of attention determines what we see. *Visual*

- Cognition*, 14(4), 411–443. <http://doi.org/10.1080/10810730902873927>. Testing
- Treisman, A. M., & Gelade, G. (1980). A feature-integration of attention. *Cognitive Psychology*, 12(1), 97–136. [http://doi.org/10.1016/0010-0285\(80\)90005-5](http://doi.org/10.1016/0010-0285(80)90005-5)
- Tremblay, L., & Schultz, W. (1999). Relative reward preference in primate orbitofrontal cortex. *Nature*, 398, 704–708.
- Ullsperger, M., Bylsma, L. M., & Botvinick, M. M. (2005). The conflict-adaptation effect : it ' s not just priming. *Cognitive, Affective, & Behavioral Neuroscience*, 5(4), 467–472. <http://doi.org/10.3758/CABN.5.4.467>
- Ullsperger, M., Harsay, H. A., Wessel, J. R., & Ridderinkhof, K. R. (2010). Conscious perception of errors and its relation to the anterior insula. *Brain Structure and Function*, 214(5–6), 629–643. <http://doi.org/10.1007/s00429-010-0261-1>
- Van Dijk, H., Schoffelen, J.-M., Oostenveld, R., & Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *Journal of Neuroscience*, 28(8), 1816–1823. <http://doi.org/10.1523/JNEUROSCI.1853-07.2008>
- Van Leijenhorst, L., Zanolie, K., Van Meel, C. S., Westenberg, P. M., Rombouts, S. a R. B., & Crone, E. A. (2010). What motivates the adolescent? Brain regions mediating reward sensitivity across adolescence. *Cerebral Cortex*, 20(1), 61–9. <http://doi.org/10.1093/cercor/bhp078>
- van Steenbergen, H., Band, G. P. H., & Hommel, B. (2009). Reward counteracts conflict adaptations: Evidence for a role of affect in executive control. *Psychological Science*, 20(12), 1473–1477.
- van Veen, V., & Carter, C. S. (2002). The anterior cingulate as a conflict monitor : fMRI and ERP studies, 77, 477–482.

- Velanova, K., Wheeler, M. E., & Luna, B. (2009). The Maturation of Task Set-Related Activation Supports Late Developmental Improvements in Inhibitory Control. *Journal of Neuroscience*, *29*(40), 12558–12567. <http://doi.org/10.1523/JNEUROSCI.1579-09.2009>
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2005). Pushing around the Locus of Selection: Evidence for the Flexible-selection Hypothesis. *Journal of Cognitive Neuroscience*, *17*(12), 1907–1922. <http://doi.org/10.1162/089892905775008599>
- Volkow, N. D., Wang, G.-J., Fowler, J. S., Tomasi, D., & Telang, F. (2011). Addiction: Beyond dopamine reward circuitry. *Proceedings of the National Academy of Sciences*, *108*(37), 15037–15042. <http://doi.org/10.1073/pnas.1010654108>
- Wahlstrom, D., Collins, P. F., White, T., & Luciana, M. (2010). Developmental changes in dopamine neurotransmission in adolescence: Behavioral implications and issues in assessment. *Brain and Cognition*, *72*(1), 146–159. <http://doi.org/10.1016/j.bandc.2009.10.013>
- Wallis, J. D., & Kennerley, S. W. (2011). Contrasting reward signals in the orbitofrontal cortex and anterior cingulate cortex. *Annals of the New York Academy of Sciences*, *1239*(1), 33–42. <http://doi.org/10.1111/j.1749-6632.2011.06277.x>
- Walton, M. E., Devlin, J. T., & Rushworth, M. F. S. (2004). Interactions between decision making and performance monitoring within prefrontal cortex. *Nature Neuroscience*, *7*(11), 1259–1265. <http://doi.org/10.1038/nn1339>
- Wang, E., Sun, M., Tao, Y., Gao, X., Guo, J., Zhao, C., ... Song, Y. (2017). Attentional selection predicts rapid automatized naming ability in Chinese-speaking children with ADHD. *Scientific Reports*, *7*(1), 1–9. <http://doi.org/10.1038/s41598-017-01075-x>
- Wang, L., Yu, H., & Zhou, X. (2013). Interaction between value and perceptual salience in

- value-driven attentional capture. *Journal of Vision*, *13*(3), 1–13.
<http://doi.org/10.1167/13.3.5>
- Wei, P., & Zhou, X. (2006). Processing multidimensional objects under different perceptual loads: The priority of bottom-up perceptual saliency. *Brain Research*, *1114*(1), 113–124.
<http://doi.org/10.1016/j.brainres.2006.07.071>
- Westbrook, A. J., & Braver, T. S. (2015). Cognitive effort: A neuroeconomic approach. *Cognitive, Affective, & Behavioral Neuroscience*, *15*(2), 395–415.
<http://doi.org/10.3758/s13415-015-0334-y>
- Westbrook, A. J., Kester, D., & Braver, T. S. (2013). What is the subjective cost of cognitive effort? Load, trait, and aging effects revealed by economic preference. *PLoS ONE*, *8*(7), 1–8. <http://doi.org/10.1371/journal.pone.0068210>
- Whiting, B. F., & Oriet, C. (2011). Rapid averaging? Not so fast! *Psychonomic Bulletin and Review*, *18*(3), 484–489. <http://doi.org/10.3758/s13423-011-0071-3>
- Wilson, R. C., Takahashi, Y. K., Schoenbaum, G., & Niv, Y. (2014). Orbitofrontal cortex as a cognitive map of task space. *Neuron*, *81*(2), 267–278.
<http://doi.org/10.1016/j.neuron.2013.11.005>
- Wolfe, J. M. (1994). Guided Search 2.0 A revised model of visual search. *Psychonomic Bulletin & Review*, *1*(2), 202–238. <http://doi.org/10.3758/BF03200774>
- Wood, W., & Neal, D. T. (2007). A new look at habits and the habit-goal interface. *Psychological Review*, *114*(4), 843–863. <http://doi.org/10.1037/0033-295X.114.4.843>
- Wood, W., & Rünger, D. (2016). Psychology of habit. *Annual Review of Psychology*, *67*(1), 289–314. <http://doi.org/10.1146/annurev-psych-122414-033417>
- Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: evidence from

- visual search. *Journal of Experimental Psychology: Human Perception and Performance*, 10(5), 601–621. <http://doi.org/10.1037/0096-1523.10.5.601>
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, 16(1), 121–134. <http://doi.org/10.1037/0096-1523.16.1.121>
- Yeung, N., Botvinick, M. M., & Cohen, J. D. (2004). The neural basis of error detection: Conflict monitoring and the error-related negativity. *Psychological Review*, 111(4), 931–959. <http://doi.org/10.1037/0033-295X.111.4.931>
- Yiend, J. (2010). The effects of emotion on attention: A review of attentional processing of emotional information. In J. De Houwer & D. Hermans (Eds.), *Cognition & Emotion: Reviews of Current Research and Theories* (Vol. 1, pp. 211–275). Hove, East Sussex: Psychology Press. <http://doi.org/10.1017/CBO9781107415324.004>
- Yuan, K., Yu, D., Bi, Y., Wang, R., Li, M., Zhang, Y., ... Tian, J. (2017). The left dorsolateral prefrontal cortex and caudate pathway: New evidence for cue-induced craving of smokers. *Human Brain Mapping*, 38(9), 4644–4656. <http://doi.org/10.1002/hbm.23690>