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MOTIVATION AND VISUAL SELECTIVE ATTENTION

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Abstract

This thesis investigates how the motivational value of a visual stimulus influences selective attention. In a series of 11 experiments, I first imbued neutral faces with value by presenting them in a conventional value learning task involving monetary gains and losses. I then employed several temporal and spatial attention paradigms: attentional blink, backward masking, and visual search. I measured recognition and categorization decisions with and without constraints on attention for value-laden and neutral stimuli. I also measured recognition of value-laden and neutral stimuli while simultaneously recording electroencephalography. Evidence obtained across these experiments supported the hypothesis that visual stimuli are processed in a value-specific manner, where value is determined by both valence and motivational salience. Regardless of available attention, recognition was substantially enhanced for motivationally salient stimuli (highly predictive of outcomes) regardless of valence (gain or loss) compared to equally familiar stimuli with weak or no motivational salience. However, when attention was constrained, valence determined recognition; only information about stimuli associated with gains was accessible for high-level processing. Motivational salience acts independently of attention to modulate simple perceptual decisions but when attention is limited, visual processing is biased in favor of reward-associated stimuli.

SECTION 1

AN INTRODUCTION TO OBJECT PROCESSING, ATTENTION, AND VALUE LEARNING

CHAPTER 1

AN INTRODUCTION TO VISUAL OBJECT PROCESSING AND REPRESENTATION

Out of the vast sea of visual content that we are exposed to when we open our eyes, we select information to process depending on its relevance to our current goals. Given our limited processing resources, we must prioritize visual processing and filter out any irrelevant information. Focused goal-directed behavior depends on the interaction of bottom-up perceptual processing and the top-down control of attention. Attention is allocated to stimuli in accordance with current priorities and depends on available resources in working memory (WM).

There is abundant evidence that some higher order factors, such as emotional valence and stimulus familiarity, can affect perceptual processing and the allocation of attention. For example, familiar stimuli such as famous faces have been shown to require less attention for processing, are more efficiently encoded, and are more effectively maintained in WM compared to unfamiliar stimuli (Jackson & Raymond, 2006; 2008). However, studies investigating familiarity or emotional valence as an aid to stimulus processing typically do not control for the *value* each stimulus has for the participant, a feature that can vary enormously across participants for the same stimulus. A famous face (e.g., Margaret Thatcher) may evoke very positive associations and memories for one person and very negative associations and memories for another person.

Learning to associate the probability and value of behavioral outcomes with specific stimuli (value learning) is essential for decision-making. When interacting with an object produces a reward (gain), punishment (loss or pain), or has no outcome, learning allows the brain to acquire and store specific neural codes for predicting which outcome is most likely, should the same object be encountered again. Linked to the stimuli, these codes, known as value prediction codes, provide a common ‘currency’ for the brain that allows comparison of diverse options with diverse outcomes.

The effects of stimulus value prediction codes are commonly overlooked in studies investigating simple perceptual decisions as well as in studies examining the effectiveness of attentional processes used to select a stimulus for higher level processing – both of which are fundamental aspects of coherent perceptual experience of our visual world. There is an abundance of research on how we acquire value prediction codes for visual stimuli through associative learning, but there is a surprising lack of research on the role value learning plays in the subsequent processing of these stimuli. Thus, the objective of this thesis was to investigate the integral role of value learning in visual perceptual decisions. To do this, I first engaged participants in a conventional value-learning task (Pessglione, Seymour, Flandin, Dolan, & Frith, 2006) so that they could acquire different predicted value codes for different stimuli. I then had participants complete one of several temporal and spatial object recognition tasks in which I manipulated the selective attention and WM resources available to process these learned stimuli.

This thesis is presented in four parts. *Part I* (Chapters 1-3) provides a general review of the object (Chapter 1) and face (Chapter 2) recognition literature as well as a review of attentional capacity limits (Chapter 2) and value learning mechanisms (Chapter 3). It also introduces the value-learning paradigm used throughout the thesis along with data from the first value learning experiment. *Part II* (Chapters 4-6) focuses on the effects of value learning on subsequent target recognition in temporal discrimination and attention tasks including the attentional blink (Chapter 4, Experiments 2-3), backward masking (Chapter 5, Experiments 4-5), and a straightforward target recognition task with concurrent electroencephalography (EEG) recording (Chapter 6, Experiment 6). *Part III* (Chapters 7-8) presents a series of visual search experiments to address the effect of value learning on spatial attention. Chapter 7 (Experiments 7-8) presents two experiments of visual search among neutral distractors for emotionally valenced targets that are also value-laden. Chapter 8 presents three experiments of visual search for emotionally valenced (Experiments 9-10) or inverted (Experiment 11) targets among a set of distractors including an irrelevant value-laden stimulus. Finally, *Part IV* (Chapter 9) provides a general discussion of the findings from all temporal attention and visual search experiments.

In this first chapter, I provide a general review of the neurobiology of object representations, followed by a review of how low-level processing interacts with attention, awareness, and WM.

Neurobiology of Object Representations

Once the visual representation of an object is projected onto the retina, information about this representation travels through the midbrain to the lateral geniculate nucleus (LGN) on its way to the visual cortex. Almost all of projections pass from the retina to the LGN; a small percentage goes through the SC and pulvinar on their way to cortical areas such as the middle temporal cortex (MT), the parietal cortex, and the frontal eye fields (FEF) (Cowey & Stoerig, 1991; Tong, 2003; for a review, see Enns, 2004). From the LGN, signals are sent forward to the primary visual area (V1) and then to V2, after which they activate numerous extrastriate areas encompassing the dorsal (e.g., V3, MT, parietal cortex) and ventral (e.g., V4, inferiortemporal, IT, cortex) pathways. Neurons in V1 and V2 have small receptive fields and code simple patterns with high precision, whereas neurons in higher levels of the visual hierarchy have increasingly larger receptive fields and analyze increasingly complex information (Bullier, 2001; for a review, see Palmer, 1999).

This feedforward projection of visual information from low- to high-level areas is extremely rapid, reaching V1 by about 60 - 80 ms and all cortical visual areas by about 100 ms after visual onset (Lamme & Roelfsema, 2000; Thorpe, Fize, & Marlot, 1996). The timing of information flow through this hierarchy, however, does not directly map onto the anatomical hierarchy in a serial manner. Instead, there are multiple streams of information processing that feed forward in parallel. For example, the magno- and parvocellular pathways originating from their respective retinal ganglion cells send information to the LGN and on to V1 in parallel but at different speeds. Magno ganglion neurons are larger with higher temporal resolution and convey signals more quickly than parvo neurons, which have smaller receptive fields and higher spatial resolution (Felleman & Van Essen, 1991). Thus, activity travelling through the magnocellular pathway from LGN reaches V1 around 20 ms earlier than activity from the parvocellular pathway. This then gives the magno-dominated dorsal stream a head start over the parvo-dominated ventral stream (Foxe and Simpson 2002; Lamme & Roelfsema, 2000; Nowak, Munk, Girard, & Bullier, 1995). This has implications for top-down processing and is discussed further in the *location of feedback* section.

Early theories

Early theories of visual perception are focused on the hierarchy of processing through the visual cortex and the feedforward sweep of information that sequentially passes through these areas (e.g., Hubel & Wiesel, 1977; Marr, 1982). This view of visual perception assumes purely serial, bottom-up processing with lower level computations completed before transferring to higher levels (Van Essen & Maunsell, 1983). Neurons in V1 and V2 perform low-level local computations on a scene, and as neuronal properties become increasingly sophisticated in higher order areas, they perform more global computations. Top down information does not influence processing until later at a high level in the hierarchy.

This is a very unrealistic proposal, however, because interpretations of global representations need to return to the local level in order to be integrated with local details to clear up ambiguities resulting from low image contrast, visual noise, lighting artifacts, distractors, occlusion, and other features that complicate segmentation of objects in a scene – i.e., realistic viewing conditions. This sort of hierarchal visual system would only work if an object was unambiguous and would fail to identify objects that we readily and effortlessly recognize in cluttered, everyday scenes (Bullier, 2001).

Interactive models

Most current research on object perception recognizes the role of top-down processing in the visual cortex. Top-down information influences perception via downward connections through the visual hierarchy. These connections have been referred to by numerous names including backward, backprojection, bidirectional, corticocortical, feedback, recurrent, reentrant, and retroinjection. For the sake of clarity, I will refer to these connections as being *feedback* in nature, as information at a higher level can be fed back down to a location from which it originated or fed back to another location earlier in the hierarchy.

Connections between visual cortical areas tend to reciprocally feed information in both forward and backward directions to other areas as well as horizontally within an area (Felleman & Van Essen, 1991; Maunsell & Van Essen, 1983; Rockland and Pandya, 1979; Salin & Bullier, 1995). While low-level, sensory driven visual information about an object or scene is being sent forward during the feedforward sweep, top-down information about the object or the scene is being sent via feedback to bias this. Visual perception can occur without top-down facilitation (e.g., processing objects that "pop out"); however, it is top-down facilitation via feedback connections that probably accounts for the highly efficient visual processing that we rely on to help us interact with our visual world.

Feedback information from top-down processing – also known as hypothesis-driven or expectation-driven processing (Palmer, 1999) – can originate from both prior experience with and current attention directed at an object or part of a scene. Prior experience with an object, stored in long-term memory (LTM), modulates the activation of neurons such that they then sensitize low-level perceptual processing to representations of familiar objects over that of unfamiliar objects (Kveraga, Ghuman, & Bar, 2007; Spratling & Johnson, 2004a). In Spratling and Johnson's (2004a; 2006) neural network model of feedback (based on the biased competition model, Desimone & Duncan, 1995; Reynolds & Desimone, 1999), top-down information serves to bias the competition among visual stimuli for representation by cortical activity. Synaptic weights of neurons are learned from prior experience, which then affects subsequent perceptual processing of related information.

The role of feedback in guiding feedforward recognition processes and in helping to interpret sensory information is not only driven by existing high-level knowledge but also by current attention (spatial and featural) to an object. Attention can be grabbed by stimuli made salient by prior experience (as described above), and it can also be driven by current task demands and goals. Attention selectively enhances the processing of some visual information over others by activating a top-down signal specific to the attended information, thus biasing competition so that the resulting feedforward activation is stronger for the attended item than for other competing items (Desimone & Duncan, 1995; Lamme, 2004; Spratling & Johnson, 2004a). Activity for the attended item is then more similar to that produced by the stimulus in isolation, increasing in amplitude and duration while irrelevant information is filtered out (Moran and Desimone, 1985). This increased attention has effects similar to increasing the saliency of the stimulus (Itti & Koch, 2001; Kastner & Ungerleider, 2000; Reynolds, Pasternak, & Desimone, 2000).

There are numerous accounts of how top-down processing affects bottom-up processing and the resulting percept. All accounts converge on the idea that top-down information helps to more efficiently and rapidly solve the puzzle of what is being viewed. Information from low-level activity is sent forward to higher levels, which then generate a prediction as to what is being viewed and sends that back to lower levels to aid in subsequent processing. Di Lollo and colleagues (Di Lollo et al., 2000) refer to this as "hypothesis verification," where ascending and descending cortical information join to determine the most plausible perceptual interpretation of a visual stimulus. Feedback information from higher areas, which process visual stimuli at a more global level, is used to prune the number of candidate representations by providing predictions based on previous knowledge and experience with similar sensory data or visual contexts (Bar, 2003; Kveraga, Ghuman, & Bar, 2007; Spratling & Johnson, 2004a; Tong, 2003). For example, seeing a long, narrow cylindrical shape with a wide, cone-like shape on top next to your desk might activate representations for both a lamp and an open umbrella. However, top-down knowledge of items in an office context and of the normal characteristics of umbrellas (e.g., do not stand up, open, on their own) might lead higher cortical areas to predict that you are viewing a lamp. (The neuroanatomy of this process will be discussed in more detail in the following sections.)

In situations where the perceptual task is more difficult, or when the initial prediction is incomplete or incorrect, an error signal is sent forward to higher areas, which then create a new prediction. This is a recursive loop that continues until the prediction is compatible with the bottom-up data and is deemed correct (Friston, 2005; Grossberg, 1980). As Grossberg (1980, p. 3) described, "sensory data activate a feedback process whereby a learned template, or expectancy, deforms the sensory data until a consensus is reached between what the data 'are' and what we 'expect' them to be. Only then do we 'perceive' anything." Kersten and colleagues (Kersten, Mamassian, & Yuille, 2004) suggested two theoretical possibilities for the role of higher-level areas in this recursive prediction loop: high-level areas tell lower levels to either "shut up" or "stop gossiping." Predictions created by higher levels may act to suppress additional sensory information from earlier areas – "shut up." Alternatively, after predicting the most plausible interpretation, higher areas may reduce the activity from earlier areas that is inconsistent with this high-level interpretation – "stop gossiping." Either way, top-down influences via feedback projections help to disambiguate bottom-up sensory data and reduce the number of candidate objects that need to be considered by predicting their identity (Bar, 2003; Di Lollo et al., 2000; Friston, 2005; Kveraga, Ghuman, & Bar, 2007; Spratling & Johnson, 2004a).

Time course and location of feedback

Now that the basic role of feedback has been established, the main point of interest is when and where it influences bottom-up, feedforward processing. A feedforward sweep of information occurs within approximately 100 ms; any visual processing that takes longer than this must involve feedback connections (Fahrenfort, Scholte, & Lamme, 2008; Lamme, 2006). Feedback can occur very soon after the initiation of the feedforward sweep – as soon as information has passed through one level to another (Lamme, 2004). For feedback information to have a chance to influence ongoing feedforward processing, higher-level areas need to be rapidly activated after the onset of a visual stimulus. Also, the transfer of information to earlier areas via feedback connections needs to be sufficiently rapid so that the delay is no more than a few milliseconds (Bullier, 2001). This is exactly the case. Reviews by Bullier (Bullier, 2001; Nowak & Bullier, 1997) have shown that some cortical areas are activated within milliseconds of V1 and V2, including areas of the "fast brain" dorsal stream (e.g., MT & FEF). The transferral of information from V1 to MT for example takes roughly the same amount of time as from V1 to V2: 1 – 2 ms (Girard, Hupé, & Bullier, 2001). Computations done in these dorsal areas after visual stimulation can feasibly influence neurons in V1 and V2 during the feedforward sweep.

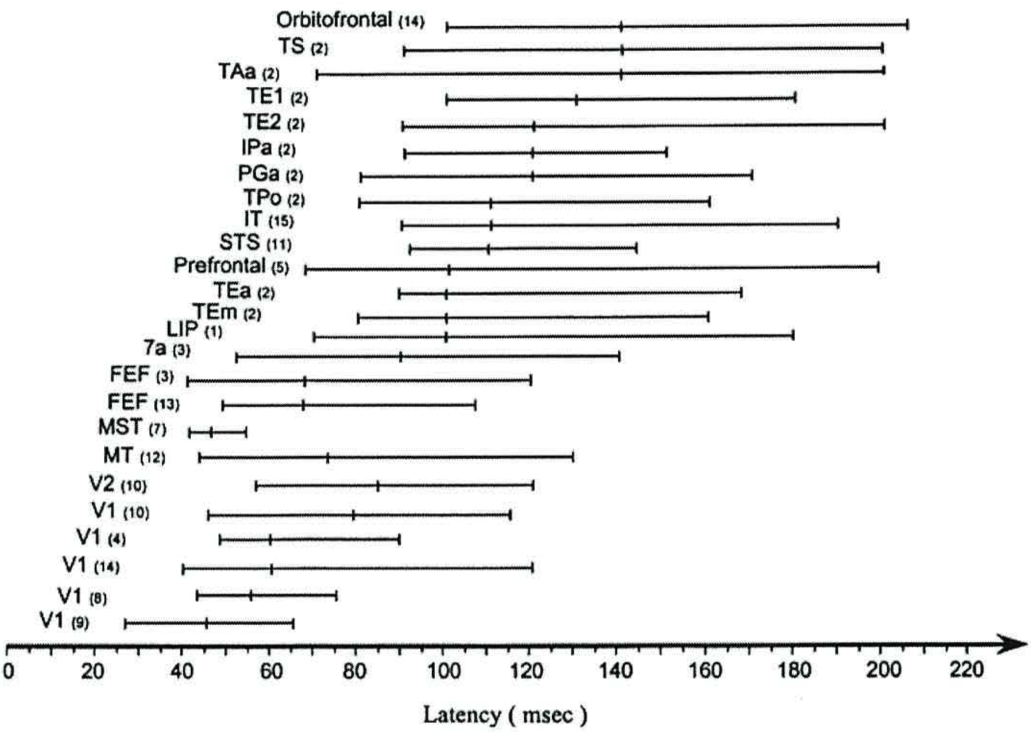

Figure 1. Latencies of visual responses of neurons in different cortical areas of the visual cortex. For each area, the central tick marks the median latency and the extreme ticks the 10 and 90% centiles. Numbers in parentheses refer to bibliographic references given in Bullier (2003). (Adapted from Bullier, 2001)

As described earlier, the magnocellular-dominated dorsal stream has a 20 ms head start over the parvo-dominated ventral stream during visual processing due to the faster conduction speed of magno ganglion neurons (e.g., Nowak et al., 1995). Using event-related potential (ERP) recordings, Foxe and Simpson (2002) investigated the temporal relationship of dorsal and ventral stream activation. They found that activation of dorsal areas preceded that of ventral stream areas by at least 10 ms, and that dorsolateral frontal cortex activation occurred within 30 ms after V1 activation (≈ 80 ms after stimulus onset). This dorsal speed advantage may then allow frontal areas to provide feedback quickly enough to then influence ventral stream areas. They conclude that there is ample time for multiple interactions among cortical areas and that frontal activation is early enough to modulate sensory processing (Foxe and Simpson 2002). Indeed, it appears that the magnocellular pathway carries the first wave of visual activity into the cortex, rapidly activating the dorsal stream. This can then influence earlier visual areas via rapid feedback connections in time for the arrival of the parvocellular wave of neural activity (Bullier, 2001).

Bar and colleagues (Bar, 2003; Bar et al., 2006; Fenske, Aminoff, Gronau, & Bar, 2006; Kveraga, Boshyan, & Bar, 2007; Kveraga, Ghuman, & Bar, 2007) have proposed a model of top-down facilitation which specifies the path of magnocellular input and subsequent feedback projections. According to their model, the magnocellular pathway rapidly sends low spatial frequency (LSF) information from early visual areas to the orbitofrontal cortex (OFC). OFC activation thus represents the cortical source of top-down bias in visual object recognition (Bar et al., 2006). The OFC generates "initial guesses" based on the global, LSF information, which are then projected to the object recognition regions in IT to provide constraints as to possible interpretations of the sensory data. The magnocellular pathway is known to convey low-resolution, high contrast, achromatic information rapidly (Bullier & Nowak, 1995; Bullier, 2001) making it well suited to carry this information to the OFC.

Why the OFC? To begin with, Bar and colleagues (Bar et al., 2001) briefly (26 ms) showed participants familiar objects, each several times throughout the experiment, which were preceded and followed by masks. These objects were quite difficult to recognize the first time, but were more easily recognized after top-down information was accumulated that could then be used process them. Functional magnetic resonance imaging (fMRI) results of cortical activity during correct object recognition showed expected activity in occipitotemporal regions (e.g., fusiform gyrus). They also found increased OFC activation during successful object recognition as compared to unsuccessful attempts, and concluded that the OFC is involved in top-down processes that facilitated successful recognition.

Bar and colleagues (Bar et al., 2006) then tested whether OFC activation occurs before activation in occipitotemporal object recognition regions so that it could then have influence on subsequent recognition. Using the same behavioral task as the previously described experiment (Bar et al., 2001) and recording activity with magnetoencephalography (MEG), they demonstrated that differential OFC activation to recognized objects occurred 50 ms earlier than activation in the object recognition regions of the occipitotemporal cortex (≈ 130 ms after stimulus onset). In a second experiment, they presented images of objects containing either LSF or high spatial frequency (HSF) information, which were all recognized at the same level (equal RTs), to compare OFC activation. Using fMRI, they found that LSF objects elicited a significantly larger signal in the OFC than the HSF images, in the same region where they found earlier activation in the previous experiment. LSF images and regular images (containing both LSF and HSF information) showed highly similar OFC activity, suggesting that the early OFC activation is driven by LSF in images (Bar et al., 2006).

These findings have since been replicated (Kveraga, Boshyan, & Bar 2007) using magnocellular-biased (low-luminance contrast and achromatic) and parvocellular-biased (red-green and isoluminant) object images. They found faster recognition of magnocellular stimuli (105 ms), which correlated with a larger fMRI signal in the OFC than that produced by the parvocellular stimuli. The OFC activation site was again close to the sites activated in previous experiments (Bar et al., 2001; Bar et al., 2006). In contrast, parvocellular stimuli differentially activated the ventral occipitotemporal object recognition regions (e.g., middle and posterior fusiform gyrus). Response accuracy for both types of stimuli was similar, showing that recognition was possible without magnocellular-driven top-down guidance from the OFC but at the cost of greater effort from bottom-up object recognition regions and slower recognition time. These results support the idea that OFC activity from low-resolution information plays a critical role in top-down recognition facilitation by improving recognition efficiency (Bar, 2003; Bar et al., 2006). This only occurs when the stimuli are able to engage in magnocellular processing, which is the fast trigger of relevant top-down processing (Kveraga, Boshyan, & Bar 2007).

While the OFC is not typically associated with object recognition, many of its neurons receive visual input and many of its functions make it a prime candidate for being involved in top-down visual recognition. Of the prefrontal regions, the OFC has the strongest and most extensive connections with the object recognition regions of IT (Cavada, Company, Tejedor, Cruz-Rizzolo, & Reinoso-Suarez, 2000). It has been shown to contribute to the analysis of visual information, including encoding, maintenance (e.g., Ongur & Price, 2000; Szatkowska, Grabowska, & Szymanska, 2001) and aesthetic value judgments (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). Interestingly, the OFC plays an important role in guessing, hypothesis testing, and the generation of expectations (e.g., Bechara, Tranel, Damasio, & Damasio, 1996; Elliot, Dolan, & Frith, 2000; Frith & Dolan, 1997), and is involved in biasing task-relevant processes against strong competing alternatives (Miller & Cohen, 2001).

The OFC is also well known for its role in processing reward value information (e.g., O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Tremblay & Schultz, 1999). Many neurons in the OFC represent the learning and updating of associations made between visual stimuli and their reinforcement outcomes, including abstract rewards and punishments such as monetary gain/loss

(O'Doherty et al., 2001; Rolls, 1999). The critical role of the OFC in value judgments will be discussed further in Chapter 3.

Besides its role in processing visual stimuli, the OFC receives input from many other areas. It has strong connections with limbic areas associated with emotional and social processing including the amygdala (e.g., Amaral & Price, 1984; Barbas & De Olmos, 1990) and with medial temporal limbic structures critical for LTM including the hippocampus (e.g., Goldman-Rakic, Selemon, & Schwartz, 1984; Ramus, Davis, Donahue, Discenza, & Waite, 2007). All of these functions point to a crucial role for the OFC in integrating high-level information with activity from sensory and limbic areas to generate predictions about stimuli (Beer, Shimamura, & Knight, 2004; Kveraga, Boshyan, & Bar, 2007; Kveraga, Ghuman, & Bar, 2007).

To summarize, successful processing of a visual stimulus depends on both feedforward and feedback pathways. Sensory information is initially processed in a feedforward manner, activating neurons in lower then higher levels of the visual hierarchy. While this feedforward sweep is occurring, information is also rapidly sent to higher areas in the visual cortex to be matched with top-down information and then sent back down to influence continuing bottom-up processing. Top-down information is used to predict the identity of a visual stimulus based on learned representations. One candidate source of top-down influence is the OFC, which is known to process visual information and plays a critical role in generating expectations about and representing the value of stimuli. In the next section, I will discuss the role of V1 in receiving top-down information and in awareness of visual stimuli.

Importance of V1 in feedback processing

Most interactive models of object perception and representation posit V1's role to include more than merely the initial stages of visual processing. There are extensive feedback connections from higher levels down to V1 (Salin & Bullier, 1995; Hupé et al., 1998) and V1 is known to represent many forms of perceptual information, including stimulus orientation and position (Pollen, 1999), contrast and perceived brightness (Rossi & Paradiso, 1999), and pattern perception (Rees, Nadell, & Heeger, 2001). V1 is believed to be involved in many stages of visual analysis, receiving signals from higher-level computations and integrating them with lower level spatial and featural information (e.g., Bullier, 2001; Juan & Walsh, 2003; Lee, Mumford, Romero, & Lamme, 1998; Tong, 2003). This framework is reminiscent of Treisman and Gelade's (1980) "master map of locations," which posits a representation of the spatial location of an object's features. Attention (top-down) communicates with this map to select features and then integrates them into a current object representation. V1 has been referred to as a "master map" (Tong, 2003), a "look-up table" (Juan & Walsh, 2003), a "high-resolution buffer" (Deco & Lee, 2004; Lee et al., 1998), and an "active blackboard" (Bullier, 2001), all of which point to its role in information integration.

Lee and colleagues (Deco & Lee, 2004; Lee et al., 1998) propose that during visual processing V1 maintains high-resolution information from a stimulus and integrates it with the global spatial and object information it receives from dorsal and ventral extrastriate cortices. They tested this idea using both single-cell recordings (Lee et al., 1998) and neural modeling (Deco & Lee, 2004). Recordings of neurons in V1 of rhesus monkeys showed that when receptive fields were inside a texture-defined figure, cells in V1 first responded to local features (texture boundaries) 60 – 80 ms after onset. After 80 ms (80 – 200 ms), V1 neurons then responded to contextual information relating to higher-level computation of figure-ground segmentation, reflecting feedback from extrastriate cortices (Lee et al., 1998). Deco and Lee (2004) reproduced this with their neural model of recurrent interaction. They concluded that V1 must be involved in the integration of fine featural and spatial detail with global feedback information by acting as the integration location. V1 neurons express different aspects of visual processing at different times, with earlier responses reflecting physical, receptive field based properties, and later responses reflecting the perceptual organization of a visual stimulus (Lamme, Supèr, Landman, Roelfsema, & Spekreijse, 2000; Stoerig, 2001).

Other researchers have echoed this idea. For instance, Bullier's (2001) idea of V1 as an "active blackboard" sees V1 integrating its large and detailed representations of visual stimuli with the computations done in higher order areas. Tong (2003) describes V1's role as a system for binding perceptual information across separate extrastriate areas or pathways (i.e., dorsal and ventral) into a coherent percept. The reverse hierarchy theory of visual perception (Ahissar & Hochstein, 2000; Juan & Walsh, 2003) states that higher extrastriate areas first compute a preliminary analysis of visual attributes which is then sent back to V1 to integrate with a more detailed report of features and spatial localization. Lee and colleagues (Lee et al., 1998) postulate that this use of feedback by V1 is all for the sake of efficient processing: some details are overlooked in the initial rapid feedforward pass of information and processing must return to the high-resolution data from a stimulus to confirm its identity. This converges with Bar's (2003; Bar et al., 2006) model of top-down facilitation where coarse, LSF information is sent through first to initiate a top-down guess from internal representations, which is then sent back to lower levels for confirmation.

Additional support for this hypothesis comes from the interruption of conscious stimulus perception using experimental interventions, such as transcranial magnetic stimulation (TMS) and visual masks. TMS applied to a location briefly disrupts its activity; therefore, by applying TMS to V1 at different times during and after stimulus onset, researchers can determine when V1 activity is necessary for stimulus perception. Corthout and colleagues (Courthout, Uttl, Walsh, Hallett, & Cowey, 1999) asked participants to identify quickly presented letters while they applied TMS at one of several time periods during the task. A pulse applied 20 – 60 ms after onset reliably disrupted letter perception, as well as when it was applied 110 – 140 ms after onset. The authors concluded that there are two necessary processing periods in V1: one corresponding with feedforward processing, and the other with feedback.

Backward masking is an elegant behavioral way to impair feedback processing and subsequent perception. Targets that are highly visible when briefly presented alone become invisible when a non-target object is presented soon after in the same (or nearby) location. This is due to a disruption of feedback signals to V1 during processing of the target (Di Lollo et al., 2000; Fahrenfort, Scholte, & Lamme, 2007; Lamme, Zipser, & Spekreijse, 2002). By the time higher-level activation of target processing has been fed back to V1, V1 has been updated with spatial and featural information about the mask. Subsequent processing involves mask information only, rendering the target invisible to a conscious percept. The longer the stimulus onset asynchrony (SOA) between the target and the mask, the more time there is for feedback processes to occur and the better perception is, resulting in a J-shaped function of performance (with the lowest performance at a mask onset SOA of zero) (Enns & Di Lollo, 2000). Impressively, this effect has even been found with a mask of only four dots surrounding (but not touching) the image, using a technique called object-substitution masking (Di Lollo et al., 2000).

Adding to these findings is a study that examined the effects of TMS applied to both V1 and V5 on the elicitation of motion phosphenes. TMS applied to the visual cortex can induce flashes of light called phosphenes, and when applied to V5/MT induces movement of them. Pascual-Leone and Walsh (2001) applied TMS to V1 and V5 to examine the temporal relation between processing events in the two areas by measuring the resulting perception of the induced phosphenes. More specifically, they sent pulses to V5 to create a motion phosphene and sent a V1 pulse (which was below the threshold for producing a phosphene) some time before or after the motion phosphene-eliciting pulse. TMS applied to V1 before V5 did not affect perceived motion of the phosphene. However, motion perception (awareness) was eliminated when TMS was applied to V1 5 – 45 ms after V5 stimulation. Rapid feedback projections from V5 to V1 appear to be necessary for perception and awareness of motion. Bullier (2001) interprets these findings as evidence of V1 organizing motion information fed back from V5 and sending it to other areas that lead to the conscious percept of motion. These findings have also been replicated with blindsight patient GY (Cowey & Walsh, 2000). TMS to V5 in the hemisphere with a V1 lesion does not induce moving phosphenes; TMS applied to V5 in the intact V1 hemisphere does. These results demonstrate the necessary role of V1 in feedback processing and visual awareness, a possibility that will be discussed further in the next section.

Before I continue my discussion of the role of V1 in awareness of perception, however, it is prudent to mention an exciting recent discovery about V1's role in reward expectancy. Shuler and Bear (2006) demonstrated that expectation of a reward modulates the perceptual response of V1 neurons in rats. Rats wore goggles that delivered flashes of light to either the left or right eye when the rats approached a water tube for a reward. Action potentials in response to the light flashes were recorded via implanted microelectrodes in V1. After a flash was presented, the rats could lick the tube a certain number of times for a reward, depending on which eye received the flash of light. Flashes to the left eye meant that water could be obtained in half the number of licks (short waiting time for reward) as for flashes to the right eye (long waiting time for reward). Half of the trials were unrewarded to control for whether neural response changes resulted from the reward itself or from the expectation of a reward. The response of V1 neurons in naïve rats related only to the physical properties of the light flashes. However, after learning the reward contingencies, a significant proportion of V1 neurons responded to the expected reward delays such that neuronal responses generated by flashes to the left eye predicted a short reward delay and right-eye responses predicted a long reward delay. This timing activity was evoked exactly the same on both rewarded and unrewarded trials, suggesting that post-stimulus V1 activity was directly related to reward delay-time prediction. Moreover, eye-specific flashes continued to evoke reward-timing activity in V1 neurons when the rats were no longer performing the task. van Ooyen and Roelfsema (2006) speculate that V1 learns the timing of reward payoff via feedback connections (e.g., OFC). Reward signals sent back to V1 could be used to improve visual perception by increasing neuronal sensitivity to distinguishing stimuli features (i.e., ones that indicate potential reward) and aid in subsequent confirmation of top-down guesses during processing.

V1 and awareness

Visual awareness, or what we are conscious of in our immediate sight, is the end result of visual perception. However, not all cortical activity results in conscious perception, nor does it have to in order to guide behavior. For example, stimuli that are not consciously perceived can unconsciously prime subsequent behavior. Blindsight patients – those with damage to V1 – can make visual discriminations in their "blind" visual field, yet they typically report no conscious visual experience of it (Sahraie, Weiskrantz, Barbur, Simmons, Williams, & Brammer, 1997; Weiskrantz, 1986; see Cowey, 2004 for a review).

The lack of conscious visual perception occurring from a lesioned V1 suggests that V1 may be necessary for producing a conscious percept. Many scientists posit, though, that while V1 is necessary for conscious visual perception, it alone is not sufficient (e.g., Crick & Koch, 1995; He, Cavanagh, & Intrilligator, 1996; Logothetis & Schall, 1989). That is to say, activity in V1 may not give rise directly to visual awareness but is instead reliant on further processing in extrastriate areas. However, this can be said about any other cortical area as well: no single cortical visual area (V1, extrastriate areas, or any other in dorsal or ventral stream) alone appears to be sufficient to produce awareness (Lamme et al., 2000; Tong, 2003).

Recent investigations into binocular rivalry have provided experimental evidence that V1 is directly involved in visual awareness. When different images are simultaneously presented to the two eyes, they compete for perceptual dominance such that perception alternates between the images, with one image visible for a few seconds while the other is suppressed. Since perceptual experiences change over time but the retinal stimuli remain constant, the neural mechanisms underlying binocular rivalry have been used to infer the neural basis of visual awareness (e.g., Crick & Koch, 1995). fMRI recordings during binocular rivalry show correlations between subjects' perceptual experiences and neural activity in V1, with significant increases in eye-specific V1 activity when the corresponding monocular stimulus becomes dominant and decreases when it is suppressed (Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005; Tong & Engel, 2001; Wunderlich, Schneider, & Kaster, 2005). These results indicate that rivalry is fully resolved between monocular neurons in V1 and, thus, activity in V1 is indeed correlated with visual awareness.

There are at least two possible explanations for the role of V1 in visual awareness. It is possible that V1 activity contributes to awareness directly, with aspects of conscious vision emerging at this earliest stage of cortical processing (see Silvanto, 2008 for an argument against this). More probable is V1's role as a "gatekeeper" of visual awareness (e.g., Pascual-Leone & Walsh, 2001; Silvanto, Cowey, Lavie, & Walsh, 2005; Tong, 2003; Tong & Engel, 2001), filtering what information reaches higher-level extrastriate areas and, thus, gains access to awareness. Extrastriate activity feeds back to V1 in order to be consciously perceived (see previous section), and disruption to V1 disrupts awareness indirectly.

This hypothesis puts feedback connections between V1 and higher areas in the crucial role for conscious visual perception. If a key function of visual awareness is to produce the best current interpretation of the visual scene, in the light of past experience either of ourselves or of our genetic past (Crick & Koch, 1995), it makes sense that V1, being the hub and gateway of feedback, is crucial to visual awareness. Indeed, there is a growing amount of experimental evidence supporting this idea (e.g., Boehler, Schoenfeld, Heinze, & Hopf, 2008; Lamme et al., 2002; Pascual-Leone & Walsh, 2001; Rees, Backus, & Heeger, 2000; Silvanto et al., 2005). Lamme and colleagues (Lamme & Roelfsema, 2000; Lamme, 2000) suggest that the initial feedforward sweep of information processing is unconscious, and it is feedback interaction between high- and low-level areas that gives rise to conscious visual perception (see also Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006).

Awareness and attention

If the visual representation of a stimulus has been projected onto the retina, has travelled through to V1, has then been fed forward through to extrastriate areas and then fed backward and horizontally, the stimulus is ready to be consciously perceived. However, due to the limited processing capacity within the visual system, not all stimuli, even extremely salient ones, reach visual awareness (Broadbent, 1958; Mack & Rock, 1998; Rensink, 2002; Schneider & Shiffrin, 1977; Simons & Levin, 1997). Multiple stimulus representations compete for access to this limited capacity system, and in most cases, a selection process is necessary to choose which stimuli gain access to awareness for conscious report. This selection process is called attention.

As described earlier, attention modulates the processing of stimuli such that neural activity in response to an attended stimulus is enhanced and activity of competing stimuli is filtered out, thus biasing information processing in favor of stimuli appearing at an attended location or containing an attended stimulus attribute (Desimone & Duncan, 1995; Moran and Desimone, 1985; see Kastner & Ungerleider, 2000 for review). In plain terms, when we attend to something, we are aware of it. This idea has led some researchers to equate attention and awareness (e.g., Posner 1994; Merikle & Joordens 1997; O'Regan & Nöe, 2001).

However, attention does not always lead to awareness and awareness might exist without attention, suggesting that they are two dissociable and distinct neural mechanisms. Attention can be focused on a stimulus event that is not consciously perceived, as with masked stimuli (Enns & Di Lollo, 2000), stimuli made invisible by continuous flash suppression (Kanai, Tsuchiya, & Verstraten, 2006), and invisible monocular stimuli (Bahrami, Lavie, & Rees, 2007). Likewise, in instances of masked priming in healthy observers (Naccache, Blandin, & Dehaene, 2002; McCormick, 1997) and neglect patients (Danziger, Kingstone, & Rafal, 1998), attention can be captured by unconscious primes or cues that subsequently generate a response or influence behavior. Blindsight patients are also capable of localizing stimuli in their blind field when forced to do so, as well as guess above chance all kinds of attributes of the unseen stimuli (Weiskrantz, 1997; Stoerig & Cowey, 1997).

Experimental support for the possibility that awareness can exist without attention is found in change blindness (CB) experiments that cue the relevant to-be-changed item before onset of the change (Becker, Pashler, & Anstis, 2000; Landman, Spekerijse, & Lamme, 2003). CB occurs when observers fail to see an item within a scene change position, color, identity, or even disappear (Rensink, 2000, 2002; Simons, 2000b; Simons & Levin, 1997). CB experiments typically separate the two versions of a scene with a brief blank interval between the two. Cuing the relevant item in the first display that might change in the second display protects it from CB, by directing attention to that item. Interestingly, cuing the relevant item long after the first display disappeared but before onset of the second display also protects it from CB (Becker, Pashler, & Anstis, 2000; Landman, Spekreijse, & Lamme, 2003). Lamme (2003, 2004) interprets this as evidence of awareness in the form of a neural representation of the scene after it disappeared, which can be accessed via attention before it is replaced by a new scene. He refers to this as consciousness without attention, or "phenomenal awareness" (Block, 1996).

In his model of visual consciousness and its relation to attention (see Figure 2), Lamme (2004) posits that visual inputs can reach consciousness or not (unconscious) via feedforward and feedback processing (see previous section). Attention does not determine whether representations of stimuli reach a conscious state, but instead operates at an independent stage. Attention is needed for a conscious *report* of stimuli that have reached a conscious state (called "access awareness"). Representations of stimuli that have reached the level of consciousness but are not attended to are fleeting and are quickly erased and forgotten. Attention can be focused on unconscious stimuli, as described above.

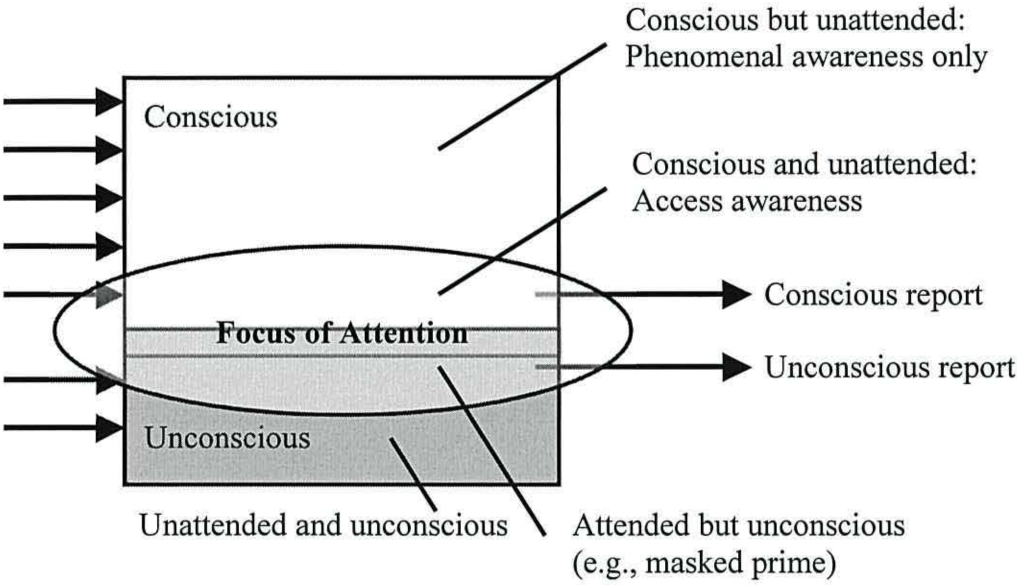

Figure 2. Lamme's (2004) model of visual consciousness and its relation to attention. The dichotomy of conscious/unconscious is orthogonal to the attended/non-attended dichotomy. Visual input can reach four different states: 1) conscious and attended, resulting in a conscious report, 2) conscious and unattended, 3) unconscious and attended, resulting in an unconscious report, 4) unconscious and unattended.

This model is closely paralleled by a proposal of Dehaene and colleagues (Dehaene et al., 2006), who posit that there is a transient "preconscious" state (or "potentially conscious") between unconscious and aware. Information is in this state when it potentially carries enough activation for conscious access, but top-down attention is not devoted to it. This information can quickly gain access to conscious report when attended, but is easily replaced with new information if not attended.

Preconscious processing corresponds to Lamme's state of phenomenal awareness, in that information in this state can gain access to conscious report when attended to, but is otherwise fleeting. However, Lamme's and Dehaene's ideas differ as to whether this information is conscious in any form. Dehaene et al. (2006) state that consciousness at this stage without the ability to report is not currently a scientifically addressable question. Lamme (2003, 2004; see above for description) cites cuing in CB experiments as evidence for its existence.

Awareness, attention, and working memory

For a visual stimulus to be processed consciously, information about it has to be sustained in an active representation to be available for use. It is commonly accepted that we maintain and update visual representations in WM – a limited capacity memory system that temporarily stores information for use in current cognitive tasks. The prevailing model of WM (Baddeley & Hitch, 1974; Baddeley, 2000) breaks it down into four major components: the *phonological loop*, the *visuospatial sketchpad* (labeled *slave systems* to the central executive), the *episodic buffer*, and the *central executive* (CE). The phonological loop stores acoustic or verbal information, maintaining it via rehearsal. The visuospatial sketchpad stores visual and spatial information. The episodic buffer, also controlled by the CE, integrates information from a variety of sources (including the slave systems and LTM) into a space- and time-locked, highly accessible, temporary representation. Independent of task modality, the CE is the attentional control system overseeing the slave systems and in charge of updating information, shifting attention toward relevant information and inhibiting irrelevant information, and dividing attention between tasks to facilitate simultaneous encoding and storage.

The CE accesses the episodic buffer and retrieves its content through conscious awareness (Baddeley, 2000). It also influences the content by attending to a given source of information over others. According to Baddeley, a crucial feature of the CE is that "it allows the organism to operate in a reflective mode, using past experience to understand the present and model the future before selecting an action" (Baddeley, 1992a, p. 5). In other words, the selection of specific items for conscious, controlled processing is a central role of the WM system. WM uses attention as its selection mechanism to enhance relevant information processing, inhibit irrelevant processing, and maintain representations for additional processing.

Experimental evidence for the direct role of WM in controlling selective attention comes from a seminal study by de Fockert and colleagues (de Fockert, Rees, Frith, & Lavie, 2001) in which they manipulated WM load to show its effects on reducing distractor processing. Participants performed a selective attention task where they classified famous written names as pop stars or politicians while ignoring distractor faces that appeared underneath the names. Distractor faces could be congruent or incongruent with the target name. Concurrently, participants maintained a digit order in WM that was either fixed (e.g., 12345; low load) or a different order (e.g., 03124; high load), which was reported at the end of each trial. A high WM load significantly enhanced distractor interference (measured in RTs) compared to a low load, indicating more distractor processing. fMRI recordings of the fusiform gyrus and extrastriate visual cortex revealed greater activity in these areas under conditions of high than of low WM load, confirming the occurrence of more extensive distractor face processing when WM is loaded. Taken together, these results provide very compelling evidence that WM actively maintains stimulus priorities and uses this information to direct attention to relevant rather than irrelevant stimuli. When WM is loaded, its ability to sustain stimulus priorities for attention is compromised, resulting in less attentional inhibition of irrelevant stimuli. These distractors are then more extensively processed than they would be under conditions of low WM load.

Desimone and Duncan's (1995) biased competition model of attention describes WM as a biasing agent for attention. Different sources of information compete for attention, and the successful ones are those with the strongest sources of support (Miller & Cohen, 2001). Task relevant representations receive top-down attentional bias within WM (Lepsien, Griffin, Devlin, & Nobre, 2005; Lepsien & Nobre, 2007). The short-term, task relevant description of visual information that is held in WM is then used to bias competition in the visual system such that inputs in V1 matching WM contents (e.g., task goals) are favored (Bundesen 1990, Duncan & Humphreys, 1989). This is true for both featural and spatial information. Attentional competition is not only biased by WM, but also by familiarity, long-term learned importance (Desimone & Duncan, 1995), and value associations (e.g., reward; Braver & Cohen, 2000), which can act in a bottom-up fashion and overturn top-down selection biases of a current task. This will be discussed in more detail in the following sections.

The prefrontal cortex (PFC) is considered to be the neuroanatomical source of the CE processes and resulting attentional top-down bias (e.g., Braver & Cohen, 2000; Cohen et al., 1997; Desimone & Duncan, 1995; Goldman-Rakic, 1996; see Miller & Cohen, 2001, for a review). More specifically, the lateral PFC has been linked to strong memory-related activity and is considered to be the main source of top-down control signals to the visual cortex of both macaque and humas (Funahashi, Bruce, & Goldman-Rakic, 1991; see Corbetta & Shulman, 2002, for a review). The PFC has extensive reciprocal connections with sensory systems, motor systems, and the limbic system, allowing it to maintain multimodal information about the current environment while having access to information stored in LTM. The key feature of the PFC that makes it ideal for WM maintenance is its ability to sustain task-relevant neural activity in the absence of sensory input and in the face of irrelevant distractor input (Cohen et al., 1997; Courtney et al., 1998; Miller, Erickson, & Desimone, 1996). Miller and Cohen (2001) describe the function of the PFC as "active memory in the service of control," not only maintaining task-relevant information against distraction but also flexibly updating information and integrating it into a new representation of task demands (see Knudsen, 2007 for a review; Frank, Loughry, & O'Reilly, 2001; O'Reilly, Braver, & Cohen, 1999, for computational models of PFC's role in WM and cognitive control).

To summarize, WM, attention, and awareness work together to create conscious experiences of our visual world. Rapid feedback processing in V1 and extrastriate areas (including OFC), which eventually enables awareness, shapes early visual descriptions, which are then accessed and manipulated by attention via further feedback processing to generate an accessible description in visual WM.

CHAPTER 2

ATTENTIONAL CAPACITY LIMITS AND THE ATTENTIONAL BLINK

Locus of Selection

As previously discussed, attention is vital for selecting and inhibiting visual information over space and time to limit processing to a subset of the vast amount of visual information available to us at any given moment. Historically, selection is thought of as occurring either early or late in processing – the classic "locus of selection" question. Early selection theories propose that selection occurs based on filtering physical attributes during early perceptual processing (Broadbent, 1958). Attention acts to enhance physical featural analyses and selection precedes stimulus identification. Late selection theories (Deutsch & Deutsch, 1963; Duncan, 1980b) argue that perceptual processing is not limited in capacity and operates without voluntary control. Attentional selection occurs at postperceptual stages after categorization and semantic analysis of visual input is completed.

More recent theories suggest selection can occur at either early or late stages of processing (or both) depending on whether parallel processing and perceptual gating are possible (for reviews, see Luck & Hillyard, 1999; Pashler, 1998). Luck and Hillyard give a good example of this. In task A, red and green letters are presented individually at fixation for a second each, and the task is to remember and report only the red letters at the end of a 15-second block. Here, green and red letters would be easily distinguished at a perceptual level and no selective processing would be needed at this stage. However, limited WM capacity would make remembering all 15 letters difficult, so only the red letters would be selected for WM storage (late selection). In task B, 14 green letters and one red letter are presented simultaneously in a densely packed array, and you have to quickly report the identity of the red letter. In this case, the green letters may interfere with perception of the red letter and would need to be filtered out at the perceptual level (early selection). In other words, selection occurs at the stage in which interference occurs. If there is no interference at all (e.g., pop-out), then attentional selection is not needed.

Lavie (1995; 2005) proposed a related account of the locus of attentional selection, showing that perceptual load determines the requirements for selection. She suggested that perception has limited capacity (early selection theory) but automatically processes all stimuli (late selection theory) when there is available capacity. Selective processing becomes necessary whenever the relevant information exceeds the capacity limit. When relevant stimuli do not take up all of the available attentional resources, any spare capacity is automatically allocated to irrelevant stimuli. In her experiments (1995), perceptual load was manipulated by either increasing the number of distractor items that are similar to the target to be perceived or by maintaining the number of items but increasing the attentional demands of the processing requirements (e.g., detect presence of color vs. presence of pre-specified color and shape conjunction). When perceptual load was low, incompatible distractors – those that compete for response – were able to interfere with target processing (measured by increase in RT as compared to the presence of a neutral distractor). A high perceptual load task engaged full attention to the target, with no attentional capacity left over for processing distractors, and thus eliminated distractor interference effects. Lavie concluded that attentional selection appears to be dependent on the perceptual load imposed by current task demands.

Limited capacity

Attentional resources themselves are thought to be limited in capacity, existing in the form of a central pool containing a finite but variable capacity of attention that can be allocated to relevant, attention-demanding tasks (e.g., Broadbent, 1958;

Kahneman, 1973; Navon & Gopher, 1979). As the demands of a task increase, more attention is allocated to its execution. The presence of an additional, concurrent, attention-demanding task will often lead to impaired performance if there is insufficient attention to devote to both tasks. This is referred to as dual-task cost or dual-task interference.

Theories of dual-task interference can be divided into two categories: postponement models and capacity-sharing models (Pashler & Johnston, 1989). In postponement models (Broadbent, 1958; Norman & Shallice, 1985; Welford, 1980), the processing of two tasks can be done in parallel, but interference arises because certain cognitive operations require exclusive dedication from a single mechanism to that operation until completion. When two tasks are competing for access to that mechanism, they reach a bottleneck where processing of one task is postponed until processing of the other task is complete.

The level of cognitive operations at which interference arises has been up for debate. Broadbent's (1958) early selection theory of attention proposed that this bottleneck occurs at the sensory level. More recent theories (e.g., Norman & Shallice, 1985; Welford, 1980) have suggested that interference arises at the response stage (late selection). The act of selecting and executing a response relies on a single mechanism, which is exclusively dedicated to only one operation at a time. Response competition results in a bottleneck that postpones selection of the second task response until after response for the first task is selected.

In capacity theories of attentional limits (Kahneman, 1973; Norman & Bobrow, 1975; Wickens, 1983), there is no stage that requires exclusive dedication to a single mechanism. Instead, each task draws on the central pool of attentional resources. If tasks together do not exceed the central capacity, they will not interfere. Once the attentional pool has been depleted, processing becomes impaired.

Attentional Blink

The cost of performing two tasks in rapid succession is best illustrated by the well-studied attentional blink (AB) effect (Raymond, Shapiro, & Arnell, 1992). In a typical AB task, an observer is required to detect two target items embedded in a rapid serial visual presentation (RSVP) of images. Detection of the second target (T2) is severely impaired when it is presented in close temporal succession to the first target (T1). This deficit in perception is referred to as a “blink” in attention because attentional resources are devoted to T1 with insufficient capacity left to process T2, thus causing T2 not to be seen as if missed by an actual eye blink.

In Raymond et al.’s (1992) seminal paper demonstrating the AB effect, randomly chosen black letters were presented for 15 ms in a RSVP stream with an interstimulus interval (ISI) of 75 ms (see Figure 3a). After 7 – 15 letters (this number was randomly chosen and varied across trials), a white target letter appeared (T1). Eight letters always succeeded the target. On half of the trials, one of the succeeding letters was an X. In the single-task control condition, observers ignored T1 and reported the presence or absence of the X (T2). In the dual-task condition, observers were required to name the T1 letter and report the presence or absence of T2. The key manipulation was the serial position of T2 relative to T1, known as T2 lag. Both T1 and T2 tasks were reported at the end of each trial. In the control condition, observers correctly detected T2 on 85% or better of trials, regardless of its serial position. In the dual-task condition, T2 performance (conditional on correct T1 performance) was significantly impaired when it appeared in lags 2 – 6, which fell between 180 and 450 ms (Figure 3b). T2 performance when presented in lags 7 – 8 was not impaired, mirroring T2 performance in the control condition. Detection impairment for T2 in the dual-task condition was determined to be attentional in nature as opposed to sensory because, while the observer's visual system was stimulated by a novel white target in both conditions, performance decrement did not occur when T1 detection was not required. Thus, varying the T1-T2 lag makes a tidy manipulation of available attentional resource for T2, without concurrently changing demands on sensory or response systems.

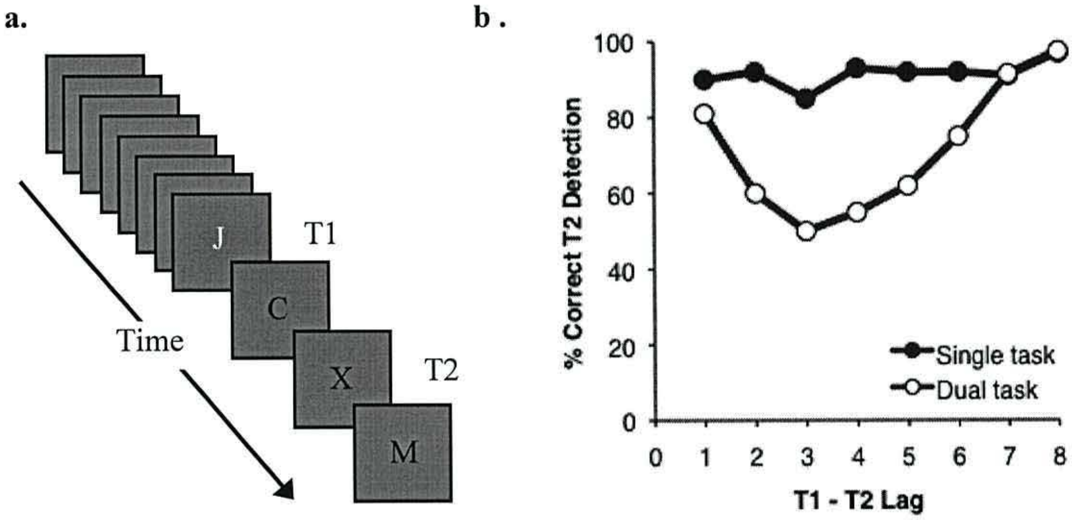

Figure 3. (a) Example of an AB trial from Raymond et al. (1992). T1 was a white letter; task was to report identity. T2 was always a black X, presented at a variable serial position after T1 on half of trials; task was to report presence or absence. (b) Example data from an AB task (Raymond et al., 1992). When only detection of T2 was required (single task), performance was not affected by serial position. When detection of T2 followed identification of T1 (dual task), performance was impaired 180 – 450 ms after T1 display and then recovered at the last two lags. This U-shaped function is characteristic of the AB effect.

Raymond and colleagues (1992) also found that the AB effect does not result from the presence of a T1 task only, but instead depends on the presence of a non-target item in the first serial position following T1 (called "T1 mask"). In two additional experiments, they found no AB effect when a blank screen followed T1 presentation. This suggests that attentional suppression, resulting in a post-target processing deficit, occurs only when novel visual input is presented before target-identification processes are complete. This is also true for T2; the AB effect only occurs when T2 is masked (Giesbrecht & Di Lollo, 1998).

Initially, the AB was explained by an early selection account of attention (Raymond et al., 1992), labeled the "inhibition model." The detection of T1 initiates an attentional episode at which point T1 processing commences. This attentional "gate" stays open until T1 processing is complete (Reeves & Sperling, 1986), during which time the T1 mask is presented. This results in features of the T1 mask being stored in WM along with features of T1, which is a source of potential confusion. To eliminate further confusion from subsequent items, an attentional suppression mechanism is initiated, thus "shutting and locking" the gate to stop further attentional processing and entry into WM. This disables T2 processing when it appears before processing of T1 is complete. Attentional selection in the AB is early because it filters information at a featural level according to similarities among targets and distractors.

Evidence against a perceptual locus of the AB was reported in Raymond and colleagues' subsequent AB papers (Shapiro, Raymond, & Arnell, 1994; Raymond, Shapiro, & Arnell, 1995). They found that presenting T1 for detection still produced an AB effect of similar magnitude as when T1 had to be identified (Shapiro et al., 1994). This was the case even when T1 was a non-letter, random-dot target and identification was not possible. They concluded that processing any T1 containing pattern information could produce an AB, and as such, the AB must not arise from the avoidance of a conjunction problem during entry into WM. Instead, deficits in T2 detection are thought to occur because of competition for retrieval from WM.

In this interference model, based on an adaptation of similarity theory (Duncan & Humphreys, 1989) and Bundesen's "theory of visual attention" (TVA; Bundesen, 1990), T1 first gains entry to WM, with preferential attentional weighting, based on its match to a T1 template. The T1 mask gains entry, with a lesser attentional weighting, due to its close temporal proximity to T1 as well as its similarity to the T2 template (Raymond et al., 1995). T2 gains access based on congruence with its template, as does the T2 mask due to temporal proximity. Retrieval problems arise from the degree of similarity between items in WM as well as from their respective weightings at the time of retrieval. When the visual similarity between T1 and T2 increases, they compete for retrieval. Since T1 and its mask always appear before T2, they receive preferential weighting and little resource is left over to consolidate T2 in WM. If the T1-T2 interval is short (less than 500 ms), T2 does not have enough attentional resources to successfully compete for consolidation in WM and subsequent retrieval, resulting in an AB. If the interval is long, sufficient time has passed for the representations of T1 and its mask to be cleared from WM, thus eliminating competition. This is also the case when T1 and T2 are featurally dissimilar (Raymond et al., 1995; Shapiro et al., 1994).

According to the interference model of the AB, T2 is perceptually processed but is "unseen" due to retrieval competition. Further evidence for this postperceptual deficit comes from studies demonstrating that semantic information from T2 is still processed during the AB. Shapiro, Driver, Ward, and Sorensen (1997) used three targets in an RSVP task to show that semantic information from T2 can prime response of a third target. Semantic priming occurs when viewing an object or word facilitates the processing of a subsequently presented object or word, based on their semantic link. In Shapiro et al.'s (1997) study, they found a significantly better T3 identification when it was semantically matched with T2 (e.g., coffee-cup) than when it was semantically unrelated (e.g., coffee-cat). T2 identification was at chance, signifying an AB. However, T2 performance (correct or incorrect) did not affect its semantic priming of T3, thus indicating that semantic information was processed even when T2 could not be consciously reported. These results demonstrate that attentional competition takes place only after substantial stimulus processing has occurred. Additional evidence for T2 semantic information processing during the AB has been shown using ERP recordings (Luck, Vogel, & Shapiro, 1996; Rolke, Heil, Streb, & Hennighausen, 2001).

Chun and Potter (1995) proposed a two-stage model to account for the AB. In the first stage, all stimuli are rapidly processed in parallel for relevant features and meaning such that identity is briefly available for subsequent processing. These initial representations are not sufficient for report, and they are subject to rapid forgetting when there is interference from subsequent RSVP stimuli. Thus, they must be selected (attention) for further processing and consolidation into WM in order for conscious response. This is congruent with the aforementioned models of visual attention and awareness (Lamme, 2004; Dehaene et al., 2006) where relevant visual input reaches a level of activation sufficient for conscious access but must be attended to avoid replacement by new information.

If an item is selected in Stage 1, it moves on to Stage 2 for additional processing. Here, it is transferred into a more durable representation by consolidation into WM and is then available for subsequent report at the end of the trial. This stage is considered to be limited in capacity and processes stimuli in a serial fashion – a consolidation bottleneck. Once an item (e.g., T1) moves to the second stage of processing, no subsequent items are processed beyond Stage 1 until the processing of the initial item in Stage 2 is complete. When T2 appears before Stage 2 is free (during a short T1-T2 lag), its consolidation into WM is delayed. The longer the delay, the more likely the T2 representation is lost, due to the fleeting nature of information in the first stage and its vulnerability to replacement.

Giesbrecht and Di Lollo (1998) introduced a revised two-stage model to account for the finding that a "blinked" T2 can semantically prime a T3, and therefore must not have been erased while waiting in Stage 1. The revision includes a Stage 1 output buffer, where the output of Stage 1 can be stored if Stage 2 is busy. Information remains here until it can be processed in Stage 2, or it is replaced by the next input (T2 mask) from Stage 1 (see Vogel, Luck, & Shapiro, 1998, for a similar account). They found that when T2 is not masked, no AB occurs. If there is no visual information presented after T2, its perceptual representation is still available when consolidation of T1 has been completed (Stage 2), at which point it can be transferred into WM. When T2 blinks but semantically primes a T3, the T2 mask erases the T2 representation from the buffer without interfering with the residual semantic activity of Stage 1 that had been triggered during T2 processing at that level.

Recently, neurophysiological studies using the AB paradigm have also given support to the two-stage model. fMRI has been used to uncover the neural fate of a missed T2 by comparing activation during an AB to when T2 is consciously perceived. In numerous studies (Gross et al., 2004; Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Marcantoni, Lepage, Beaudoin, Bourgouin, & Richer, 2003; Marois, Chun, & Gore, 2000; Marois, Yi, & Chun, 2004; Shapiro, Johnston, Vogels, Zaman, & Roberts, 2007), PFC activation is shown to be larger on trials when T2 is consciously perceived and detected compared to when it is undetected (AB) or when it is absent. For example, Kranczioch and colleagues (2005) used fMRI to measure activation during an AB letter discrimination (T1) and detection (T2) task similar to Raymond et al. (1992). They found consistently larger activation in the lateral PFC when T2 had been detected; when T2 was undetected, lateral PFC activation was no different than when T2 was physically absent. Marois et al. (2004), who found similar results, suggested that lateral PFC activation is associated with the consolidation and maintenance of targets in WM. Marcantoni et al. (2003) proposed that larger lateral PFC activation for consciously perceived T2s reflects the resolution of dual-task interference. Since Kranczioch et al. (2005) did not find an increase in lateral PFC activation when T2 was detected as compared to absent at a long T1-T2 lag, they concluded that this activation represents a combination of WM processes and interference between target items.

In addition to lateral PFC activation, Kranczioch et al. (2005) also found larger activation for detected T2s in superior and inferior prefrontal areas and inferior parietal lobules (IPL) compared to when T2 was undetected or absent. However, unlike the lateral PFC activation, activation in these areas was significantly higher when T2 was missed than when it was absent, suggesting that the processing of target-related information occurs but is incomplete when T2 is missed.

A third interesting finding from Kranczioch et al.'s (2005) study is that activation in regions in the occipitotemporal cortex (OTC) (including the left and right lateral occipital complex, LOC, and left and right fusiform gyrus, FFG), thought to be involved in the processing of letter stimuli (Joseph, Gathers, & Piper, 2003), was significantly larger when T2 was missed than when it was detected. They suggest that attentive search for T2 in the letter stream was aborted early when T2 was detected; when undetected or absent, the stream was searched until its end.

Taken together, these findings give neuroanatomical support for the revised two-stage model of the AB (Giesbrecht & Di Lollo, 1998; Vogel et al., 1998). During Stage 1, both detected and undetected visual items engage high-level stages of visual representation in ventral regions of the OTC (e.g., perceptual and semantic processing). Consolidation and maintenance of items into WM (Stage 2) occur later along the information-processing pathway in the lateral PFC (consistent with research on the neuroanatomy of WM maintenance, see previous chapter), allowing retrieval for conscious report at the end of the trial. Areas in the PFC reflect explicit perception of T2 rather than its physical presentation. Prior to WM consolidation, activation in superior and inferior prefrontal areas parietal areas might reflect storage in a Stage 1 output buffer.

Top-down and bottom-up attentional guidance

As discussed in previous sections, selection of visual information can be biased and facilitated by top-down, goal-driven attention. Top-down biases, based on overt expectations of current task goals, reflect voluntary (endogenous) control over attention. Visual objects, features, and locations are selected based on a match to top-down goals and are preferentially processed in WM for subsequent retrieval.

However, information does not have to be modulated by top-down attention to gain access to WM. Salient physical stimulus properties can capture attention in an involuntary, bottom-up (exogenous) fashion, regardless of (or in spite of) current task goals. Stimuli can be highly salient when they differ substantially from the rest of a visual array in one or more simple visual attributes (e.g., color), known as a feature singleton (Egeth, Jonides, & Wall, 1972; Treisman & Gelade, 1980). These stimuli are said to "pop out" from their background, and capture attention during a task that requires searching for a singleton (Pashler, 1988; Theeuwes, 1991a; 1992).

Unexpected stimuli, such as those with abrupt visual onsets (sudden luminance changes), also preferentially draw attention (Yantis & Jonides, 1984). Featural information actively held in WM can also automatically focus attention on visual stimuli that share this feature (Downing, 2000; Olivers, Meijer, & Theeuwes, 2006). Additionally, there is a great deal of evidence suggesting that emotional valence can influence the allocation of attention (e.g., Fox, Russo, Bowels, & Dutton, 2001; Georgiou et al., 2005; Smith, Most, Newsome, & Zald, 2006).

Both bottom-up and top-down processes almost invariably work together to influence the attentional consequences of a given attentional event (Egeth & Yantis, 1997; Corbetta & Shulman, 2002). For example, irrelevant feature singletons do not pop out when an observer has an incongruent top-down goal of searching for a specific feature (Jonides & Yantis, 1988). Folk et al. (1992) proposed that the interaction between goal-driven attentional control and stimulus-driven attentional capture is contingent on the feature property that is critical to the performance of the task at hand. In support of this, Folk et al. (1992) used a spatial cuing paradigm in which a visual abrupt onset cue predicted the subsequent target location in some block of trials (valid) and did not predict target location in other blocks (invalid). In invalid trial blocks, a shift of attention to the cue depended on whether the cue shared the critical target property (as measured by an increase in RT to locate the target). When the target was an abrupt onset, the abrupt onset cue captured attention. When the target was a color singleton, the abrupt onset cue no longer captured attention. They concluded that involuntary orienting of attention to a stimulus event can occur only if that event shares a critical target property. This is called contingent capture of attention.

In a similar vein, Wolfe (1994a) proposed the Guided Search model to account for the guidance of attention. According to Wolfe, preattentive stages of vision process basic features in parallel until they reach a processing bottleneck, at which point processing is essentially serial. It is at this point that attention is directed to objects serially, in order of priority. Attentional priority is determined by the interactions between the bottom-up activation – how much an object differs within a given dimension – and how closely it matches the top-down perceptual set.

Familiarity aids attentional selection

Familiar stimuli have been shown to have a competitive advantage over unfamiliar stimuli when competing for attention, exerting early exogenous control over visuospatial attention. Information of learned importance or of general significance from LTM can act in a bottom-up fashion to bias attentional competition. When discriminating changes in a visual display, changes at the location of familiar words are detected more rapidly than changes at the location of novel letter combinations (Christie & Klein, 1995). Observers are also more likely to detect changes with familiar faces than with novel faces in brief, masked displays (Buttle & Raymond, 2003).

Long-term experience or practice with visual stimuli makes them hard to ignore when they are subsequently irrelevant in a task (Shiffrin & Schneider, 1977). West Chanon and Hopfinger (2008) recently investigated the effects of previous experience with objects on the subsequent allocation of attention to them in an eye-tracking experiment. At the beginning of the experiment, observers deeply encoded a set of every-day objects by making semantic judgments about them. After encoding, observers viewed scenes containing both learned and novel objects in preparation for a memory test. Objects in the encoding stage were counterbalanced such that a learned item (e.g., towel or sink) for some observers was a novel item for other observers, and vice versa. One group was told that memory recall would be for individual items from the scene, which was meant to bias fixation time toward new items. The other group was told that the memory task would entail change discrimination for the whole scene, meant to bias observers to use the old items as memory aids. Regardless of instruction, learned objects were fixated sooner than novel comparisons and attention dwelled on learned objects longer before disengagement (as measured by fixation duration). These results support the idea that LTM for visual objects creates salient bottom-up activation that biases the guidance of attention. A similar finding has been shown to occur in target detection in natural scenes for targets appearing in previously memorized locations (stored in LTM) compared to search for targets in familiar scenes without a previously memorized location (Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006).

Personal relevance is another source of long-term importance that can bias attention. Moray's (1959; Wood & Cohen, 1995) well-known "cocktail party effect" shows that attention can be attracted to one's own name in an ignored auditory channel. An observer's own name has also been shown to attract visual attention (Bundesen, Kyllingsbaek, Houmann, & Jensen, 1997; Harris, Pashler, & Coburn, 2004), and can successfully escape the AB as T2 while other names and nouns do not (Shapiro, Caldwell, & Sorensen, 1997). Similarly, one's own name can be detected under conditions of inattentional blindness (Mack & Rock, 1998) and show reduced repetition blindness (Arnell, Shapiro, & Sorensen, 1999).

Tong and Nakayama (1999) proposed the idea that highly familiar visual stimuli show a processing advantage because observers have acquired a "robust representation" for them. In a series of visual search experiments, Tong and Nakayama (1999) had observers search for their own face or an unfamiliar face among displays of unfamiliar distractor faces. They found that search for one's own face was substantially faster than recognition of a stranger's face, even after hundreds of presentations made the stranger's face familiar. This was true for different views of the faces, including atypical ones (e.g., inverted, profile, & three-quarter views). Also, distractor rejection rates during search for an unfamiliar face among own face distractors were considerably faster than during search for one's own face among unfamiliar distractors (all the same unfamiliar face) (Experiment 3).

Tong and Nakayama (1999) propose five defining properties of a robust visual representation: (1) mediate rapid asymptotic visual processing; (2) require extensive visual experience to develop; (3) contain some abstract or view-invariant information; (4) facilitate a variety of visual and decisional processes across tasks and contexts; (5) demand less attentional resources. Of interest here is the role of familiarity in competing for attention. Faces require attention to be processed (Brown, Huey, & Findlay, 1997; Jackson & Raymond, 2006; Landau & Bentin, 2008; Pessoa, McKenna, Gutierrez, & Ungerleider, 2002) and hold attention once processed (Bindemann, Burton, Hooge, Jenkins, & de Haan, 2005). It is still unclear whether faces themselves are able to capture attention exogenously (e.g., Hershler & Hochstein, 2005; Langton, Law, Burton, & Schweinberger, 2008; Ro, Russell, & Lavie, 2001; Theeuwes & Van der Stigchel, 2006; Van Rullen, 2005; Wolfe & Horowitz, 2004). However, evidence does suggest that highly familiar faces (i.e., those with robust representations) require less attention to be processed than unfamiliar faces (Jackson & Raymond, 2006; Tong & Nakayama, 1999).

Tong and Nakayama (1999) hypothesize that extensive visual experience with a face (Property 2) in multiple contexts and from different viewpoints (Property 3) results in a reduction in the number of active neurons required to code it, which leads to efficient, or "compact" visual codes for the face (Property 1). The visual system then processes the compact face code more quickly when the face is next encountered (Property 5), irrespective of task or context (Property 4). The robust representation of a face in LTM might then allow better maintenance once in WM, less likely to decay or experience interference from other visual stimuli before report is required (Cowan, 2001; Jackson & Raymond, 2008).

Visual expertise with faces

We can become experts for objects within any category of visual stimuli, able to make fine within-category distinctions, after a prolonged experience with thousands of exemplars under the aforementioned conditions of robust representations. For example, there are dog experts (Diamond & Carey, 1986), bird experts (Tanaka & Curran, 2002), car experts (Gauthier, Skudlarski, Gore, & Anderson, 2000), and even Greeble experts (a homogeneous set of artificial stimuli organized into genders and families, Gauthier & Tarr, 1997). However, we are natural experts at recognizing individual faces, having practiced this skill since the first time we opened our eyes and spending most of our lives looking at faces than at any other type of object. While human faces vary only subtly, we are remarkably able to recognize those for whom we have acquired robust representations despite changes in those faces with time.

With the immense biological and social importance that faces hold, there has been much debate over whether faces constitute a "special" category for which we have developed domain-specific perceptual processing mechanisms. One striking line of evidence is that a specific brain area, the fusiform face area (FFA) within the fusiform gyrus, appears to be selectively activated by faces, with activation about twice as strong when viewing faces compared with other objects (Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; see McKone, Kanwisher, & Duchaine, 2007, for a review). The FFA also shows greater sensitivity to identity differences in upright face than in inverted faces, referred to as the face inversion effect. Behaviorally, the face inversion effect is demonstrated by a dramatic impairment for face recognition when faces are inverted compared to recognition for other inverted objects (Farah, Tanaka, & Drain, 1995; Tanaka & Farah, 1993; Yin, 1969). In addition, damage to the FFA leads to severe deficits in face recognition, a condition called prosopagnosia (Damasio, Damasio, & Van Hoesen, 1982; McNeil & Warrington, 1993).

There is counter evidence for all the above face-specificity claims. This evidence suggests that the special processing of faces merely reflects our expertise at performing within-class discriminations of faces as compared to other objects. Researchers advocating the "expertise account" claim that it is our extensive experience with faces that makes them special, and expertise developed for any other visual object category would result in the same behavior (e.g., within-category discrimination, inversion effects) and FFA activity. For example, experts in other object categories experience behavioral inversion effects for those objects (dog experts: Diamond & Carey, 1986; Greeble experts: Gauthier & Tarr, 1997); however, the inversion effect with dog experts has failed to be replicated (Robbins & McKone, 2007). Significant FFA activity has also been shown for bird, car, and Greeble experts compared to novices (Gauthier & Tarr, 2002; Gauthier et al., 2000; Xu, 2005;

Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). The expertise account of FFA activation has been put into question, though, and increased activation has been explained as reflecting an overall increased attentional engagement for these non-face stimuli (Grill-Spector et al., 2004; see McKone et al., 2007, for a review).

Whether face processing is always different from object processing due to domain specificity or whether it is because of our expertise with faces is beyond the scope of this thesis. Regardless, we are experts at faces and we have robust representations for many that are familiar, important, and/or significant in our visual world. We can learn individual identities rapidly, and we seem to have the capacity to perceive the unique identities of an unlimited amount of different faces. This special relationship with faces makes them ideal stimuli to use when investigating the effects of learning on perception and attention. I used faces as stimuli in all of my thesis experiments to capitalize on the innate human ability to rapidly learn individual face identities, and not as a specific investigation into face processing mechanisms. The results of these studies are meant to generalize to all types of visual stimuli.

A comprehensive review of face processing is also outside the scope of this thesis, so I will just review some fundamental characteristics. First, it is generally thought that upright faces are processed configurally (sometimes referred to as holistic processing) and inverted faces are processed featurally (e.g., Tanaka & Sengco, 1997; Young, Hellawell, & Hay, 1987). Young et al. (1987) tested the idea of configural face processing by creating new faces from the top and bottom portions of two different famous faces that were either aligned or misaligned horizontally. Observers were asked to make recognition judgments on the top half of the face. When the faces were upright, observers were slower to identify the top half of the face when the halves were aligned compared to when they were misaligned. This "composite face effect," the disruption of face identity processing caused by aligning face halves from two different identities, is thought to occur because configural face processing creates the perception of a novel face configuration making it difficult to recognize the individual identities. When the face halves are misaligned, configural processing is disrupted and the individual identities are perceived much easier and quicker. When the composite faces are inverted (aligned and misaligned), however, there is no longer a disadvantage when the faces are aligned compared to misaligned. This suggests that inverted faces are processed featurally; hence, the top half features can be distinguished from the bottom half regardless of alignment. Further evidence for the role of configural processing in face recognition in studies showing a robust right hemisphere advantage for face recognition in behavioral (Hillger & Koenig, 1991; Rhodes, 1993), fMRI (Young, Hay, & McWeeny 1985; Haxby, Ungerleider, Horwitz, Maisog, Rapoport, & Grady, 1996), and ERP (Sagiv & Bentin, 2001) studies. The right hemisphere has been shown to be biased for processing global and configural information (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Martinez, Moses, Frank, Buxton, Wong, & Stiles, 1997).

Determining that an item in the visual world is a face is a rapid process. ERP recordings during face perception show a reliable large negative component that peaks between 150 – 220 ms after the presentation of a face, called N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996; found also with MEG, M170; Liu, Higuchi, Marantz, & Kanwisher, 2000). The N170 occurs at occipitotemporal sites and, when elicited by faces, is believed to reflect a late pre-categorical structural encoding stage prior to recognition and identification (Bentin et al., 1996; Eimer, 2000). According to Bruce and Young's (1986) functional model of face processing and an updated model of a distributed neural system for face perception (Haxby, Hoffman, & Gobbini, 2000, discussed in more detail in the next section), faces are first processed by a core, structural encoding system responsible for early perceptual processing of facial features before they are configured into representations able to inform emotional expression interpretation and identity. In line with this, recent studies have shown that the N170 is unaffected by familiarity with face identity (celebrities vs. novel faces) (Bentin & Deouell, 2000; Eimer, 2000; Henson et al., 2003) or by emotional face expression (Eimer & Holmes, 2002; Eimer, Holmes, & McGlore, 2003; Holmes, Vuilleumier, & Eimer, 2003; Holmes, Winston, & Eimer, 2003; but see Blau, Maurer, Tottenham, & McCandliss, 2007; Miyoshi, Katayama, & Morotomi, 2004), both processes believed to occur after structural face encoding.

In contrast to evidence suggesting that the N170 is insensitive to face identity, Liu and colleagues (Liu, Harris, & Kanwisher, 2002) found that the face selective M170 component is correlated with successful face recognition (Liu et al., 2002; although see Ewbank, Smith, Hancock, & Andrews, 2008, for evidence that the M170 is not sensitive to face familiarity). MEG recordings also indicate that the categorization of a stimulus as a face occurs as early as 100 ms after face onset (Liu et al., 2002). Given that the initial feedforward sweep of visual information processing occurs within 100 ms, it is probable that face categorization is carried out mainly by feedforward mechanisms. Face identification requires at least an additional 70 ms, supporting the idea of distinct stages of face perception (Haxby et al., 2000).

Locus of face processing

As mentioned earlier, the FFA is thought to be a face-processing area within the visual extrastriate cortex, specialized in processing the invariant aspects of faces such as identity (Hoffman & Haxby, 2000; Kanwisher et al., 1997; McCarthy et al., 1997). In addition to the FFA, functional imaging studies have identified the inferior occipital gyri and the posterior superior temporal sulcus (pSTS) as face-responsive regions, also within the visual extrastriate cortex. The pSTS is thought to process the changeable aspects of faces (biological movement), such as expressions, mouth movements, and eye gaze (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). The inferior occipital gyri (IOG) are involved in the early perception of basic facial features and may provide input to the FG and the pSTS (Puce, Allison, Gore, & McCarthy, 1995; see Haxby et al., 2000, for a review).

Haxby and colleagues (2000; Hoffman & Haxby, 2000; see also Winston, Henson, Fine-Goulden, & Dolan, 2004) proposed a neuroanatomical model to account for the organization of the face processing system in humans. Compatible with Bruce and Young's (1986) functional account of face perception, Haxby et al.'s model describes a distributed neural system, consisting of core and extended systems, that processes facial identity and expression via functionally and neurologically independent parallel pathways (see Figure 4; although see Calder & Young, 2005, for a review on how the separation of neural mechanisms is relative rather than absolute). According to the model, the aforementioned IOG, FFA, and pSTS constitute the core system of face perception. After the initial structural and visual analysis of faces in the IOG, there is a separation (functional and neural) in processing of the invariable facial aspects (i.e., identity; FFA) and the variable aspects (i.e., eye gaze, expression, lip movement; pSTS). The extended system includes projections from the STS to the intraparietal sulcus, which processes spatial attention from the face, to the auditory cortex for the perception of speech sounds, and to brain regions involved in emotion processing including the amygdala, insula, and limbic system. It also includes projections from the FFA to the anterior temporal cortex, where biographical/semantic information and personal identity are used to recognize the identity of a familiar face. An extended version of this model (Gobbini & Haxby, 2007) also includes a set of extended system areas involved extracting further information from a face to aid familiar face recognition, including personal traits, attitudes, intentions, episodic memories, and reward information (see Figure 5).

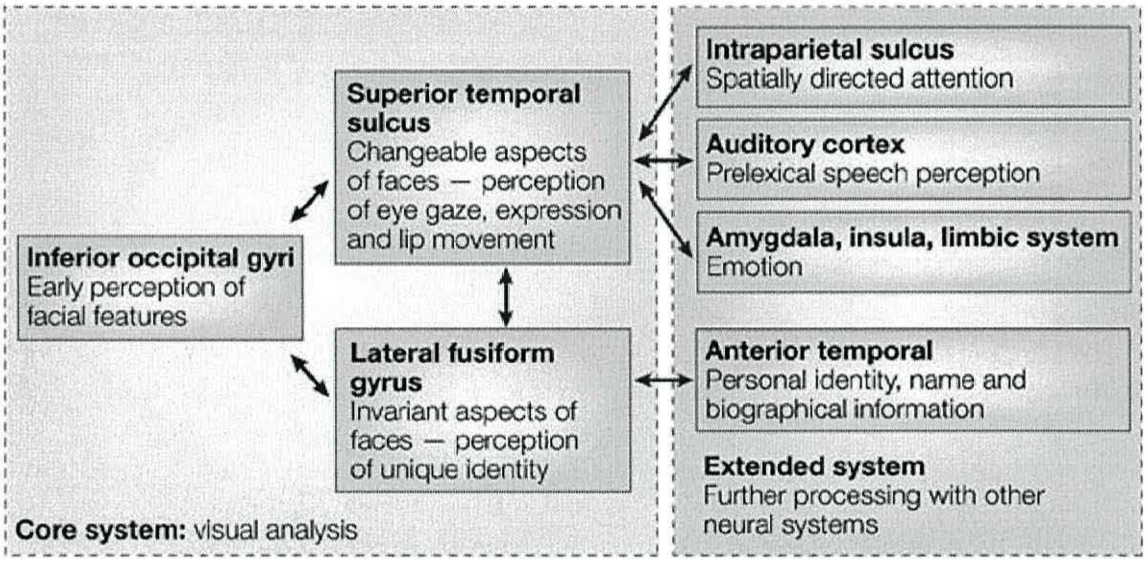

Figure 4. Haxby et al.'s (2000) model of the distributed human neural system for face perception, reproduced from Calder & Young (2005).

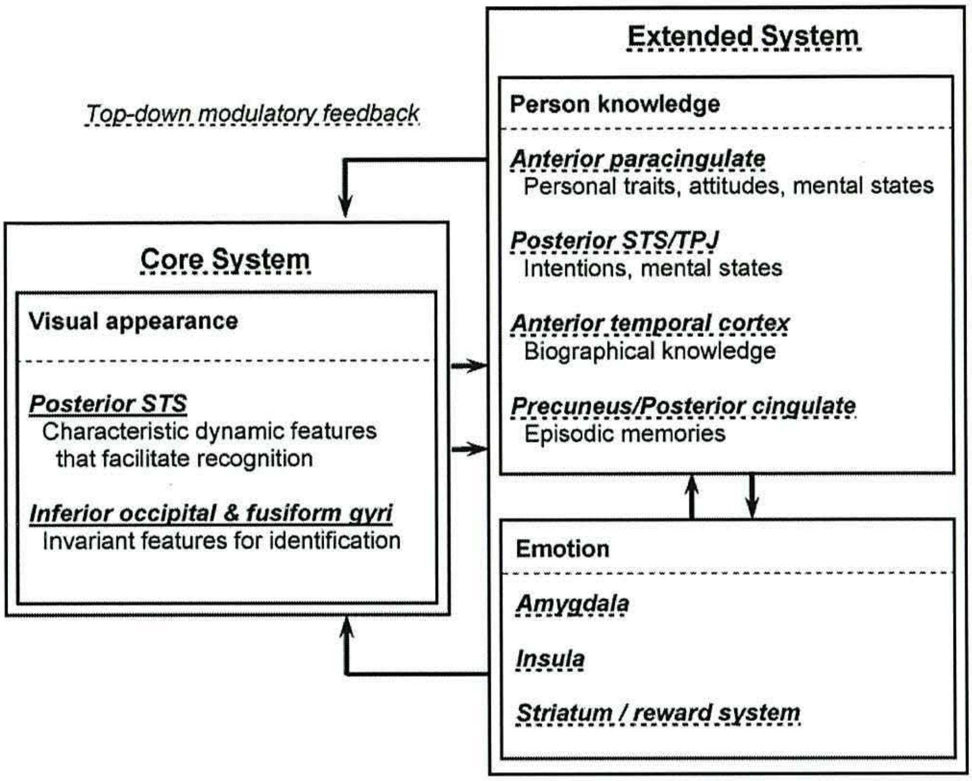

Figure 5. Extended model of distributed human neural system for face perception, including areas that mediate familiar face recognition. Reproduced from Gobbini & Haxby (2007).

It remains to be determined whether familiar faces have a different distribution of neural activation compared to unfamiliar faces, or whether different neural activity for familiar faces is a result of the representations of biographical and semantic information associated with these faces. In ERP studies where face familiarity is tangential to the visual task, familiar faces elicit a greater negativity 400 ms post-stimulus followed by a greater positivity 600 ms post-stimulus (N400 and P600, respectively), as compared to unfamiliar faces (Bentin & Deouell, 2000; Eimer, 2000a, 2000b; Schweinberger, Pickering, Burton, & Kaufmann, 2002; Trautner et al., 2004). This later activity is interpreted as reflecting the access and retrieval of person-specific semantic memory information (Eimer, 2000b; Trautner et al., 2004). Consistent with this, neuroimaging studies directly comparing the activation of familiar and unfamiliar faces using identity tasks describe increases of activity for familiar faces in the anterior middle temporal region, suggested to be related to the analysis of semantic knowledge associated with the familiar face rather than to the differences in familiarity (e.g., Gorno-Tempini et al., 1998; Leveroni, Seidenberg, Mayer, Mead, Binder, & Rao, 2000; Sergent, Ohta, & Macdonald, 1992). Recent neuroimaging studies where tasks orthogonal to familiarity were used (e.g., gender categorization task), however, have failed to find differential activation between familiar and unfamiliar faces, most consistently in the FFA (Dubois et al., 1999; Gauthier, Tarr, Moylan, Skudlarski, Gore, & Anderson, 2000; Rossion, Schilts, Robaye, Pirenne, & Crommelinck, 2001). Activity for familiar faces has been shown to decrease compared to that for unfamiliar faces in the right middle occipital gyrus (Dubois et al., 1999; Rossion et al., 2001) including V1 (Dubois et al., 1999), possibly reflecting efficient visual codes for robust face representations (Tong & Nakayama, 1999).

Faces, familiarity, and attention

As mentioned previously, a visual stimulus can be categorized as a face (rather than another visual item) very rapidly, but some extra time and attention is needed to process information about an individual face identity (Bentin et al., 1996; Liu et al., 2002). However, evidence suggests that less attention is needed to process the identity of a highly familiar face than an unfamiliar face (Jackson & Raymond, 2006; Tong & Nakayama, 1999). In a series of three experiments, Jackson and Raymond (2006) demonstrated that highly familiar (famous) faces escape the AB, providing support for the efficient visual code hypothesis. In each experiment, T1 was an abstract pattern composed of either circles or squares and observers were asked to discriminate the shapes. The T2 task was to detect the presence of a pre-defined unfamiliar (Experiment 1, 3) or familiar (Experiment 2, 3) face presented amongst unfamiliar (Experiment 1 & 2) or familiar (Experiment 3) distractor faces. The T2 face could appear at one of five lags after T1 (one lag = 85 ms), creating both short and long T1-T2 intervals. Of main interest was observers' ability to detect a T2 face at short and long lags following correct T1 shape discrimination.

In the first experiment, unfamiliar faces were susceptible to the AB, with T2 detection significantly impaired at short lags and recovered after a long T1-T2 interval. This provides clear support for an attentional requirement during face identification. In Experiment 2, T2 faces were extremely familiar to one group of observers and somewhat familiar to a second group. For the extremely familiar group, T2 detection was not significantly affected by attentional constraints during short lags and no AB for these faces was found. This immunity occurred regardless of the familiarity of the distractor faces presented before and after a familiar T2 (Experiment 3), suggesting that it is not a result of T2 uniqueness or pop out. In contrast, these same faces were highly susceptible to the AB at short lags when they were only slightly familiar (Experiment 2), as were unfamiliar T2 faces among familiar distractors (Experiment 3). These experiments show that, while successful face identification (awareness) requires attention, visual experience with a face determines the amount of attention needed. A more robust experience with a face, and thus a robust representation stored for it, reduces the amount of attentional resources needed to consciously identify it.

As discussed earlier in this chapter, research on perceptual load has demonstrated that the perception of irrelevant distractors depends on the level of perceptual load in the current task. In situations of high perceptual load, conscious perception of distractors is prevented; with low load, spare capacity is automatically used to process the irrelevant item(s) resulting in perception (Lavie, 1995, see 2005 for a review). Congruent with this theory, the ability of irrelevant faces to capture attention has been shown to also depend on perceptual load (Jenkins, Lavie, & Driver, 2005).

Investigating the effects of perceptual load on face processing, Jenkins and colleagues (2005) presented low load and high load letter tasks (shape discrimination) superimposed across unfamiliar faces. RTs for correct letter discrimination increased with an increase in task difficulty, indicating successful perceptual load manipulation. Observers completed a surprise recognition test at the end of the experiment to determine the effect of load on subsequent explicit recognition. This was completed for either all faces used as distractors (long term recognition, Experiments 1 & 2) or for the face used as a distractor only on the last trial (immediate recognition, Experiment 3). In both cases, correct recognition from memory of previously seen distractor faces depended on perceptual load at exposure. Faces seen under a high load were recognized at chance, whereas performance was significantly better for faces seen during a low load. Jenkins and colleagues (2002) also used familiar (famous) faces in a very similar procedure. They found that long-term explicit recognition memory for famous faces also depends on the level of load at encoding. Together, these experiments suggest that explicit conscious recognition of faces, regardless of familiarity, depends on the amount of available attention when they are viewed.

In contrast to explicit recognition, more implicit face recognition processes seem to be less dependent on attentional load. For instance, Lavie and colleagues (Jenkins, Lavie, & Driver, 2003; Lavie, Ro, & Russell, 2003) found that interference by familiar (famous) distractor faces on a famous name-categorization task (politician vs. pop star) was independent of perceptual load. When the distractor was the face of the person named, categorization RTs decreased as compared to when the face was from the incongruent category. Critically, the congruency effect did not vary as a function of perceptual load (increase in set size of name search), indicating that the familiar faces were perceived and recognized in all conditions. The authors conclude that face processing is automatic, independent of general capacity limits (Lavie et al., 2003).

Due to limitations in the design, however, the authors could not repeat the experiment with unfamiliar faces. Thus, it is unclear whether the processing of all faces is resistant to perceptual load manipulations or just familiar ones. In light of the findings that faces require attention to be processed and only highly familiar faces escape the AB (Jackson & Raymond, 2006), these results most likely stem from the familiarity of the distractor faces. The need for attention was reduced for these faces, but most likely not entirely eliminated – as would be the case if face processing were truly automatic.

In addition to an attention advantage, evidence suggests that familiar faces benefit from enhanced WM capacity as compared to unfamiliar faces. Traditional estimates of WM capacity report a limit of around 3 – 4 items (Luck & Vogel, 1997; Todd & Marois, 2004; Wheeler & Treisman, 2002). In a WM task with a concurrent verbal WM suppression task, Jackson and Raymond (2008) found that WM capacity for faces was between 2 – 3 items, depending on face familiarity. Interestingly, WM capacity for familiar (famous) faces was significantly higher than capacity for unfamiliar faces in conditions of low and high verbal WM load. When robust visual representations exist in LTM for a face, this can enhance storage of that face in WM.

In summary, attention is a limited capacity resource that can be captured by bottom-up stimulus features or deployed using top-down guidance. When attention is divided between the processing of two (or more) visual inputs, the cost of this division often results in a deficit in processing the second item (an AB). Visual stimuli that we are familiar with through extensive experience tend to hold a competitive advantage over unfamiliar stimuli when competing for attention, especially familiar faces. Faces benefit from specialized neuroanatomical processing regions and we tend to create robust representations for numerous faces we see throughout our lives, making them ideal visual stimuli when investigating the interactions of familiarity and attention.

When we become familiar with a person, we learn their identity through many encounters with them either in person or vicariously (i.e., a celebrity). These encounters are rarely void of a context, which can be good or bad. For example, when meeting someone for the first time, them smiling and shaking your hand would result in a much different experience than shouting at you and slapping your face. When you remembered the encounter later on, you would probably have different associations and feelings about them depending on the type of encounter you experienced. Thus, familiarity with a visual item is not just whether you know it or not. Instead, it encompasses the good and/or bad experiences you have learned to associate with that item. This can be expressed in terms of reward and punishment, both incorporated into a learned value. In the next chapter, I discuss how the learned value associated with a visual stimulus is processed and might affect the subsequent visual processing of that stimulus.

CHAPTER 3

DECISION MAKING AND VALUE LEARNING: EXPERIMENT 1

In addition to having limited cognitive resources, our physical resources are also limited. We plan our actions in life in attempt to optimize our investments of time and energy. At a basic level, we have to seek out the essentials for our survival (e.g., food). As humans, we are also motivated to control non-vegetative behaviors to ensure our well being, above and beyond merely surviving. Primarily, in order to service our desires and needs, our ultimate behavioral goals are to seek out rewards and to avoid punishments (Cohen & Blum, 2002). In this chapter, I will discuss how we learn to associate our actions with their outcomes in terms of instrumental conditioning, and how these outcomes of reward and punishment and the expected value of subsequent actions are coded in the brain. I will then discuss some studies that attempt to study motivation and attention. Finally, I will present the learning paradigm through which I was able to establish stable value codes for visual stimuli in order to then investigate how these value-laden stimuli affect perception and attention in a variety of cognitive tasks.

Rewards, punishments, and instrumental conditioning

Rewards for animals are principally vegetative in nature: food, liquid, and sex. Only the first two of these are commonly used as controlled rewards in a laboratory setting, the third being impossible to deliver in situations requiring hundreds of daily trials. Primary rewards are essential for humans as well, but we also seek to obtain a wide variety of non-vegetative rewards, such as money, beauty, and power. A key function of non-vegetative rewards is to induce subjective feelings of pleasure and positive emotion (Schultz, 2006). Rewards function as positive reinforcers: we learn to increase the frequency of a behavior that results in a reward in order to more frequently obtain the reward (Law of Effect; Thorndike, 1911). In contrast, punishers decrease the frequency of behavior that results in the punishment in attempt to avoid the aversive outcome of that behavior. We also learn to increase the frequency of behaviors that help us avoid aversive outcomes, which function as negative reinforcement (Skinner, 1939). Our ability to direct our actions according to specific goals and control our environment in pursuit of these goals is essential for adaptive behavior.

As previously mentioned, humans are motivated to seek both primary and higher order rewards. We learn the behaviors that are necessary for achieving these rewards, and we learn to avoid the behaviors that prevent us from acquiring desired rewards or that result in punishment. We learn to associate our behaviors with the outcomes they produce (rewards and punishments), and the contingencies necessary to produce the outcome, through a process called instrumental (or operant) conditioning (Skinner, 1939; Thorndike, 1911). Unlike Pavlovian (classical) conditioning where no action is required to learn a stimulus-response association, the key aspect of instrumental conditioning is that it requires the execution of a behavioral response. Without a response, there is no outcome; thus, no reward. When we learn the contingencies between responses and outcomes, we can alter our behavior and control our environment such that we maximize rewarding outcomes.

Instrumental conditioning occurs as a result of three factors: contiguity, contingency, and prediction error (Schultz, 2006). Contiguity is the need for near simultaneous occurrence of an action and an outcome. When observing an action-outcome relationship, the outcome needs to occur within a few seconds of response in order for the casual connection to be learned (Siegler & Liebert, 1974; Shanks, Pearson, & Dickinson, 1989). Contingency refers to the need for an outcome to occur more frequently in the presence of a response (or stimulus) compared with no response in order to become a predictor of that outcome. Finally, conditioning occurs only when an outcome is unpredicted. When an outcome is fully predicted, any action or stimulus paired with it will fail to become associated with that outcome because it is predicted to occur regardless of the presence or absence of the action/stimulus – no new learning occurs. Stated in terms of a *reward* prediction error, if an unpredicted reward occurs after an action, then the prediction error is positive and we learn a relationship between the action and the reward. Once the relationship is learned, such that the reward is predicted to follow subsequent repetitions of that action, the prediction error goes back to zero and no new information about the relationship is learned. If the expected reward is not received after a subsequent repetition of the action, then the prediction error becomes negative and leads to extinction of the behavior. In other words, behavior changes when an outcome of an action is different from that predicted to ensure more accurate future expectations, and behavior stays the same when the outcome is as predicted. Prediction errors are thought to play a crucial role during learning (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Schultz, 2000, 2006; Sutton & Barto, 1998).

Dickinson and Balleine (1994) state that behavior can be goal-directed (in search of reward) if it meets two conditions: 1) the instrumental contingency between the response and the outcome is known, and 2) the outcome is represented as a current goal. In other words, a reward can become a goal if it is relevant to a current motivational state and if its contingent relationship to a response is already known. A rat presses a lever for food because it is hungry and it has learned that lever pressing results in food. When the food is paired with taste aversion (e.g., injecting the food with lithium chloride), the food is no longer a valued goal and the rat is no longer motivated to continue its lever pressing behavior (Adams & Dickinson, 1981; Colwill

& Rescorla, 1985). The same decrement in behavior can occur with satiation. Thus, rewards do not always have an absolute value and instead can be dependent on current motivational states (Dickinson & Balleine, 1994).

Reward value following instrumental performance is not always automatically updated, however, and is often dependent on another direct experience with the reward after a change in motivational state. For example, the "resistance to satiation" phenomenon occurs when an action-reward contingency is learned in a deprived state (e.g., reward = food, state = hunger) and the reward is not immediately devalued during a subsequent sated state. A hungry rat trained to respond for food will continue to respond like a hungry rat after satiation until it directly experiences the reduced value of food in this new motivational state (Balleine, 1992). Dickinson and Balleine (1994) refer to this as incentive learning, where we learn the changes in incentive or subjective value of an outcome as a result of motivational shifts only after we re-experience the outcome in the altered state.

Expected value

In addition to variations in motivational valence, outcomes can vary in other aspects including delay in occurrence, magnitude, and predictability. Rewards that occur immediately can hold a different value than those that are delayed. For instance, receiving an immediate reward of $5 after an action is a greater incentive than receiving the $5 a year after producing the action (a phenomenon called temporal discounting, Kirby & Herrnstein, 1995). Magnitude refers to the amount or intensity of the reward or punishment received, and the probability of occurrence of a specific reward or punishment after an action is called its predictability. The myriad different rewards we encounter, with varying magnitudes and probabilities, are so diverse that there is no natural way to compare them. In order to make choices among them, we must compare them using a common scale, or "currency," which allows the comparison of diverse options with diverse outcomes (Montague & Berns, 2002; Padoa-Schioppa & Assad, 2006).

The neuroeconomic approach to the problem of common neural currency for rewards is the convention of expected value (EV; von Neumann & Morgenstern, 1944). First discussed by Blaise Pascal around 1650 (see Glimcher, 2003, for details), EV is the result of considering both the potential outcome of different actions and the probability that the desired outcomes will occur (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Schultz, 2006). In mathematical terms, EV is the product of the reward magnitude (value) and the reward probability. Evidence suggests that people's actions do not always maximize EV and therefore decision-making using EV does not follow a linear function (Bernoulli, 1738; Kahneman & Tversky, 1979, 1984). Instead, the value function is concave for gains and convex for losses with less weight placed on high probability outcomes and more weight placed on low probability outcomes (see Figure 6). Also, the function is generally steeper for losses than for gains, with a more extreme response to losses than to equivalent gains (called loss aversion, e.g. more displeasure losing an amount than winning the same amount; Tversky & Kahneman, 1981, 1991).

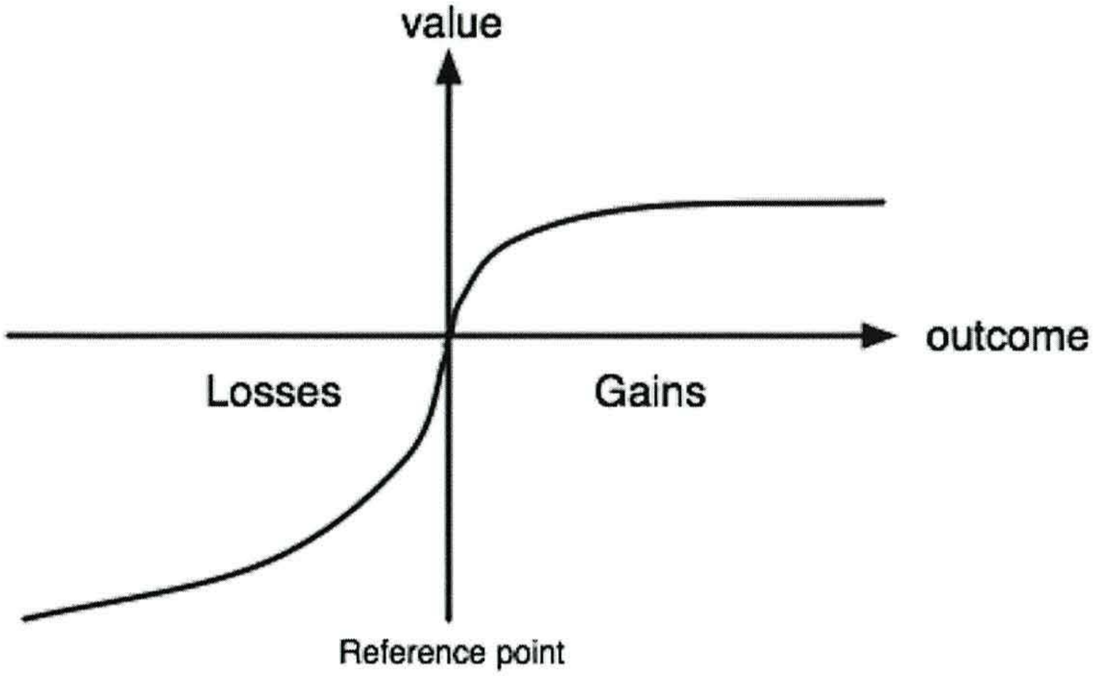

Figure 6. A hypothetical value function, according to prospect theory (Kahneman & Tversky, 1979).

Neuroanatomy of valuation

The common currency needed for making decisions about diverse outcomes can be translated into common neural circuitry for diverse rewards and punishments (although not the same circuitry for both, see below). The acquisition, updating, and use of these neural codes relies on a complex neural network, involving prefrontal cortical areas, especially the orbitofrontal cortex (Gottfried, O'Doherty, & Dolan, 2003; Ongur & Price, 2000; Rolls, 2000), the ventral striatum, including the nucleus accumbens (Knutson et al., 2001), the amygdala (Gottfried et al., 2003; Kahn et al., 2002; Paton, Belova, Morrison, & Salzman, 2006), and the anterior insula (Kuhnen & Knutson, 2005; Paulus, Rogalsky, & Simmons, 2003). Initially, the stimulus-outcome value is coded; the outcome is then subsequently predicted the next time the stimulus is encountered.

Evidence suggests that the networks coding value and subsequent prediction are different for rewards and punishments. When an unexpected reward is initially received, the mesocortico-limbic dopamine system is activated, with projections from neurons in the ventral tegmental area (VTA) in the midbrain to a number of regions including the dorsal striatum, nucleus accumbens (NAcc), OFC, hippocampus, amygdala, and hypothalamus (Schultz, 1998; see Hyman, Malenka, & Nestler, 2006; Ressler, 2004, for reviews). These areas are thought to mark the motivational significance and magnitude of the reward (Hyman et al., 2006). For example, the hippocampus may integrate the reward with stored contextual information relating to the stimulus that generated it, and the amygdala may help to integrate the reward with emotion information (Ressler, 2004) as well as help determine the magnitude of the reward (Pratt & Mizumori, 1998).

The OFC encodes current relative outcome value and magnitude (Gottfried et al., 2003; Knutson, Fong, Bennett, Adams, & Hommer, 2003; O'Doherty, Kringelbach, et al., 2001; Rogers et al., 1999; Rolls, 2000; Tremblay & Schultz, 1999) as well as unexpected breaches in expectation (Nobre, Coull, Frith, & Mesulam, 1999), and can flexibly adjust and reverse responses rapidly according to changes in stimulus-outcome contingencies (Rolls et al., 1996b; Thorpe, Rolls, & Maddison, 1983). The OFC maintains representations of both primary and conditioned rewards from all sensory modalities (see Rolls, 2004, for review). As discussed in Chapter 1, the OFC receives visual input to many of its neurons, and it has been suggested that these neurons represent the reward association of visual stimuli (Rolls, 2004). The OFC appears to have a major role in maintaining active representations of stimuli predictive of reward and punishment at any given time. Through its extensive reciprocal connections with sensory, motor, and limbic systems including amygdala, dorsal striatum, NAcc, hypothalamus, and insula, the OFC is in an ideal position to integrate this motivational (reward/punishment) information with object representations held in WM and create reward-associated memories in LTM (see Chapter 2).

The medial OFC appears to be involved in the representation of positive outcome values while the lateral OFC represents negative outcome values (e.g., Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; O'Doherty et al., 2001; Rolls, Kringelbach, & De Araujo, 2003). For example, O'Doherty and colleagues showed that activity in medial OFC correlates with monetary gain and activity in the lateral OFC correlates with monetary loss (O'Doherty et al., 2001). In addition to the OFC, punishment also activates the ventral striatum (Becerra, Breiter, Wise, Gonzalez, & Borsook, 2001; Jensen, McIntosh, Crawley, Mikulis, Remington, & Kapur; 2003; Seymour et al., 2004), dorsal ACC (Bush et al., 2002; O'Doherty, Critchley, Deichmann, and Dolan, 2003), and the amygdala (as loss-related EV, Yacubian, Gläscher, Schroeder, Sommer, Braus, & Büchel, 2006; as fear, Phelps, O'Connor, Gatenby, Gore, Grillon, & Davis, 2001; see LeDoux, 2002). In contrast to rewards, only a few dopamine neurons show activation when punishers are presented (Mirenowicz & Schultz, 1996).

Once the stimulus-reward relationship is well learned, we are then able to predict the reward for subsequent occurrences of the stimulus and modify our behavior accordingly. Neuroimaging studies have shown activation in the NAcc, OFC, amygdala, and anterior cingulate cortex (ACC) during reward anticipation (e.g., Gottfried, O'Doherty, & Dolan, 2002; Knutson et al., 2001a, 2001b; O'Doherty, Deichmann, Critchley, & Dolan, 2002; Tremblay & Schultz, 1999). For example, Knutson and colleagues (Knutson et al., 2001a, 2001b; Kuhnen & Knutson, 2005; see also Breiter et al., 2001; Galvan, Hare, Davidson, Spicer, Glover, & Casey, 2005) demonstrated that NAcc activation is proportional to the magnitude of an anticipated monetary reward. The NAcc is also activated during risk-taking behavior in which a reward is expected but not received (Kuhnen & Knutson, 2005). In contrast, the anterior insula is activated during expectation of punishment and loss (Buchel, Morris, Dolan, & Friston, 1998; Elliott, Dolan, & Frith, 2000b; Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003; Seymour et al., 2004), including monetary loss both real (Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006) and predicted (Kuhnen & Knutson, 2005).

A crucial feature of dopamine neurons is their sensitivity to the unpredictability of rewards (see Schultz, 1998, for review). When a reward is first encountered, it is by nature unpredicted, and dopamine neurons are activated in response. When learning is underway, dopamine neurons begin to be responsive to the earliest reliable predictor of the reward rather than the reward itself (Schultz, Dayan, & Montague, 1997). After the stimulus-reward association is learned and the reward is now well-predicted, dopamine neurons no longer fire when the reward is re-encountered (Mirenowicz & Schultz, 1994). Instead, dopamine neurons react to unpredicted rewards and changes in predicted rewards. When a reward occurs unexpectedly, or better than expected, then dopamine neurons respond positively (activation; Mirenowicz & Schultz, 1994). When a reward is expected, but it does not occur or is less than predicted, then dopamine neurons respond negatively (depression of activation; Hollerman & Schultz, 1998). Thus, dopamine neurons are thought to encode the reward prediction error (as discussed earlier; Schultz et al., 1997; Schultz, 1998), acting as a teaching signal to guide behavior for maximizing reward (Pessiglione et al., 2006). Given dopamine's major role in the formation of WM

(Aalto, Brück, Laine, Någren, & Rinne, 2005; Fried et al., 2001; Goldman-Rakic, 1996; Muller, Cramon, & Pollmann, 1998; Williams & Goldman-Rakic, 1995) and LTM (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Knecht et al., 2004; Schott et al., 2004; Wittmann, Schott, Guderian, Frey, Heinze, & Düzel, 2005), it is an ideal candidate to assist the OFC in memory maintenance for goal-directed behavior.

Dopamine neurons are activated by an unexpected change in reward contingencies. They send signals to the OFC, which responds to reward value, magnitude, and probability (i.e., EV; Hollerman, Tremblay, & Schultz, 2000; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Rolls, McCabe, & Redoute, 2008; Tremblay and Schultz, 1999). The OFC and dopamine neurons, along with the amygdala, update WM with current task representations. The OFC and amygdala send dense reward projections to the NAcc (Haber, Kunishio, Mizobuchi, & Lynd-Balta, 1995; Shultz et al., 2000), and dopamine gates these inputs such that the strongest inputs are enhanced and prioritized and the weaker (task-irrelevant) signals become ineffective (see Horvitz, 2002; Schultz, 2006; for reviews). Reward prediction errors are encoded in the NAcc for gain-related EV (Abler, Walter, Erk, Kammerer, & Spitzer, 2006; O'Doherty et al., 2003; Rolls et al., 2008; Seymour et al., 2004; Yacubian et al., 2006), as well as in the midbrain (O'Doherty et al., 2006; Rolls et al., 2008) and ACC (Amiez, Joseph, & Procyk, 2005; Holroyd and Coles, 2002; Matsumoto, Matsumoto, Abe, & Tanaka, 2007), and in the amygdala for loss-related EV prediction errors (Yacubian et al., 2006).

Thus, dopamine response to reward prediction is thought to be a bottom-up detection signal that rapidly informs these structures about surprising or omitted rewards, enhancing and focusing processing of these inputs over others (Schultz, 2002). Additional reward processing mechanisms in the OFC, amygdala, and NAcc act in a top-down fashion to discriminate and evaluate rewards, anticipate future rewards, make decisions about which rewards to pursue, and initiate goal-directed behaviors.

Interaction of motivation with perception and attention

Although numerous recent studies have addressed how value prediction codes are acquired, we know little about how these codes are subsequently used to aid and control simple decision processes, especially during demanding cognitive conditions. For example, surprisingly little is known about how value prediction (another way of referring to motivation) might affect simple perceptual decisions, such as judging whether a visual object is novel or familiar. Similarly, few studies have asked whether value prediction codes might modulate the effectiveness of attentional processes used to select a stimulus for higher level processing. In the few studies that have investigated the interactions of reward and attention, they have not modulated EV and no actual learning takes place.

Using a negative priming task, Della Libera and Chelazzi (2006) demonstrated that visual selective attention to a target can be modulated by the value of a monetary outcome associated with it. In two experiments, observers were shown a visual display (called the "prime") containing a pre-defined target and a distractor for which they had to identify the target and ignore the distractor. Correct responses were then followed by a reward, which could be high or low (1 cent or 10 cents). This amount was said (to the observers) to be based on performance level (a combination of speed and accuracy), but it was actually pre-determined such that high and low rewards occurred with the same probability (50%) balanced across conditions. After being rewarded (correct trials only), observers responded to a "probe" display, in which the target could be from three possible conditions: a) attended repetition, in which the probe target was previously the prime target; b) ignored repetition, in which the probe target was previously the prime distractor; or c) control, in which the probe target was not previously seen in the prime display.

In the control condition, the amount of reward had no effect on subsequent probe RTs or accuracy. When the probe and the prime targets were the same (attended repetition), positive priming (faster RTs compared to control RTs) occurred but this effect was unaffected by reward value (Experiment 1). Interestingly, when the probe target was a previously ignored prime distractor (ignored repetition), negative priming (increased RTs compared to control RTs) was dependent on the reward amount received in between prime and probe. When the reward amount was high, a large negative priming effect was found in both experiments. When the reward amount was low, response to the probe target was actually faster than in the control condition, in a positive priming-like way (Experiment 1; RTs were not different from control RTs in Experiment 2). Selective attention was thus enhanced by reward value such that greater rewards produced larger negative priming effects. The authors suggest that when a response was poorly rewarded, inhibition applied to the distractor was quickly lifted in an attempt to "reset" the attentive system after feedback indicating unsuccessful performance. As the EV of each stimulus was not actually being learned throughout the experiment, however, these results can be explained by a modulation of the prediction error after each correct probe response.

In a similar vein, Small and colleagues (Small, Gitelman, Simmons, Bloise, Parrish, & Mesulam (2005) used monetary rewards and punishments as motivational incentives to direct visual spatial attention in a target detection task. Observers were able to win money or avoid losing money (trials blocked by condition) by responding to a visual target faster than a specified cut-off time (determined by mean RT during a control condition). The target location was indicated by a directional cue that was valid on 80% of trials. Overall, observers responded faster to targets when there was a monetary incentive compared to no incentive. On valid trials, there was a modest trend toward faster RTs in the win condition compared to the no-outcome (neutral) control condition. On invalid trials, RTs were faster when money could be lost compared to the no-outcome condition. These behavioral results were coupled with increased fMRI activity in the OFC when money could be won and increased activity in the dorsal ACC and insula when money could be lost. Expectation of reward or punishment acted as a top-down motivational incentive to enhance spatial attention; however, heightened arousal can also explain this result.

Research on how emotional content in stimuli affects attentional processes indirectly addresses the issue of value prediction code influence, although these studies make *a priori* assumptions about the value of emotional stimuli (e.g., photos of expressive faces or dramatic scenes). They generally show that threat-related stimuli (e.g., angry or fearful faces) appear to capture attention to a greater extent than emotionally neutral or positive stimuli (Fox et al., 2006; Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004; Öhman, Flykt, & Esteves, 2001; Vuilleumier & Schwartz, 2001b), although other studies indicate that arousal may be the determining factor (Anderson, 2005; Arnell, Killman, & Fijavz, 2007). In a related vein, studies of attentional selection when interfering stimuli are present show that in addicts task-irrelevant words and images related to the object of addiction preferentially gain access to conscious awareness compared to control items (Hogarth, Mogg, Bradley, Duka, & Dickinson, 2003), suggesting that items with positive motivational or predicted value (and probably high arousal) may require little attentional resource for selection.

Animal learning theorists (e.g., Hall, 2003; Mackintosh, 1975) have long held that stimuli that are highly predictive of outcomes (i.e., are motivationally salient) should gain more attention than those less predictive, regardless of valence; but these ideas have not been tested on humans using conventional measures of visual selection and attention. In fact, most visual attention studies (on animals and humans) confound motivation and attention (see Maunsell, 2004, for a review). Humans devote more attention to stimuli that are more likely to be associated with reward and behavioral performance (RTs and detection thresholds) tends to be superior for attended stimuli (Posner, 1980) and for stimuli associated with larger rewards (e.g., Kawagoe, Takikawa, & Hikosaka, 1998; Ramnani & Miall, 2003).

In this thesis, the main aim was to investigate how previously established value prediction codes for specific stimuli influence subsequent top-down visual selection processes. In each experiment, participants first learned to associate monetary reward or punishment outcomes of different probabilities (high and low) with visual stimuli (Experiment 1). Then, participants interacted with these value-laden stimuli as targets (Experiments 2-8), or distractors (Experiment 9-11) in temporal and spatial visual discrimination tasks. The first half of the thesis is focused on temporal tasks (Experiments 2-6), including the AB and backward masking, using RSVP. In these experiments, value-laden information was task relevant (except in Experiment 5) and results show influence of learned value on attentional resource allocation and perceptual processing. The second half of the thesis is focused on spatial visual search tasks (Experiments 7-11). Here I was interested in how value-laden stimuli effect processing when value information is orthogonal to the task.

Similar to the temporal discrimination tasks, results from the visual search tasks show effects of value learning on attention capture and target recognition.

In the remainder of this chapter, I will describe the general learning methods employed throughout the thesis experiments, followed by the specific details of the learning phase of Experiment 1. The main goal in the learning task was for the participants in each experiment to learn the correct valence and probability outcomes associated with each stimulus above a chance level of performance. Across 11 experiments, participants' ability to choose the optimal stimuli in order to maximize winnings and minimize losses was at 80% (SE = 2%) and 71% (SE = 1%) respectively. Stimuli in no outcome pairs were chosen at an equal probability (50%, SE = 1%).

General Learning Methods

Participants

Participants were recruited from the Bangor University Student and Community Subject Panels and participated in exchange for course credits and money. All were Caucasian adults who reported normal or corrected to normal vision and were naïve to the purpose of their experiment. Informed consent was obtained prior to participation.

Apparatus

A Pentium-4 computer, running E-prime 1.0 (Schneider, Eshman, & Zuccolotto, 2002), recorded data and presented stimuli on a 51 cm monitor (85 Hz refresh; 1024x768 resolution) at a viewing distance of 70 cm. Responses were recorded via the computer keyboard. Testing was conducted in a small, dimly lit room.

Stimuli

Stimuli used in all learning experiments were static, grayscale faces of young adults (hair, teeth, and neck not visible), subtending approximately 2.9° x 3.6°.

Design & Procedure

On each trial, two faces were presented above and below a central fixation cross (Figure 7). After choosing a face (by pressing one of two designated keys), the screen immediately displayed "WIN" in green (plus "bing" sound), "LOSS" in red (plus "bong" sound), or "NOTHING" in black (no sound), depending on the face pair just presented and the probability governing outcome. A running total of earnings also appeared. Each face always appeared with its mate but location was randomized from trial to trial. Wins and losses were always 5 pence occurring with a probability of .8 or .2; no outcome was the default. Each pair (two for wins, two for losses, and two without any monetary outcome) was presented 100 times in a self-paced, random order. Assignment of each face pair to outcome pair type (win/loss/nothing) was counter-balanced across participants to eliminate image effects. Participants were instructed merely to choose the face in each trial that would maximize payoff, which they could keep as winnings at the end of participation. Speeded response was not emphasized. Instead, participants were encouraged to study each face for as long as they wanted to throughout the experiment and attempt to learn each individual identity as early on as possible. All participants left with the same fixed amount (£5), which was higher than the total possible winnings.

Data Analysis

Learning was assessed by calculating (for each participant and face pair) the probability of optimal choice (high-probability gain faces and low-probability loss faces) within 10-trial bins. Final learning level was defined as the average probability for the last three bins. A repeated measures ANOVA on probabilities using these bins and valence (win/loss) as factors was used to compare win versus loss learning. Paired-sample, 2-tailed *t*-tests were used to compare means. Alpha levels were set at .05.

Experiment 1: Value learning choice game[1]

In each trial of the choice game, participants selected one face from a pair in an effort to maximize winnings (Figure 7). For some face pairs, choice sometimes resulted in a win or no outcome; for others pairs, choice sometimes led to a loss or no outcome; and for a third pair type (controls), monetary outcomes were never forthcoming, regardless of choice. For win and loss pairs, one face produced a monetary outcome with a probability of 0.80 and its mate with a probability of 0.20. These response contingencies produced value prediction codes for each face that varied in valence (predicting wins versus losses) and motivational salience (probability of 0.8, 0.2, or 0). To concisely express this in economic terms, I use the convention of EV, using positive and negative to refer to win and loss, respectively. The learning procedure thus yielded five different nominal EVs: $-0.8x$, $-0.2x$, 0, $0.2x$, and $0.8x$ where x is the cash value involved. Choice was forced between pairs of faces

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[1] The majority of this thesis write-up for Experiments 1 & 2 originates from Raymond & O'Brien (in press), but I have expanded some sections for further clarity.

with the same valence so that I could efficiently imbue different levels of motivational salience for both loss and gain stimuli.

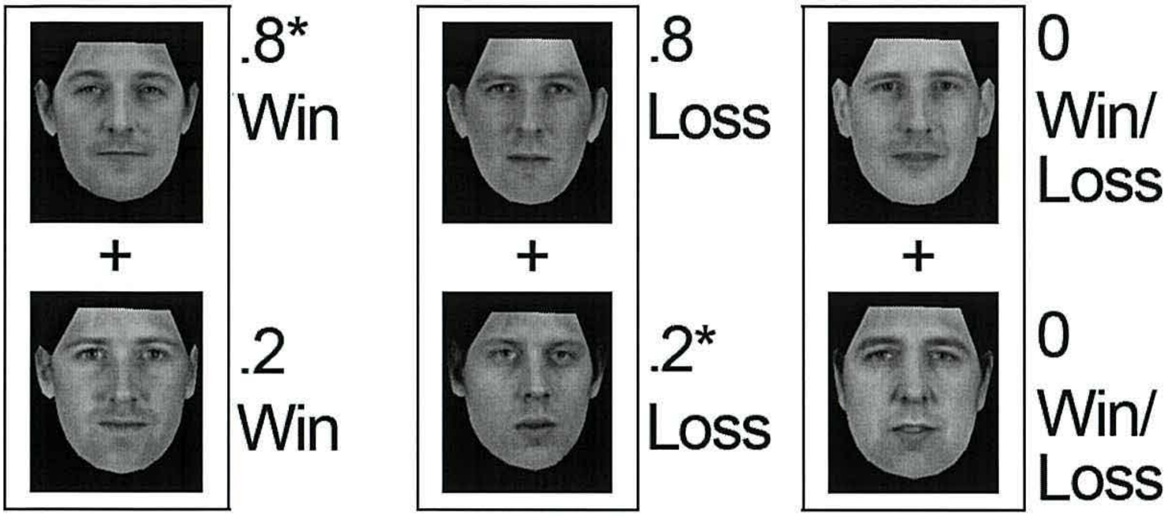

Figure 7. An example of win, loss, and no-outcome face pairs presented in the choice game. Probability of outcome for each choice is shown, with optimal choice indicated by an asterisk (not seen by participants). Vertical location of the optimal face was randomized on successive trials. Different outcome probabilities were assigned to different faces for different participants.

Methods

Participants

Twenty-four healthy young adults (15 females; mean age 19 years) participated in exchange for £5 and course credit. All achieved at least a minimal level of learning (significantly better than chance) in the choice game for both win and loss pairs.

Stimuli

Face stimuli were static grayscale, computer-generated (GenHead 1.2; Genemation, Inc.) faces of young adult males (hair, teeth, and neck not visible); subtending approximately 2.9° x 3.6° with minor deviations (max. .4°), and shown in frontal view. Faces were generated from a base face with a randomness setting of 7, an age setting of 30's - 50's, a male gender setting of 1.25 (extreme), an ethnicity setting of Caucasian, and facial expression weights set to zero.

Results & Discussion

At the end of the learning session, (i.e., after 100 randomly ordered trials for each of six face pairs) performance approached asymptote (Figure 8) and learning approximated the outcome contingencies similarly for win and loss pairs ($F(1,23) = 2.45$, $p = .131$). For win pairs, the high-probability win face ($EV = 0.8x$) was chosen on average on 74% (SE = 3%) of trials; for loss pairs, the low-probability loss face ($EV = -0.2x$) was chosen on 67% (SE = 2%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 49% of trials (SE = 5%).

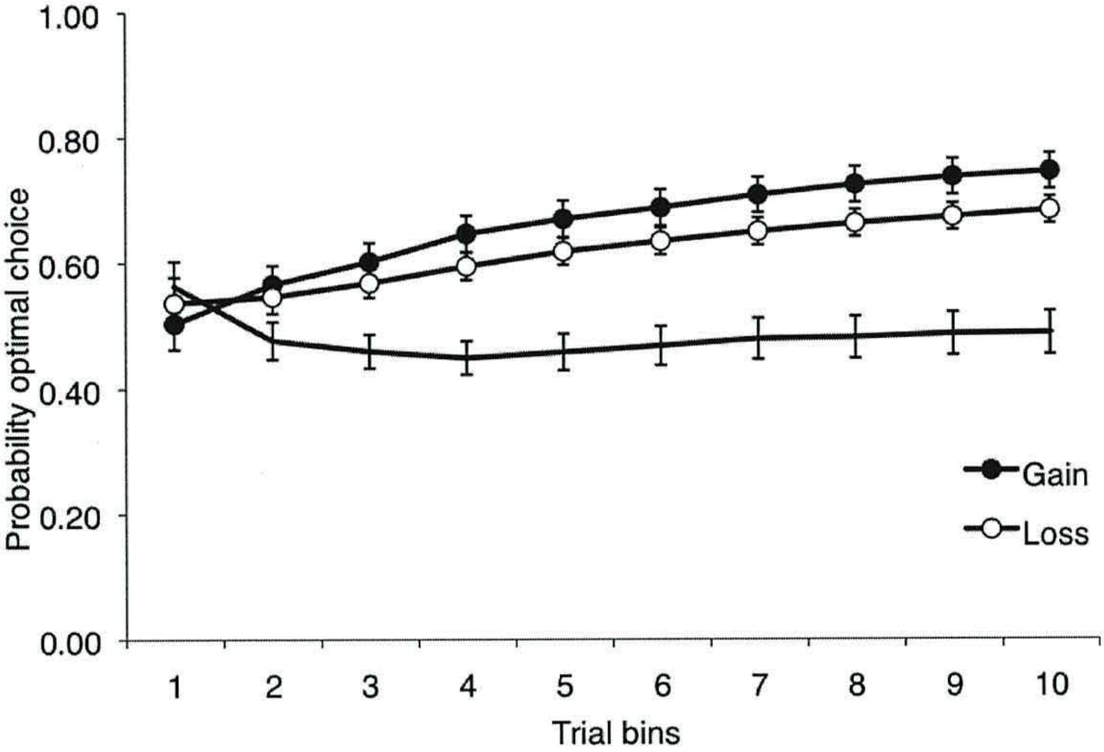

Figure 8. Average probability of choosing the optimal face for each 10-trial bin for win (closed circles) and loss (open circles), and no-outcome (dashed line) pairs. Error bars are +/- 1 SE.

Participants were encouraged to spend as much time as needed studying each pair choice, and the average time spent doing so differed by pair type. Less time was spent viewing gain face pairs (M = 1391 ms, SD = 89 ms) than loss (M = 1614 ms, SD = 1000 ms) or neutral (M = 1557 ms, SD = 101 ms) face pairs), *p*'s < .002. Time spent viewing loss pairs was not significantly different from time spent viewing neutral pairs, *p* > .25.

In summary, participants were able to learn the value contingencies associated with the face stimuli well above chance performance. As can be seen in Figure 8, participants began choosing optimally (above chance) after 20 – 30 trials for gain and loss pairs. Gain pair EVs were learned as well as loss pair EVs, although time spent viewing the different pair types was significantly different.

There are three hypotheses as to which aspects of the value-laden faces learned in the choice game will be important in these temporal and spatial attention experiments: 1) Choice, 2) Predictability, or 3) Valence. First, stimuli associated with high probability gain and low probability loss outcomes are consistently chosen more often in the choice game in an attempt to maximize payoff. It is possible that the stimuli chosen most often will predict subsequent recognition and dominate attention when presented in different contexts. Second, it is possible that stimuli with highly reliable outcomes (predictability) will gain more attention than those less reliable, regardless of valence. Finally, it is possible that the expected valence of a stimulus will determine the attentional resources needed to process it. In each experiment, I will be highlighting the outcomes in regard to these three hypotheses.

In the next chapter, I present data investigating how learned EV codes can affect subsequent selective visual attention, WM, and visual perception. Results from these experiments support the hypotheses that generating positive and negative EVs uses different brain mechanisms and that motivation and attention are indeed separable.

SECTION 2

VALUE LEARNING AND RSVP: EFFECTS ON TEMPORAL VISUAL ATTENTION, MOTIVATION, AND PERCEPTION

CHAPTER 4

SELECTIVE VISUAL ATTENTION AND MOTIVATION: THE CONSEQUENCES OF VALUE LEARNING IN AN ATTENTIONAL BLINK TASK: EXPERIMENTS 2 & 3

The goals in these first two attention experiments were twofold. First, by measuring recognition performance with value-laden stimuli in an AB task (old/new), I wanted to see if value prediction codes are capable of modulating recognition decisions under varying attentional demands. Instead of visual decisions being determined by current attentional demands, it is possible that learned value codes lead to efficient processing during conditions of both full and limited attention. For example, we know that highly familiar faces escape the AB (Jackson & Raymond, 2006), but it is yet unknown whether this is due to their motivational salience or to a value attribute associated with each face. In demanding cognitive conditions such as during the AB, access to learned values might be constrained by limited attentional capacity. Knowing that gain and loss EVs are coded by different neural mechanisms, it is possible that constraints on attention might affect access to these learned values differently. Second, I wanted to replicate the Jackson and Raymond (2006) findings of an AB with faces to further support the idea that face processing does not rely on a special attentional mechanism and instead depend on the efficiency of the visual codes (acquired by experience) for each face.

Before describing Experiments 2 and 3, I first detail some general methods used in all the experiments in this section on temporal attention.

General RSVP Methods

Participants

Participants were recruited from the Bangor University Student and Community Subject Panels and participated in exchange for course credits and money. All were Caucasian adults who reported normal or corrected to normal vision and were naïve to the purpose of their experiment. Informed consent was obtained prior to participation.

Apparatus

A Pentium-4 computer, running E-prime 1.0 (Schneider, Eshman, & Zuccolotto, 2002), recorded data and presented stimuli on a 51 cm monitor (85 Hz refresh; 1024x768 resolution) at a viewing distance of 70 cm. Responses were recorded via the computer keyboard. Testing was conducted in a small, dimly lit room.

Stimuli

Stimuli used in all RSVP experiments were static, grayscale faces of young adults (hair, teeth, and neck not visible), subtending approximately 2.9° x 3.6°.

Experiment 2: Value-laden stimuli as T2 in the AB

(Raymond & O'Brien, in press)

The goal here was to systematically investigate how value prediction might modulate a simple visual perceptual decision (familiar or novel) when selective attention resources were more or less available. Based on the animal learning literature and the studies of attention with arousing stimuli (reviewed in Chapter 3), I predicted that stimuli highly predictive of outcome (wins or losses) might lead to enhanced recognition when attention was fully available for capture by these stimuli. However, based on reports of intrusive awareness of task-irrelevant but addiction-related (high value) items in addicts, I predicted that gain versus loss association should determine performance when attentional resources are limited.

This was accomplished using a two-phased approach: Participants first learned the valence and probability of possible outcomes from choosing faces in a conventional value learning session (Experiment 1). This enabled me to establish in each participant a set of stable value prediction codes for faces used subsequently as T2 in the attentional blink task. Moreover, this design allowed me to determine whether EV, valence, motivational salience, or repeatedly choosing the optimal stimulus (i.e., high probability gain and low probability loss stimuli) determined subsequent behavior in the AB task.

After participants acquired different predicted value codes for different faces in the value learning task, I measured recognition for these value-laden faces presented within an attentional blink (AB) task, which is a well-established procedure for modulating the availability of attention (Raymond, Shapiro, & Arnell, 1992). In an adaptation of this technique, participants viewed a rapid sequence of briefly presented images in which two targets, an abstract object (T1) and a face (T2), were imbedded (Figure 9). I incorporated a variant of the AB task in which the RSVP stream was abbreviated to contain only the T1 and T2 images and their masks, separated by a short or long blank SOA (known as a skeletal AB, cf. Ward, Duncan, & Shapiro, 1996).

Participants were required to discriminate the texture of T1, and then to decide whether T2 was a face seen in the prior value learning task (old) or not (new). Critically, the lag between successive target presentations was either short (285 ms; half of trials), creating a reduced-attention condition, or long (885 ms; remaining trials), making a full-attention condition, thus allowing manipulation the availability of cognitive resources at the time of face presentation. In stimulus sequences like this, short lags (less than 500 ms) between successive targets cause a large impairment in perceptual awareness of T2 that can be completely eradicated by extending the lag to longer than 500 ms (Chun & Potter, 1995; Jackson & Raymond, 2006; Raymond et al., 1992). This lag-dependent dip in awareness of T2 (AB) indexes temporal changes in the limited availability of attentional resources initiated by processing T1. Thus, varying the T1-T2 lag makes a tidy manipulation of available cognitive resource for T2, without concurrently changing demands on sensory or response systems (Raymond et al., 1992).

Method

Participants & Apparatus

Same as Experiment 1.

Stimuli

Face stimuli included the 12 value-laden faces used in Experiment 1 and an additional 24 similarly generated novel faces. Twenty different stimuli used as masks in the AB task were created by dividing a digital face image (not otherwise used) into a 5 by 4 grid and then rearranging the pieces in a non-face-like presentation, whilst preserving the outer shape of the face. A set of 20 computer-generated, grayscale, abstract, elliptical patterns (composed of either small circles or squares) matched in global size to the faces of the choice game were used as T1 stimuli.

Procedure

A few minutes after completing the choice game (Experiment 1), participation in the AB task began, starting with 24 practice trials. In each experimental trial, four elliptical stimuli (T1, mask, T2, mask; Figure 9), matched in size to the faces of the choice game, were presented (85 ms each) in rapid succession at the centre of the screen. The T1 image was equally likely to be composed of circles or squares but was otherwise randomly selected on each trial from a set of 20 possible images. The T2 face was selected on half the trials from the 12 value-laden faces used in the choice game and on remaining trials from 24 similarly generated novel faces. Face masks were randomly selected on each trial. After a 1000 ms central fixation cross, T1 and its mask were presented successively (with no interstimulus interval, ISI). A blank screen was then displayed for either 115 or 715 ms, followed by T2 and its mask (with no ISI), making the short lag (stimulus onset synchrony, SOA, between T1 and T2 = 285 ms) and long lag (T1-T2 SOA = 885 ms) conditions, respectively. At the end of the stimulus sequence, without time pressure, participants pressed one of two keys using the left hand to identify the T1 pattern as ‘circles’ or ‘squares’ and then pressed one of a different two keys using the right hand to report their recognition decision (old/ new) regarding the T2 face. Trials were self-paced; neither feedback nor monetary outcomes were provided. T1 type, lag, and T2 type (old/new) trial combinations were pseudo-randomly presented in a fully crossed design. Within this design, each value-laden face appeared as T2 ten times, randomized across trials. There were 480 trials, 20 for each lag and T2-EV combination (except for control faces, where there were 40 trials).

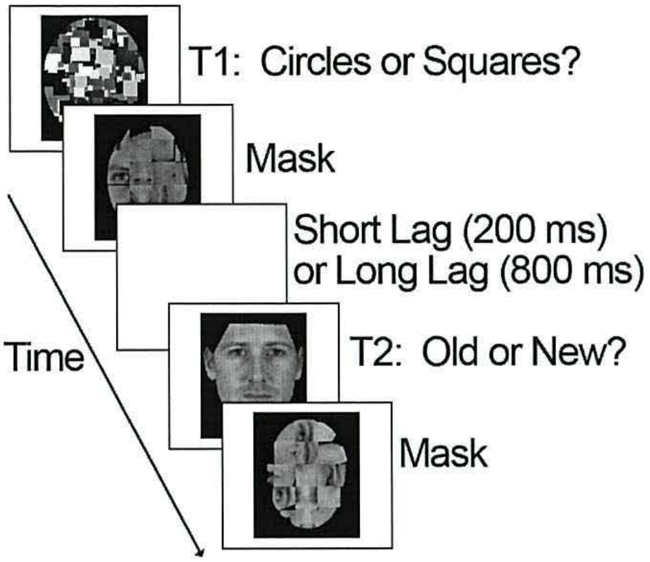

Figure 9. Stimuli and sequence of events in the AB task. Each stimulus was displayed for 85 ms. The first task was to judge whether the T1 stimulus was comprised of small circles or squares. The second task was to decide whether the T2 face was from the prior choice game (old) or not (new).

Data analysis

Recognition performance, conditional on correct T1 performance, was measured using *d*', calculated for each participant and condition as the difference in the *Z*-transformed probability of making a hit (reporting 'old' when the stimulus was 'old') and the *Z*-transformed probability of making a false alarm (reporting 'old' when the stimulus was 'new'). *d'* provides a criterion-free measure of recognition (Green & Swets, 1966); zero indicates chance performance and values greater than zero index recognition. Two ANOVAs of recognition performance for value-laden faces were conducted; the first used EV (-.8, -.2, 0, .2, .8) as a factor, and the second used valence (win/loss) and motivational salience (high/low) as factors (and excluded data for EV = 0). Additional corresponding ANOVAs using lag were also conducted. Paired-sample, 2-tailed *t*-tests were used to compare means. The presence of AB effects was determined by comparing short versus long lag *d'* values using *t*-tests (corrected for multiple comparisons). Pearson's correlation coefficient, *r*, was used to relate individual learning scores with short lag *d'* values. Alpha levels were set at .05. Within-subject SE was calculated using the methods of Cousineau (2005).

Results & Discussion

T1 Performance

Probability of a correct T1 response was modestly but significantly better for the long (M = .90, S.E. = .02) versus the short (M = .88, S.E. = .018) SOA condition ($F(1,23) = 9.22, p < .006$). However, performance was not affected by T2's EV ($F(5,23) = 1.08, p = .373$) and the effects of SOA and T2-EV did not interact significantly ($F(5,115) = 1.95, p = .150$).

T2 Performance

Two robust and interesting results were found in the T2 recognition data of the subsequent AB task (Figure 10). First, in the full-attention condition (long lag), T2 recognition strongly depended on EV ($F(3,63) = 9.09, p < .001$). When the data were re-analyzed for valence and motivational salience effects, recognition (*d'*) of 'old' faces was found to be more accurate for high probability win and loss faces regardless of valence than for low probability faces (mean hit rate = .57; $F(1,23) = 28.96, p < .001$). Moreover, these faces were also better recognized than faces never associated with a monetary outcome (mean hit rate = .50; $F(1,23) = 8.92, p < .01$) even though all had been seen the same number of times before. These results clearly show that prior value learning can modulate perceptual recognition decisions in a subsequent unrelated task. Interestingly, which face was chosen most often in the choice game did not predict subsequent recognition. In the choice game, low-probability loss faces were appropriately chosen more often than high-probability loss faces, yet the former were more poorly recognized than the latter in the long lag condition of the AB task

($t(23) = 2.97, p < .01$). Note also, recognition accuracy did not depend on valence ($F(1,23) = 2.214, p = .150$); recognition of high-probability win stimuli did not differ from that of high-probability loss stimuli ($t(23) = 1.17, p = .254$). These effects of value learning in the full-attention condition are especially interesting considering that all faces, regardless of their prior history, were equally task-relevant in the recognition task and as such should have engaged top-down attention similarly (Desimone & Duncan, 1995).

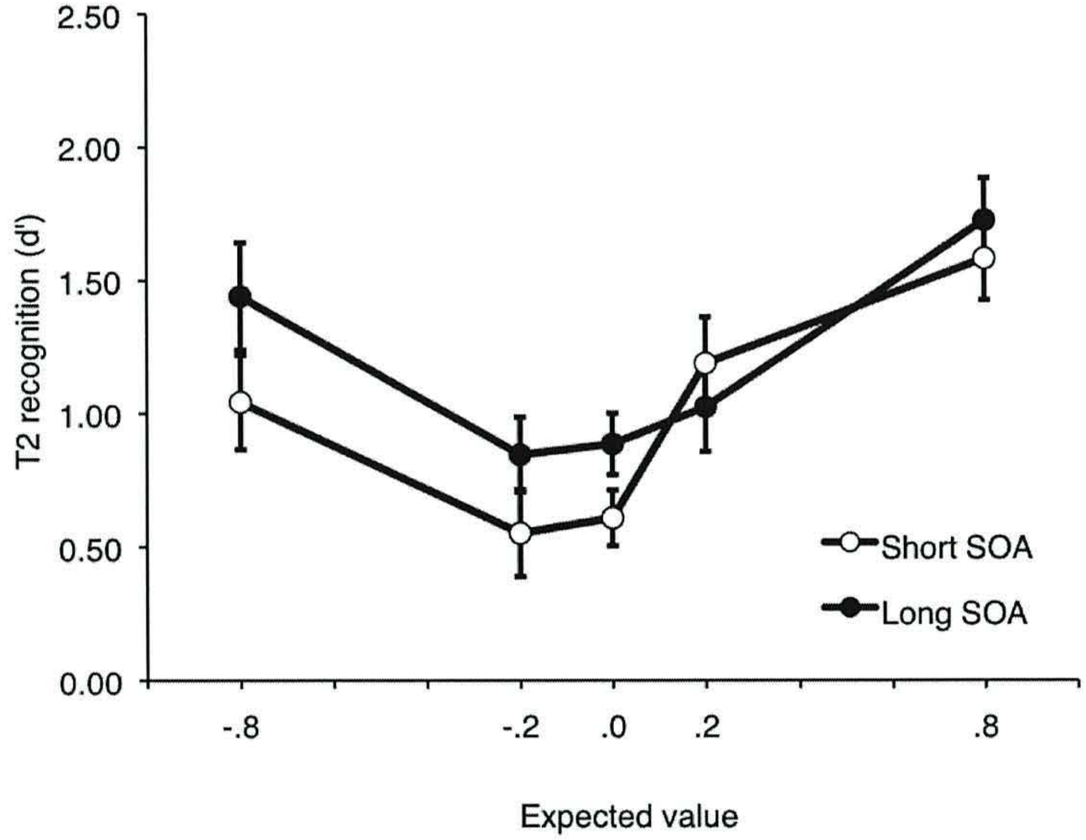

Figure 10. Mean recognition of T2 faces (*d'*) as a function of expected value of the T2 stimulus: closed circles for long T1-T2 interval and open circles for short T1-T2 interval. Error bars are within-subject SE.

A second and even more interesting result is evident when the cost of reducing attention (short versus long lag condition) on recognition is compared for win- versus loss-associated T2 stimuli. For faces associated with loss or no outcome, recognition became dramatically impaired in the short versus long lag condition ($p < 0.01$ in all cases), indicating a typical attentional blink effect (Raymond et al., 1992). In stark contrast, recognition of win-associated stimuli, regardless of their motivational salience, showed no cost of divided attention. A three-way ANOVA using lag, valence, and motivational salience as factors (excluding the control condition) showed significantly better recognition for win- versus loss-associated stimuli ($F(1,23) = 7.33, p < .05$) and a significant interaction of lag and valence ($F(1,23) = 18.72, p < .001$) that did not interact with motivational salience ($F(1,23) < 1$). In other words, the size of the attentional blink effect was determined solely by valence, being present for loss-associated stimuli and absent for win-associated stimuli. Note, however, even in the reduced-attention condition, monetary outcome probability modulated recognition performance for both win- and loss-associated stimuli ($F(1,23) = 17.04, p < .001$), indicating that codes for motivational salience facilitate recognition independently of attention. Our finding that the valence (win/loss) of prior value learning plays a role in subsequent stimulus recognition when attentional resources are scarce is supported by a significant correlation ($r = .43, p < .05$) between asymptotic win learning performance in the choice game and individual recognition scores for high-probability win stimuli in the short lag condition. The corresponding correlation between loss learning performance and recognition of high-probability loss stimuli was non-significant ($r = .08, p = .710$).

Experiment 3: Value-laden stimuli as T1 in the AB

(Raymond & O'Brien, in press)

In Experiment 3, I swapped T1 with T2 to determine whether the motivational significance of T1 stimuli might influence the AB. Previous studies using emotional words (Arnell, Killman & Fijavz, 2007; Huang, et al., 2008) and faces (Stein, Zwickel, Ritter, Kitzmantel, & Schneider, in press) as T1 stimuli have shown larger AB effects with emotional targets, suggesting that motivational significance might have a similar effect. To test this idea, I repeated Experiment 1, but switched the stimuli used as T1 and T2. T1 were the value-laden faces from the choice task and T2 stimuli were abstract patterns.

Methods

Participants

Seventeen different adults (13 females, mean age = 23 yrs) participated.

Procedure

The learning procedure was identical to that used in Experiment 1 and the AB procedure was also identical except that the stimulus sets for T1 and T2 were swapped. T1 required a recognition response (old/new) and T2 required a texture discrimination response (circles/squares).

Results & Discussion

Learning Task

As in Experiment 1, learning approximated the outcome contingencies similarly for win and loss pairs ($F(1,16) = 1.28$, $p = .276$). For win pairs, the high-probability win face (EV = $0.8x$) was chosen on average on 77% (SE = 4%) of trials; for loss pairs, the low-probability loss face (EV = $-0.2x$) was chosen on 71% (SE = 3%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 51% of trials (SE = 5%).

AB task

As can be seen in Figure 11, T1 recognition depended on the EV associated with each face ($F(3,44) = 3.98, p < .05$) in much the same way as did the T2 data for the long lag condition of Experiment 1. Recognition did not depend on lag ($F < 1$) and lag and EV did not significantly interact ($F < 1$). Recognition was more accurate for high probability win and loss faces, regardless of valence than for low probability faces ($F(1,16) = 5.56, p < .05$) or for faces never associated with a monetary outcome ($t(16) = 8.86, p < .0001$).

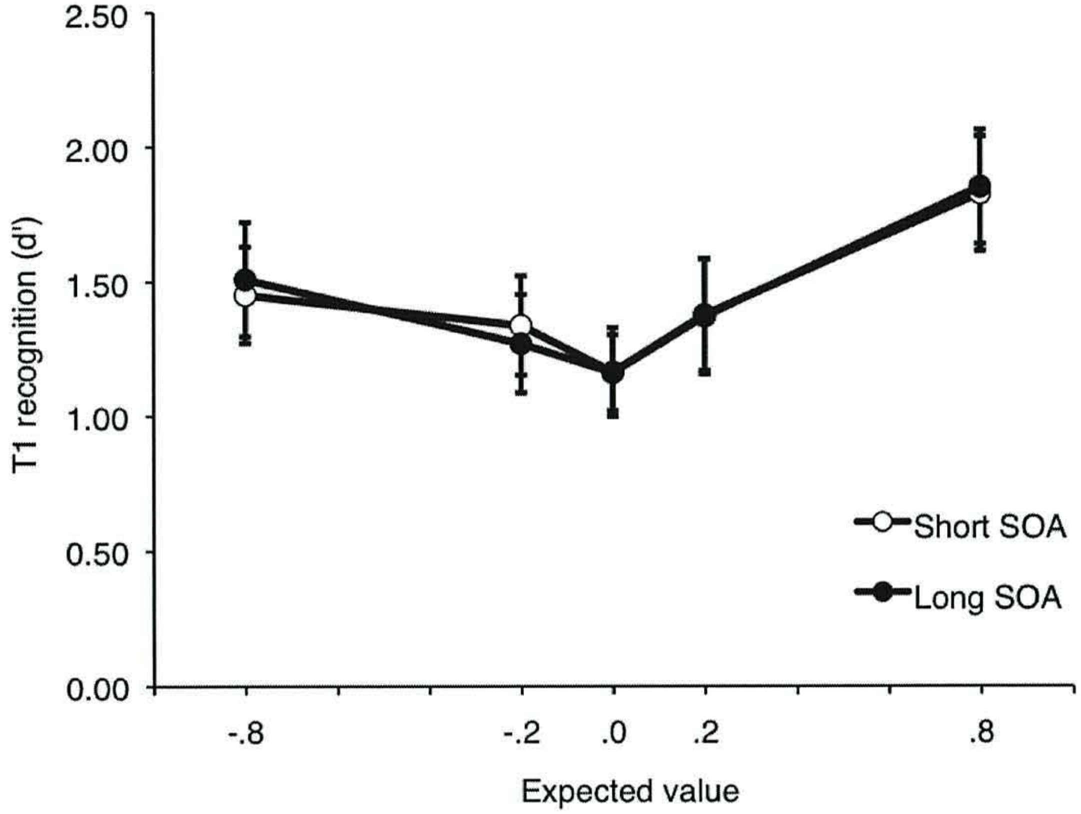

Figure 11. Mean recognition of T1 faces (d') as a function of expected value: closed circles for long T1-T2 interval and open circles for short T1-T2 interval. Error bars are within-subject SE.

Accuracy of discrimination for T2 stimuli was analyzed using a repeated measures ANOVA using T1-EV and lag as factors. As can be seen in Figure 12, T2 performance was unaffected by T1-EV ($F < 1$). The AB effect was obvious ($F(1,16) = 36.612, p < .0001$), but its magnitude was unaffected by T1's EV ($F < 1$). These results provide no support for the notion that gain-associated stimuli presented within a trial provide some generalized, albeit short-term, processing enhancement able to eliminate the AB (as seen in Experiment 1). If that were the case, then the AB should have been absent when gain-associated T1 stimuli were presented. The results indirectly indicate that EV did not modulate difficulty of the T1 task, at least not sufficiently to modulate the AB.

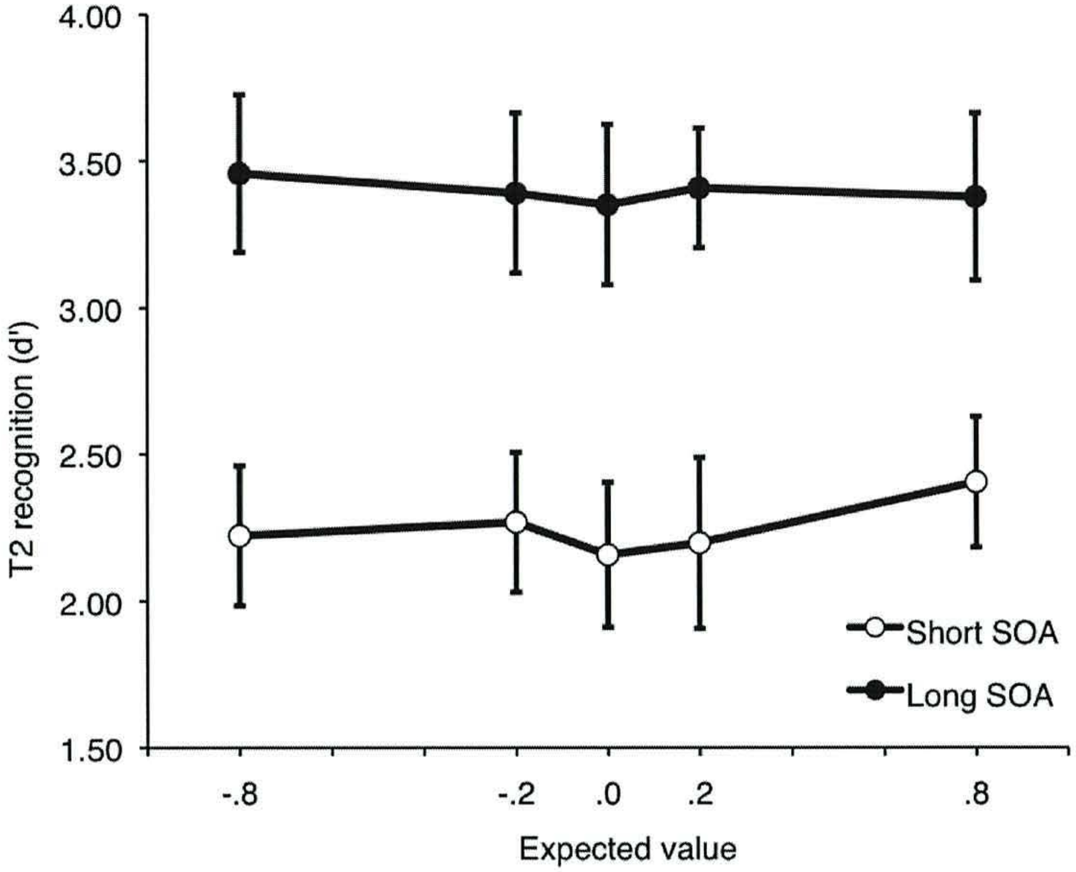

Figure 12. Mean identification of T2 shapes (d') as a function of expected value of the T1 stimulus: closed circles for long T1-T2 interval and open circles for short T1-T2 interval. Error bars are within-subject SE.

Chapter Discussion – Experiments 2 & 3

In two experiments I used a simple choice game to imbue novel face stimuli with different levels of expected value. Through this procedure, stimuli became associated with a high or low probability of a monetary win or loss (or certainty of no outcome). When these stimuli were then used within an attentional blink paradigm either as T2 (Experiment 1) or as T1 (Experiment 2), two interesting effects of acquired expected value on recognition performance were found. First, when attention was fully available (in the long lag condition of Experiment 1 and in both conditions of Experiment 2), recognition was significantly better for stimuli associated with a high probability of outcome (i.e., motivationally salient stimuli), regardless of the valence of that outcome. Second, when attentional resources were constrained (during the AB in Experiment 1), the same dependence on motivational salience was observed as when attention was unconstrained, but now large blink effects were observed for loss-associated and no-outcome stimuli but were completely absent for win-associated stimuli.

Finding that recognition varies with motivational salience, even when attention is unconstrained, is important because it shows that simple visual decisions are not determined solely by current attentional demands directed at available sensory data. Rather, value prediction information, specifically the probability of an outcome, appears to provide an additional 'top-down' signal that can facilitate processes necessary for recognition, such as perception or long-term memory. These interesting findings are supported by recent neurobiological studies indicating that value prediction can greatly determine activity in visual cortex in rats (Shuler & Bear, 2006) and in lateral intraparietal cortex in monkeys (Bendiksby & Platt, 2006). They are also consistent with recent studies indicating a neural mechanism in the basal forebrain of rats that is selectively activated by motivationally salient stimuli independently of their valence and is capable of affecting the activity of widespread cortical circuits (Lin & Nicolelis, 2008), akin to mechanisms thought to mediate top-down control in humans.

The second important finding, a valence effect of value learning on the AB in Experiment 1, is surprising because it is not readily predicted from the effect of motivation salience seen when attention is unconstrained. It is, however, consistent with neurobiological evidence that value coding for reward and punishment may be mediated by different neural networks (Kahn et al., 2002; Yacubian et al., 2006) and suggests that these may differentially interact with attentional networks. Without results from the reduced-attention (short lag) condition, findings from the full-attention condition (long lag) could be interpreted as indicating that motivational salience, in addition to current task relevance (Desimone & Duncan, 1995), determines how successfully a stimulus can compete for attentional resources. However, if this were the case, then in the harder, reduced attention condition, high-probability stimuli, regardless of valence, should have retained their competitive advantage and "escaped" the AB. Instead, there were large AB effects for high-probability loss stimuli and none for high-probability win stimuli. Clearly, association with gains but not losses enhances attentional competitiveness of stimuli, whereas outcome probability modulates other processes important for recognition, independently of attention. These findings thus supply dramatic evidence that attention and motivation provide separable, independent top-down signals for controlling perceptual awareness. The demonstration that reducing attention has differential effects on access to value codes has important implications for decision-making under cognitive stress. If, as reported here, reward-associated stimuli are more likely to be recognized than punishment-associated ones when attentional resources are scarce, then irrational biases in favor of prior rewarding experiences are likely to guide behavior under duress.

CHAPTER 5

THE EFFECT OF VALUE LEARNING ON PERCEPTION IN A BACKWARD MASKING TASK: EXPERIMENTS 4 & 5

The experiments in the previous chapter demonstrated that the value associated with a stimulus determines its ability to be recognized when it is the second of two targets under conditions of full attention and constrained attention. Regardless of available attention, recognition was substantially enhanced for motivationally salient stimuli (highly predictive of outcomes) regardless of valence (win or loss) compared to equally familiar stimuli with weak or no motivational salience. However, when attention was constrained (by presenting stimuli during an AB), valence determined recognition; only win-associated faces showed no AB, all other faces showed large ABs. Motivational salience acts independently of attention to modulate simple perceptual decisions but when attention is limited, visual processing is biased in favor of reward-associated stimuli.

In both Experiments 2 and 3, targets were presented for 85 ms and then masked. While recognition was enhanced for motivationally salient stimuli when full attention was available, recognition of all value-laden stimuli was well above chance. This suggests that under conditions of full attention enough visual information was accessible for recognition of all the stimuli at presentation duration of 85 ms. Subsequently, what is left unclear from these experiments is the role of stimulus presentation duration in recognition. More specifically, how does stimulus value affect its perceptual accessibility? How long does exposure to value-laden stimuli need to be for conscious perception? Does the duration of exposure needed for perception of value-laden stimuli differ depending on the value?

It is well established that prior experience with complex visual stimuli enhances performance on visual perception tasks, such as discrimination among highly similar objects (e.g., “Greebles”; Gauthier & Tarr, 1997b). However, it remains unclear from these perceptual learning studies whether the cumulative outcomes, or values, learned through prior experience with stimuli plays a role in the subsequent benefit of prior experience for perception. In most laboratory-based studies of perceptual learning, experience with a stimulus set or task is gained either via passive exposure or through simple feedback (e.g., correct or wrong) based on the perceptual task in question. This means that with practice, every stimulus ultimately predicts the same equal value outcome (implicit approval for a correct response), making it impossible to determine how the value of an interaction outcome might modulate perception. A handful of studies have examined the effect of reward on performance in speeded response attention tasks (e.g., Della Libera & Chelazzi, 2006) but such studies neither measured perceptual performance, nor varied the value of the outcome.

There are sound neurophysiological reasons to expect that value associations learned for specific stimuli could modulate perceptual processing. Reports that EV coding involves prefrontal cortex and the amygdala (see Chapter 3) suggest that value codes could be allowed to influence relatively early visual processes. The amygdala has a large efferent pathway to visual cortex (Amaral and Price, 1984) and substantial evidence indicates that prefrontal activations (including OFC) feedback to modulate earlier visual processing via reentrant loops (see Chapter 1). Such pathways afford an opportunity for EV codes to modulate perception.

In this chapter, I report two backward masking experiments that aimed to investigate the role of value associations in visual perception. The first experiment used the same task as T2 (old/new) in Experiment 2, with a manipulation of stimulus presentation duration. The second experiment used a gender discrimination task with manipulation of stimulus presentation duration and a concurrent WM load (load/no load).

While RSVP provides an estimate of the rate at which successive stimuli can be processed, backward masking provides an estimate of the required duration for effective processing of a single stimulus. As described in Chapter 1, backward masking occurs when a non-target object is presented soon after a target in the same (or nearby) location. When the mask is presented shortly after the target, the behavioral result of the mask is impeded visibility of the preceding target. This is caused by a disruption of feedback signals to V1 by spatial and featural information about the mask during processing of the target (i.e., before target processing is completed). Therefore, the temporal window in which a mask can disrupt processing of a target is thought to reflect the time it takes for cortical computation (Loffler, Gordon, Wilkinson, Goren, & Wilson, 2005). Higher-level cognitive processes have been shown to modulate the magnitude of backward masking, including perceptual grouping (Kurylo, 1997; Wolf, Chun, & Friedman-Hill, 1995) and selective visual attention (Enns & Di Lollo, 1997; Ramachandran & Cobb, 1995; Shelley-Tremblay & Mack, 1999); however no previous studies investigating the effects of value learning on masking have been conducted (to the best of my knowledge).

Experiment 4: Backward masking with value-laden stimuli[2]

In Experiment 4, I measured the minimum duration between a target face stimulus and a scrambled-face mask needed for criteria recognition to see how face perception performance is modulated by learned value. Participants identified a target as “old,” a stimulus for which the participant previously learned a value code, or “new,” a stimulus the participant had not previously seen. After completing the

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[2] Experiment 4 was presented as a poster at the Vision Sciences Society (VSS) conference in May 2007. [O’Brien, J. & Raymond, J. E. (2007). Associating reward and loss with faces: Effects on rapid face recognition [Abstract], *Journal of Vision*, *7*(9):16, 16a.]

learning task, participants saw the value-laden faces for various durations before they were masked, and I measured accuracy to classify the faces as old or new.

Based on the results from Experiment 2, I predicted that there would be a significant effect of motivational salience on the ability to identify a target face as old or new at a duration of 85 ms as well as at shorter presentation durations. However, it is possible that the valence associated with target stimuli, instead of the probability of outcome, could determine perception performance. In a backward masking study done with emotional faces, Maxwell and Davidson (2004) found better expression discrimination performance for happy faces compared to angry or neutral expressions at a target-mask SOA of only 17 ms. One explanation given for a happy expression perceptual advantage is that a positive valence is more efficiently recognized than a negative valence due to a more extensive cognitive analysis triggered by negatively valenced events (Leppänen & Hietanen, 2004; Taylor, 1991). It is possible that happy faces have a positive valence similar to a face associated with gain. A lower recognition threshold for happy expressions than for fear or anger has been shown in numerous other studies as well using photographs (Esteves & Öhman, 1993; Juth, Lundqvist, Karlsson, & Öhman, 2005; Leppänen, Tenhunen, & Hietanen, 2003; Milders, Sahraie, & Logan, 2008) and schematic faces that controlled for low-level physical features (Leppänen & Hietanen, 2004), although none of these studies controlled for expected value associations.

Method

Participants

Twenty-six experimentally naïve, healthy undergraduates from the Bangor University student panel (18 females; mean age 21 years; normal or corrected-to-normal vision) participated in exchange for money and course credit. Informed consent was given prior to participation. Data from five participants were excluded for false alarm rates above three SD from the mean.

Stimuli

Face stimuli (learned, novel, and masks) were the same as used in Experiment 2. Allocation of stimuli to category was almost balanced, with three people in learning version 1, 4, and 5, and four people in learning version 2, 3, and 6 (see Appendix B for learning version details).

Procedure

Value learning. The learning procedure was identical to that used in Experiment 1.

Face recognition task. A few minutes after completing the choice game, participation in the face recognition task began, starting with a short practice session (24 trials). Each experimental trial began with a 1000 ms central fixation cross, and then a face presented in the center of the screen for 15, 30, 45, 65, or 85 ms. On half of the trials, the target face was randomly selected from the 12 value-laden faces used in the choice game; on the other half, it was randomly selected from a set of 24 novel faces. After the target face was presented, it was replaced by a scrambled face for 200 ms and then a blank screen until response. Participants were instructed to respond as accurately as possible as to whether the target face was "old" (previously seen in learning task) or "new" (not seen in learning task). Responses were unspeeded. Trials were self-paced. Within this design, each value-laden face appeared as a target 20 times, randomized across trials. There were a total of 480 trials, with 8 trials per combination of target type, target value, and target duration.

Data analysis

Face recognition task. For each participant, data in the face recognition task was included only in value conditions where the learning from the corresponding face pairs was over 60%. For value conditions where learning was over 60% for both corresponding pairs, the two data points were averaged together. Recognition performance was measured using *d*', calculated for each participant and condition as the difference in the *Z*-transformed probability of making a hit (reporting 'old' when the stimulus was 'old') and the *Z*-transformed probability of making a false alarm (reporting 'old' when the stimulus was 'new').

Two ANOVAs of recognition performance for value-laden faces were conducted; the first used duration (15, 30, 45, 65, 85 ms) and EV (-.8, -.2, 0, .2, .8) as a factor, and the second used duration, valence (win/loss), and motivational salience (high/low) as factors (and excluded data for EV = 0). Additional corresponding ANOVAs for each duration were also conducted. Planned paired-sample, 2-tailed *t*-tests (with Bonferroni corrections where applicable) were used to compare means. Alpha levels were set at .05.

Results

Learning task

At the end of the learning session, performance approached asymptote and learning approximated the outcome contingencies similarly for win and loss pairs, $p >$ .10. For win pairs, the high-probability win face (EV = 0.8x) was chosen on average on 75% (SE = 3%) of trials; for loss pairs, the low-probability loss face (EV = -0.2x) was chosen on 68% (SE = 2%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 48% of trials (SE = 4%).

Face Recognition

Figure 13 shows mean target recognition (*d*') for stimuli of each EV at each target duration. Average FA rate was 37% (SE = 2%). As can be seen, performance at 15 ms is near chance (*d*' = 0) and increases as duration increases, with a steeper increase for stimuli associated with high probability of outcome. A repeated measures ANOVA with duration and target EV as within factors revealed a significant main effect for both duration, $F(2,31) = 35.66, p < .001$, and target EV, $F(4,80) = 3.12, p < .02$, which did not interact, $p > .30$. Reanalyzing the data for target valence (gain, loss) and target probability (high, low) showed that the difference in EV is due to the target's probability, $F(1,20) = 5.67, p < .03$, and is unaffected by target valence, $p > .15$.

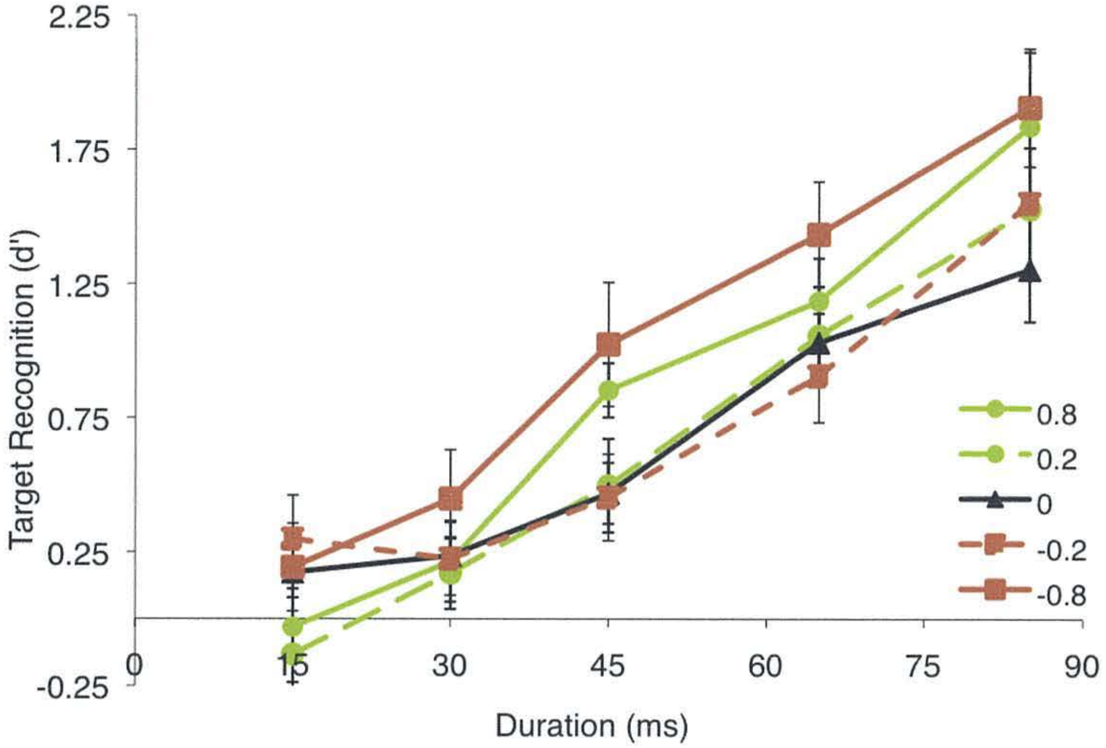

Figure 13. Mean old/new categorization accuracy (*d'*) for each target EV per target duration. Dotted lines represent low-probability associations; solid lines high probability. Error bars represent ± 1 SE.

ANOVAs of target EV at the shortest durations (15 & 30 ms) confirmed that there was no significant effect of target EV on recognition performance, $p > .30$. When the target was displayed for longer than 30 ms before masking, recognition for stimuli associated with a high probability of outcome began to increase compared to that for low-probability and no outcome associated stimuli. At both 45 ms and 65 ms, high-probability outcome associated stimuli (M = .94, SE = .14 & M = 1.31, SE = .13 respectively) were recognized significantly better than low-probability ones (M = .48, SE = .11 & M = .98, SE = .16), *p*'s < .04, and significantly better than stimuli associated with no outcome (M = .47, SE = .11 & M = 1.03, SE = .11), *p*'s < .03. At a target duration of 85 ms, recognition performances for high- and low-probability outcome associated stimuli were only marginally different from each other, $p = .089$, but high-probability outcome stimuli were still recognized better than no outcome ones, $t(20) = 4.13$, $p = .001$, whereas low-probability outcome stimuli were not, $p > .20$.

In addition to analyses of performance (*d'*), I also calculated the least squares line for the data for each EV, based on average data[3], to reach an interpolation of the critical duration necessary to yield a *d'* of 1.25. As can be seen in Figure 14, critical duration varies as a function of the motivational salience of the target.

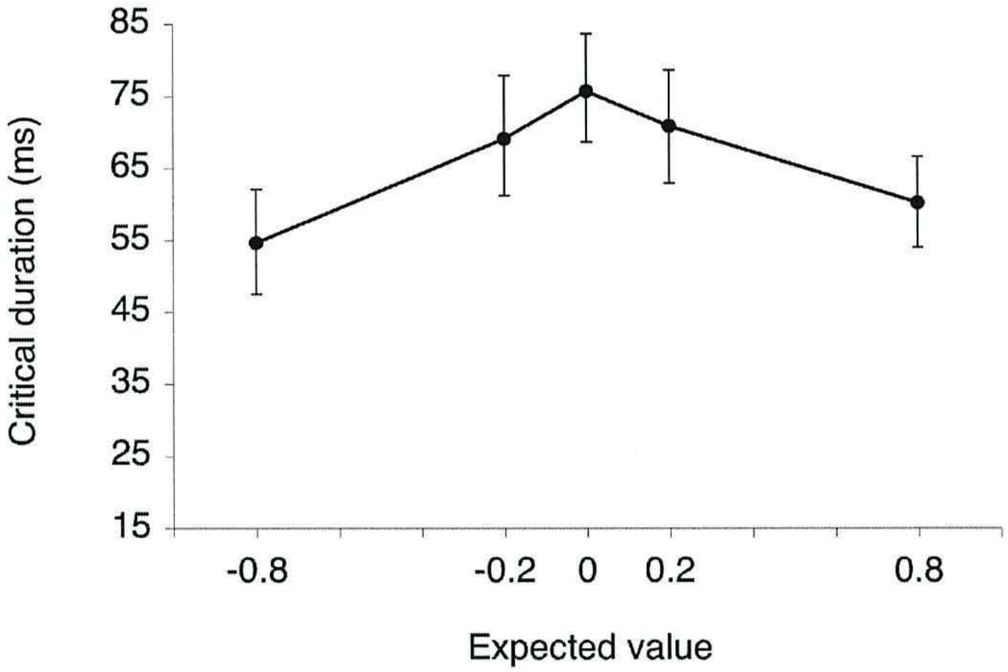

Figure 14. Presentation duration necessary for each target EV to yield a *d'* of 1.25. Error bars represent ± 1 SE.

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[3] I originally attempted to use individual data, but they were too noisy. I also attempted to plot the data on a logarithmic scale, but the line fits were inferior to those obtained using linear values.

Table 1. Critical duration (ms) and mean correlation coefficients (*r*) of the least squares per target EV

EV	Critical Duration	*r*
0.8	60.27	.78
0.2	70.87	.68
0	75.73	.79
-0.2	69.14	.70
-0.8	54.67	.73

Discussion

Experiment 4 produced two main findings. First, recognition of old faces was more accurate for high probability win- and loss-associated faces regardless of valence than for low probability faces. Thus, it appears that performance was driven by the motivational salience of the stimulus. Stimuli that are more motivationally salient are more resistant to backward masking. This is consistent with the finding in Experiment 2 that motivational salience facilitates recognition, regardless of attentional demands. As in Experiment 1, prior value learning was able to modulate perceptual recognition decisions in a subsequent unrelated task. Top-down feedback signals containing information about high predictability may be able to reach V1 (via the OFC and/or the amygdala) during the processing of the target before V1 is updated with spatial and featural information about the mask, thus making these stimuli more perceptually accessible than those with weaker top-down signals (i.e., low predictable stimuli).

This finding also suggests that valence effects are unlikely to explain results that might be attributed to happy expression superiority in face processing. Since happy facial expressions are encountered more often than other expressions outside of laboratory conditions (Bond & Siddle, 1996), it is possible that this frequency of occurrence has led to a greater motivational salience for happy faces (i.e., more predictable).

Second, recognition performance for stimuli associated with a high probability of outcome was better than for stimuli associated with a low probability of outcome when presented as quickly as 45 ms before masking. These data suggest that little time is needed to access and use information about outcome probability to aid in perception of a visual stimulus. If it takes approximately 40 ms for visual information to reach V1 (Lamme & Roelfsema, 2000; see Chapter 1), then the current data suggest that top-down information about motivational salience is possibly being accessed soon after, perhaps 85 ms after target presentation, at which time visual information about the mask overwrites V1 target information (i.e., 45 ms target duration + 40 ms after presentation of the mask for mask information to reach V1).

However, there is evidence that the mechanisms underlying face discrimination take slightly longer than this (upward of 133 ms). Loffler and colleagues (Loffler et al., 2005) suggest that the discrepancy in reported time of face discrimination is a result of the type of mask used in backward masking experiments. They presented a target face for 27 ms, which was then masked for 27 ms after a variable target-mask SOA. Observers were then shown two faces and indicated which of the two they had just seen. Loffler et al. tested the effectiveness of a variety of masks (visual noise, house, scrambled face, inverted face, upright face). They found that upright faces were the most effective, resulting in a necessary SOA of at least 130 ms before face processing is complete and accurate target discrimination can be made. This result is consistent with other studies using face masks investigating the recognition of facial expression (Esteves & Ohman, 1993) and face identification (Costen, Shepherd, Elis, & Craw, 1994). Scrambled and inverted faces were less effective as masks, but significantly more effective than houses or visual noise. The masks that I used in this study, however, were the same for all targets (scrambled faces), so the effectiveness of the mask cannot explain the effects of value learning.

A feedforward sweep of information through the visual system takes approximately 100 ms to complete, and any visual processing that takes longer than this involves feedback connections (Fahrenfort, Scholte, & Lamme, 2008; Lamme, 2006). The possibility that disambiguation of bottom-up sensory data via top-down information about outcome predictability occurs very rapidly can help explain why motivational salience facilitates recognition independently of attentional demands (Experiment 1). The associated predictability of a stimulus changes the perceptual threshold needed to see it. A highly predictable stimulus results in a lower perceptual threshold, making it accessible to conscious awareness earlier than stimuli that are less predictable of an outcome.

Experiment 5: Backward masking with concurrent WM load

In Experiment 2, when attentional resources were limited associations with gains but not losses enhanced the attentional competitiveness of stimuli. Thus, a high attentional load biases access to positive value codes over negative ones in WM. In this next experiment, I investigated how value codes are accessed during perceptual processing in a backward masking task with a concurrent WM load. Here, value codes were irrelevant to the task(s).

Value codes are essentially a form of associative memory, which can be accessed through WM. When WM is loaded, it is possible that value codes are no longer accessible. However, data from Experiment 2 suggest that when WM is used in a dual task situation, information about valence (gain) is still accessible. Since value information is irrelevant in this experiment, it is also possible that associations with valence or motivational salience (or both) may interfere with performance depending on WM load.

Lavie and colleagues (de Fockert et al., 2001; Lavie, 2005; see Chapter 1) showed that processing load in WM determines ability to filter out irrelevant stimuli during selection. As load increases, fewer resources are available to support efficient target selection and distractor rejection. In contrast to a high perceptual load, which prevents conscious perception of irrelevant distractors (see Chapter 2), a high WM load has the opposite effect: it increases competition interference from distractors. When WM load is high, availability of additional WM for maintaining stimulus priorities is limited, leading to greater intrusion of distractors in a selective attention task (de Fockert et al., 2001).

The purpose of this experiment was to determine if value codes could still be accessed within WM when there is a concurrent WM load. To do this, I used a gender categorization task (male/female) that was orthogonal to the learning-dependent object recognition task (old/new) and did not require previous knowledge of the faces. Thus, value information was irrelevant in this task. It is possible that the irrelevant value information could act as a distractor and disrupt performance. It is also possible that value codes may not be accessible when WM is loaded.

Unfortunately, after this experiment was tested, it was discovered that the design had a flaw. Trial numbers were not balanced in all conditions, and so some aspects of these results are difficult to interpret. Therefore, this experiment was considered to be a pilot study.

Method

Participants

Thirty different undergraduates from the Bangor University student panel (22 females; mean age 20 years; normal or corrected-to-normal vision) participated.

Stimuli

Faces learned in the learning task were 12 neutral faces (six female) chosen from the Karolinska Directed Emotional Faces database (KDEF; Lundqvist, Flykt, & Öhman, 1998). The switch from computer-generated faces to this database was made to avoid any ambiguity in gender discrimination. Faces subtended approximately 2.9° x 3.6° with minor deviations (max. .4°), and were shown in frontal view (hair, teeth, and neck not visible). Scrambled face masks were the same as those used in Experiment 1. Eight additional neutral novel male faces (sourced from the internet, teeth and neck not visible) and 10 computer-generated, grayscale, abstract, elliptical patterns (composed of small circles) matched in global size to the faces were used in the visual WM task. Allocation of stimuli to category was almost balanced, with three people in learning version 2 and 3, four people in versions 1, 5, and 6, and five people in version 4.

Procedure

Value learning. The learning procedure was identical to that used in Experiment 1.

Visual WM and gender categorization tasks. A few minutes after completing the choice game, participation in the face recognition task began, starting with a short practice session (15 trials). Each experimental trial (Figure 15) began with a 500 ms central fixation cross, and then four images to be remembered for the WM task. The images were presented simultaneously on the left and right of the screen, above and below fixation, for 3500 ms. On half of the trials, there were four male faces to be remembered, chosen from eight possible faces, to create a WM load condition; on the other half, four elliptical circle patterns appeared to create a no WM load condition. Participants were instructed to remember the four faces for a face-matching task at the end of each trial and ignore the elliptical circle patterns.

The WM images were then replaced with a 1000 ms central fixation cross, followed by a centrally presented male or female target face. Target faces were randomly selected from the 12 value-laden faces used in the learning game and appeared for one of three possible durations: 15, 45, or 85 ms. After the target face was presented, it was replaced by a scrambled face for 200 ms and then a blank screen until response within three seconds. Participants were instructed to respond as quickly and as accurately as possible as to whether the target face was male or female. After the male/female categorization task, participants were shown one of the eight possible working memory male faces and reported whether or not it was one of the faces shown at the beginning of the trial. Half of the WM load trials ended with a face that matched one in WM. The face remained on the screen until response, and response was not speeded.

Trials were self-paced. Within this design, each value-laden face appeared as a target 33 times, randomized across trials. There were a total of 396 trials, with 11 trials per combination of target gender, target value, and target duration.

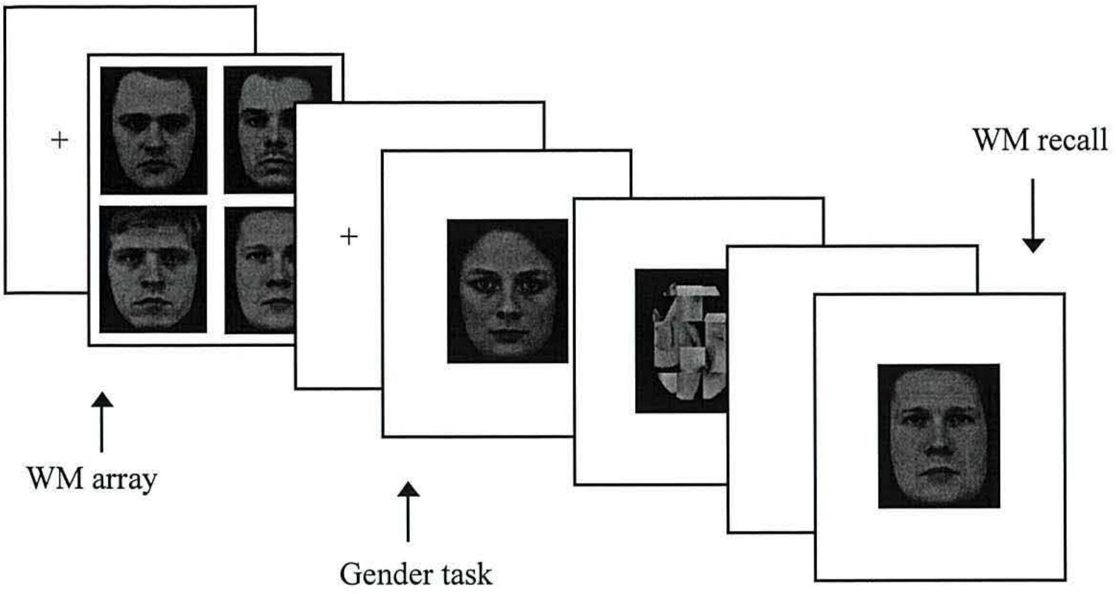

Figure 15. Stimuli and sequence of events in the WM and gender categorization tasks. The WM items were displayed for 3500. The gender categorization face was displayed for one of three possible durations: 15 ms, 45 ms, 85 ms. The face mask was displayed for 200 ms. Participants responded to the gender of the face, and then reported whether the WM recall face matched one in WM from the beginning of the trial.

Data analysis

WM. Accuracy in the WM task was measured as a probability of correct report. I excluded data from five participants for near chance performance (< 55% correct) on WM load trials.

Gender categorization. Data from two additional participants were excluded owing to a large gender bias in response (responding "female" on over 70% of trials). Accuracy in the gender categorization task was measured as a probability of correct report. Data regarding performance on the gender categorization task (accuracy and RT) were analyzed conditional on correct WM load trials. RT data was analyzed conditional on correct gender categorization response. Two ANOVAs of accuracy in gender categorization for value-laden faces were conducted; the first used duration

(15, 45, 85 ms) and EV (-.8, -.2, 0, .2, .8) as a factor, and the second used duration, valence (win/loss), and motivational salience (high/low) as factors (and excluded data for EV = 0). The same two ANOVAs were conducted for the RT data. Additional corresponding ANOVAs for each duration were also conducted. Planned paired-sample, 2-tailed *t*-tests (with Bonferroni corrections where applicable) were used to compare means. Alpha levels were set at .05.

Anticipation responses (< 200 ms) and exceedingly slow responses (>2500 ms) were removed (1.9% of all trials) from RT data. A mean RT and standard deviation (SD) were then calculated for each condition, and any RTs that exceeded the mean of its condition by more than 2.5 SDs were removed (12.2% of trials).

Results

Learning task

Learning approximated the outcome contingencies significantly more for win pairs than loss pairs, $F(1,22) = 57.91, p < .001$. For win pairs, the high-probability win face (EV = $0.8x$) was chosen on average on 87% (SE = 2%) of trials; for loss pairs, the low-probability loss face (EV = $-0.2x$) was chosen on 74% (SE = 2%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 49% of trials (SE = 3%).

Visual WM task

Performance on the WM task was .75 (SE = .02). WM accuracy did not vary as a function of target duration, EV, valence, or motivational salience in the gender categorization task, *p*'s > .30.

Accuracy

I first examined the effects of target EV on gender categorization accuracy at each target duration under conditions of WM load and no load using a repeated measures ANOVA. As can be seen in Figures 16 and 17, accuracy increased with increasing duration, $F(2,34) = 188.05, p < .001$. There were significant interactions of target duration with WM load, $F(2,34) = 3.23, p = .052$, and with target EV, $F(8,136) = 2.35, p < .05$. When the data were reanalyzed for valence and motivational salience effects, I found a marginally significant main effect of motivational salience, $F(1,17) = 3.75, p = .070$, as well as a significant interaction between target duration and target valence, $F(2,34) = 3.54, p < .05$. I then analyzed performance for each target duration separately, looking at differences caused by target valence and motivational salience (and WM load where significant).

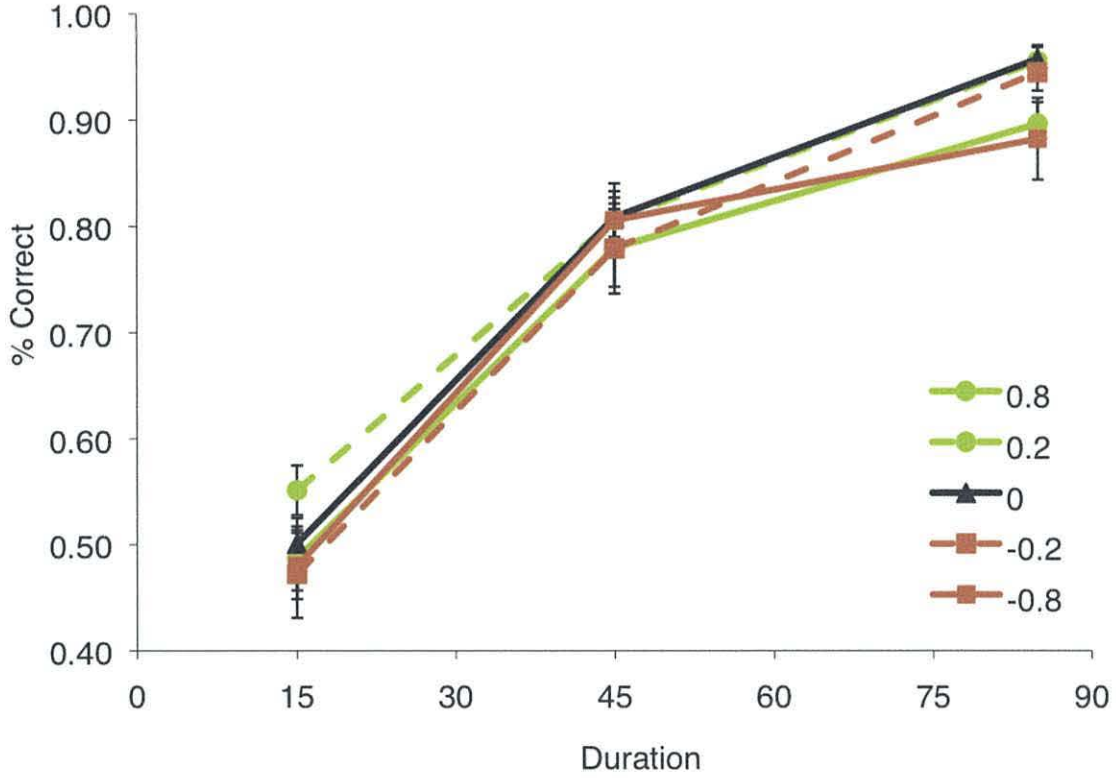

Figure 16. Mean gender categorization accuracy (proportion correct) for each target EV per target duration with no WM load. Dotted lines represent low-

probability associations; solid lines high probability. Error bars represent ± 1 SE.

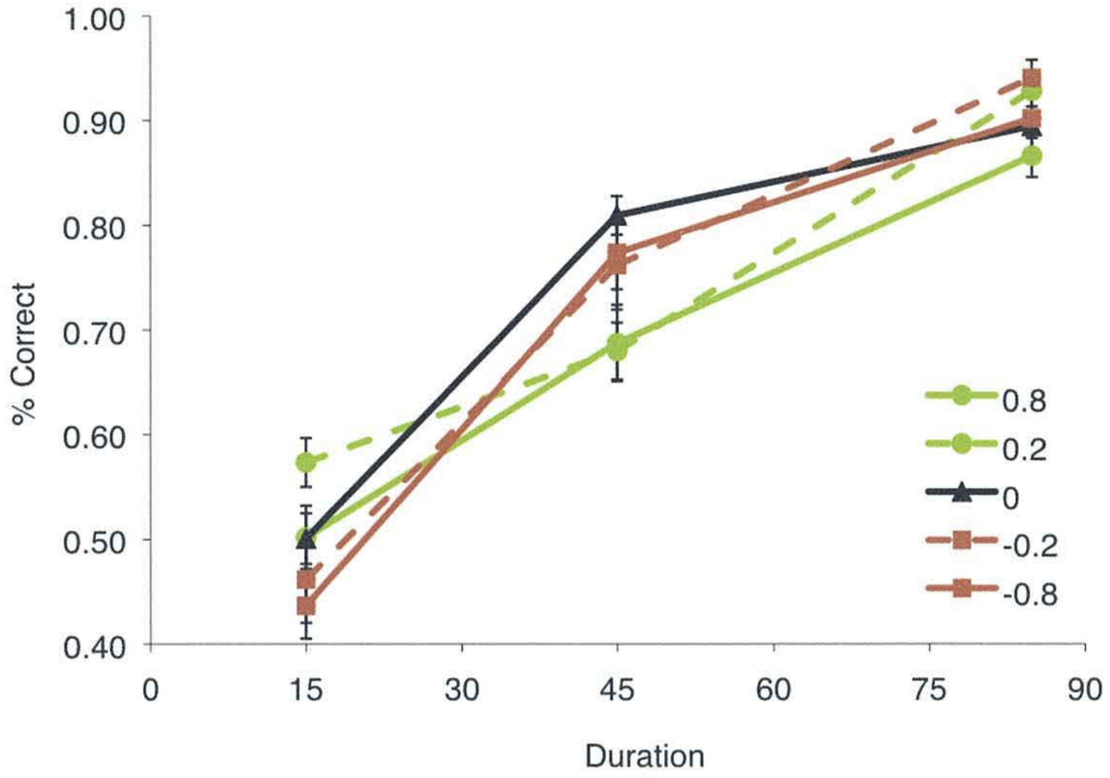

Figure 17. Mean gender categorization accuracy (proportion correct) for each target EV per target duration with a WM load. Dotted lines represent low-probability associations; solid lines high probability. Error bars represent ± 1 SE.

Duration = 15 ms. An ANOVA of WM load, target valence, and motivational salience (excluding EV = 0) revealed a significant main effect of valence, $F(1,20) = 4.73$, $p < .05$, which did not interact with WM, $F < 1$. Performance for gain-associated faces (M = .53) was significantly better than for loss-associated faces (M = .47), $t(23) = 2.66$, $p < .05$. However, as performance at both values differed from chance (.50) by only .03, it is likely that value is not actually affecting performance at this short duration.

Duration = 45 ms. Analysis of WM, target valence, and motivational salience at a 45 ms duration revealed a significant main effect of WM load, $F(1,20) = 6.21, p < .05$. Target probability did not significantly affect gender categorization, $F < 1$. The interaction between WM load and target valance was marginally significant, $F(1,20) = 3.31, p = .084$. As can be seen in Figures 16 and 17, performance for loss-associated and no-outcome associated faces does not significantly differ depending on presence of a WM load, p's > .30. However, performance for gain-associated faces with a concurrent WM load was significantly worse than with no WM load (see Table 2), $t(22) = 2.95, p < .01$. This suggests that gain information is possibly accessible and competing with gender information at this duration. However, the effect is modest and similar to what is seen at 15 ms, raising the possibly that it is spurious.

Table 2. Proportion of correct responses at 45 ms target duration per WM load and target valence.

	45 ms	
	No WM	WM load
Gain	.79	.68
Loss	.79	.77
No Outcome	.81	.81

Duration = 85 ms. An ANOVA of WM load, target valence, and motivational salience revealed a significant main effect of motivational salience, $F(1,20) = 5.82, p < .05$, which did not interact with WM, $F < 1$. Performance for low-probability outcome faces (M = .94) was significantly better than for high-probability outcome faces (M = .89), $t(22) = 2.46, p < .05$. High motivational salience may have competed as distracting information during the gender task regardless of WM load, resulting in decreased performance for those faces as compared with faces associated with low motivational salience. Again, however, the difference in performance is modest.

Table 3. Proportion of correct responses at 85 ms target duration per WM load and motivational salience.

	85 ms	
	No WM	WM load
High	.89	.89
Low	.95	.93
No Outcome	.96	.89

RTs

I then examined the effects of target EV on gender categorization RT at each target duration with WM load and no load using a repeated measures ANOVA (Figure 18 and 19). Again there was a main effect of target duration, $F(1,31) = 82.96$, $p < .001$, with RTs decreasing with increasing duration. There was also a significant interaction of target duration with WM load, $F(2,44) = 5.36$, $p < .01$. Reanalyzing the data for valence and motivational salience effects revealed a marginally significant main effect of valence, $F(1,22) = 3.58$, $p = .072$, as well as significant interactions between WM load and target valence, $F(1,22) = 6.61$, $p < .05$, and between target duration and motivational salience, $F(2,44) = 6.54$, $p < .01$. I then analyzed RTs at each duration separately, looking at differences caused by target valence and motivational salience (and WM load where significant).

Table 4. RTs at 85 ms target duration per WM load and motivational salience.

	No WM Load		WM Load	
	45 ms	85 ms	45 ms	85 ms
High	794	745	848	730
Low	835	715	867	760
No Outcome	813	732	826	743

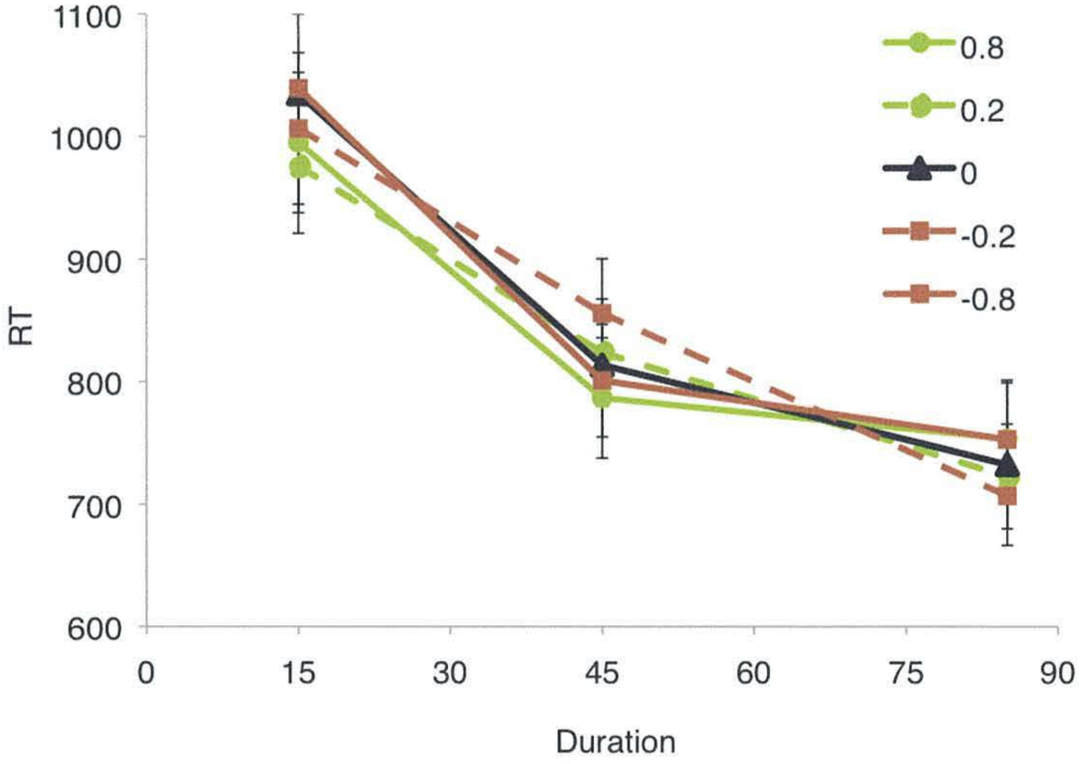

Figure 18. Mean gender categorization RT (ms) for each target EV per target duration with no WM load. Dotted lines represent low-probability associations; solid lines high probability. Error bars represent ± 1 SE.

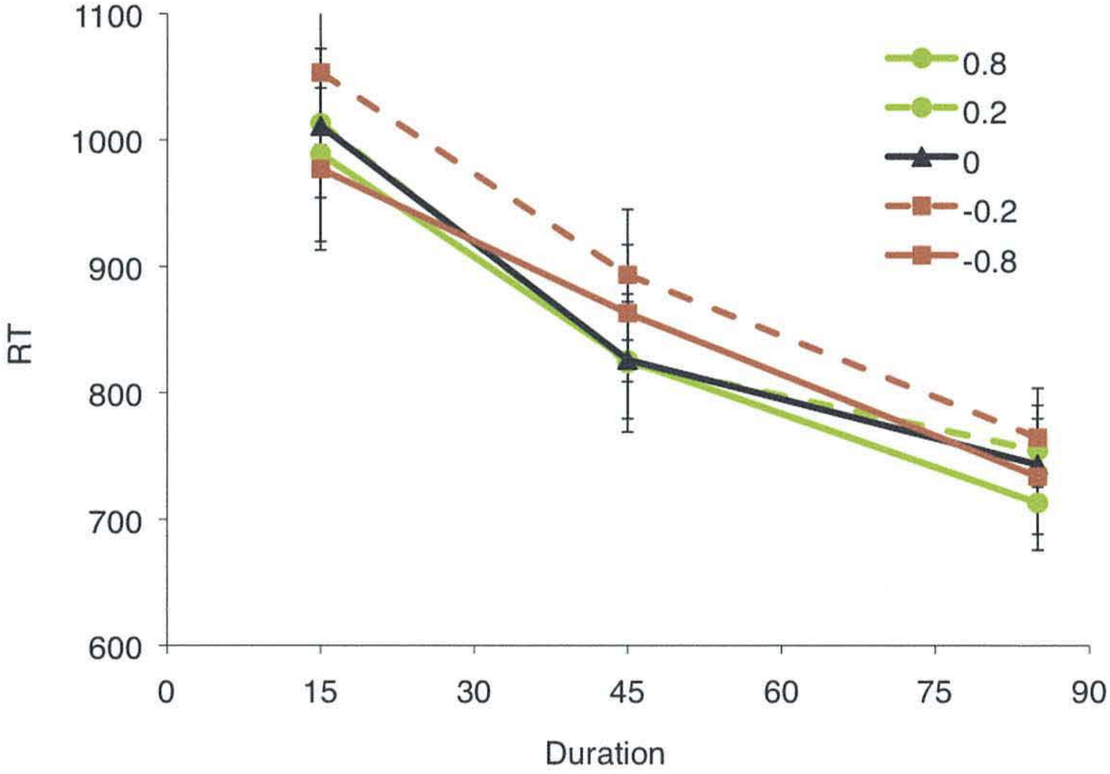

Figure 19. Mean gender categorization RT (ms) for each target EV per target duration with a WM load. Dotted lines represent low-probability associations; solid lines high probability. Error bars represent ± 1 SE.

Duration = 15 ms. An analysis of RT data at a 15 ms target duration showed that RTs did not vary by WM load, target valence, or motivational salience, *F*'s < 1.

Duration = 45 ms. An ANOVA of WM load, target valence, and motivational salience at a 45 ms duration revealed a significant main effect of motivational salience, $F(1,16) = 6.53$, $p < .05$, which did not interact with WM, $F < 1$. RTs were not significantly affected by the valence associated with each face, $p > .20$. RTs for high probability outcome faces (M = 821 ms) were marginally faster than for low probability outcome faces (M = 846), $t(22) = 1.99$, $p = .060$.

Duration = 85 ms. An ANOVA of WM load, target valence, and motivational salience at an 85 ms duration revealed a significant interaction of WM load and motivational salience, $F(1,19) = 7.87, p < .05$. With no WM load, participants are marginally quicker to categorize a face previously associated with a low probability of outcome (M = 715 ms) than a face previously associated with a high probability of outcome (M = 745 ms), $t(22) = 2.03, p = .055$. With a WM load, RTs do not differ by motivational salience, $p > .14$.

There was also a marginally significant interaction of WM load and valence, $F(1,19) = 4.34, p = .051$; however, paired samples *t*-tests did not reveal any significant differences in RTs by valence.

Discussion

When a face is presented for rapid gender categorization and then backward masked, perceptual performance is possibly affected by the value previously associated with that face, even though this information is entirely irrelevant to the task. Regardless of WM demands, ability to categorize the gender of a face is at chance when it is masked after 15 ms. When presented for 45 ms, accuracy improves but is not affected by value information when there is no WM load. However, when there is a WM load, gain-related value codes become in competition with gender information and performance accuracy for faces associated with gain is hindered. This result is consistent with the enhanced competitive advantage found for gain-associated faces in Experiment 2 under conditions of reduced attention. In Experiment 2, gain-related information was task relevant and facilitated performance. In this experiment, gain-related information is task irrelevant and had a negative effect on performance. Unfortunately, the data from this experiment are unclear and inconsistent, so the implications are only speculative.

At a presentation duration of 85 ms, motivational salience appears to compete with gender information because performance accuracy for faces associated with high probability outcomes was decreased. Data support the possibility that motivationally saliency enhanced face perception, independent of WM demands, which is consistent with the results from Experiments 2 and 4. However, since motivational saliency information was irrelevant to the task in this experiment, it had a negative effect on performance. I also expected to see interference by high probability faces at 45 ms, and it is unclear why this was absent. It is also unclear why a gain effect was not found at 85 ms when WM load was high. It is possible that with more trials in these conditions these effects would come out.

RTs for the gender categorization task were marginally affected by the expected value associated with the stimuli. At 45 ms, correct gender responses were made more quickly when the face was associated with high predictable outcomes than with low predictable outcomes, regardless of WM load. This is counterintuitive, as salient distracting information often slows performance as well as decreasing accuracy (e.g., Stroop effect, Stroop, 1935). Responses to high predictable faces were only marginally faster than responses to low predictable ones, however, so this effect may be spurious. At 85 ms, RTs were faster for low predictable faces than for high predictable ones. This effect was also marginal and only occurred when WM load was low. It appears that RTs are not as sensitive as accuracy in measuring the effects of value learning on subsequent perception under different WM loads.

The results from this experiment overall are consistent with Lavie and colleagues' (de Fockert et al., 2001; Lavie, 2005) theory on WM load and distractor interference. When WM load was high, competition from irrelevant valence and predictability value codes increased.

Bruce and Young's (1986) model of face recognition proposes that gender perception occurs independently of face (identity) recognition; therefore, face gender can be determined irrespective of whether the face is familiar or not (Bruce, Ellis, Gibling, & Young, 1987). It has also been posited that gender discrimination occurs prior to face recognition (Ellis, 1986). However, more recent studies have challenged the idea that these two processes are unrelated, providing evidence that gender identification is indeed related to face familiarity (Baudoin & Tiberghien, 2002; Bülthoff & Newell, 2004; Ganel & Goshen-Gottstein, 2002; Rossion, 2002). The results from the current experiment also support the idea that gender perception and face identity processing are linked. If gender perception occurs independently of and prior to face recognition, then gender discrimination should be carried out prior to interference from identity-specific value codes. Instead, value code information appears to be distracting in this task, supporting the idea that face recognition contributes to gender categorization.

Chapter Discussion – Experiments 4 & 5

This chapter examined the effects of value learning on stimulus perception in backward masking tasks. In Experiment 4, the prior value learning of a stimulus enhanced subsequent perception of that stimulus when value information was relevant to the task. More specifically, high versus low motivational salience of a stimulus aids perception. In Experiment 5, value learning was also shown to enhance perception, but as it was task irrelevant it was shown to interfere with the perceptual task at hand. Motivational salience again modulated perception, independent of WM load. The competitiveness of valence information was enhanced, but only when WM was loaded. These results supply further evidence for the finding that attention and motivation provide separable, independent top-down signals for controlling perceptual awareness.

CHAPTER 6

THE EFFECT OF VALUE LEARNING ON LOW-LEVEL OBJECT PERCEPTION AS MEASURED BY EEG: EXPERIMENT 6

Acquisition and storage of EV codes involves pre-frontal and limbic system circuits that have ample opportunity to interface with visual object processing networks. In the first two experimental chapters, I have shown that the interaction of value codes with object processing leads to enhanced perception of learned stimuli depending on the specific value and attentional demands.

In this next experiment, I further investigated the role of value learning in object perception by measuring ERP components elicited during categorization of previously learned stimuli as old or new. I focused my investigation on two specific components: N170 and P3. The N170 is widely seen as an automatically elicited, face-specific response reflecting pre-categorical structural encoding. Recent studies have shown that the N170 is unaffected by face identity (Bentin & Deouell, 2000) or by emotional face expression (Eimer & Holmes, 2002), both believed to occur after early structural face encoding. In contrast to this, other studies have shown that the N170 can be modulated by face identity (Jemel et al., 2003), familiarity (Caharel, Courtay, Bernard, Lalonde, and Rebaï, 2005), and top-down information such as emotional context (Galli, Feurra, & Pia Viggiano, 2006). To see if value codes modulate the N170, I used faces with previously learned EVs as stimuli, thus controlling familiarity and emotionality. Modulating the N170 by presenting stimuli with different EVs would indicate an influence of value learning at a relatively early stage of processing. The P3 (or P300) is believed to reflect the allocation of cognitive resources to stimulus evaluation processes (Johnson, 1988). It is also heightened in response to emotionally relevant stimuli, both positive and negative in valence (Schupp, Bruce, Cuthbert, Bradley, Cacioppo, Ito, & Lang, 2000). Therefore we might expect to see stimuli strongly associated with positive and negative value outcomes elicit larger P3s than stimuli less strongly associated with value outcomes (or no outcome at all).

N170

The N170 is a large negative component that peaks between 150 – 220 ms after stimulus onset at occipitotemporal sites and is believed to be an automatically elicited, face-specific response reflecting a pre-categorical structural encoding stage prior to recognition and identification (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; but see Thierry, Martin, Downing, & Pegna, 2007). According to existing face processing models (Bruce & Young, 1986; Haxby et al., 2000), faces are first processed by a core, structural encoding system responsible for early perceptual processing of facial features before they are configured into representations able to inform emotional expression interpretation and identity. In line with this, recent studies have shown that the N170 is unaffected by face familiarity (celebrities vs. novel faces) (Bentin & Deouell, 2000; Eimer, 2000; Henson et al., 2003) or by emotional face expression (Eimer & Holmes, 2002; Eimer, Holmes, & McGlore, 2003; Holmes, Vuilleumier, & Eimer, 2003; Holmes, Winston, & Eimer, 2005; but see Blau, Maurer, Tottenham, & McCandliss, 2007; Miyoshi, Katayama, & Morotomi, 2004), both processes believed to occur after early structural face encoding.

A key issue for the current experiment is whether the N170 is influenced by top-down non-visual information. While the N170 appears to be automatically elicited by visual processing of faces, there is evidence to suggest that, once triggered, it is susceptible to top-down cognitive influences such as priming, attention, and context. For example, Bentin and colleagues (Bentin & Golland, 2002; Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002) recorded N170 amplitude to meaningless stimuli, and then to the same stimuli primed as face parts (both visually and verbally). Before priming, N170 amplitude to schematic eyes was similar to those for objects. After priming, the N170 was the same as that elicited by full schematic faces, suggesting that initial face categorization was modulated by top-down information.

Holmes et al. (2003) demonstrated an enhanced N170 to faces presented in attended locations compared to when they were presented in unattended locations (as distractors). Faces were presented concurrently with houses, arranged in horizontal and vertical pairs. Attention was directed to either the horizontal or vertical locations (pre-specified at the start of the trial) to detect identical images and the other locations were actively ignored. They concluded that the structural encoding of faces can be modulated by spatial attention.

Several studies have also reported evidence that the N170 can be influenced by face familiarity and emotional content, challenging the hypothesis that the N170 is insensitive to face identity. Caharel and colleagues (Caharel et al., 2005; Caharel, Fiori, Bernard, Lalonde, & Rebaï, 2006; Caharel et al., 2002) found a larger N170 amplitude for the viewers' own face compared to novel faces when passively viewed (Caharel et al., 2002). This group also reported a larger N170 for the viewers' own face and mother's face compared to famous and unfamiliar faces regardless of whether familiarity was task relevant or not (Caharel et al., 2005). This finding is consistent with Tanaka and Curran's (2001) N170 "expertise" effect – an enhanced N170 to a non-face stimulus category for which the viewers were expert (e.g., birds). We tend to have a robust representation for faces to which we have had extensive exposure which results in more efficient and faster processing (Tong & Nakayama, 1999).

Galli and colleagues (2006) paired novel faces with emotional information to try to influence the N170 with top-down information about valenced contexts. They had participants view neutral expression faces in a newspaper context paired with either emotionally positive or negative headlines depicting an action committed by the person, and then showed the faces again without their context. They found that positive-context faces elicited larger N170 amplitudes than negative-context faces. In constrast, Righart and de Gelder (2006) reported that faces seen paired with fearful contexts (e.g., crashed car) elicit larger N170 amplitudes than faces paired with a neutral context.

If the N170 is indeed susceptible to influence by top-down factors like attention, context, and face familiarity, it is possible that the underlying influencing factor is EV. Familiar faces have learned values, especially those for which we have robust representations (e.g., your own face, your mother's face). The aforementioned experiments that presented faces paired with valenced contexts essentially paired them with a value to be learned (albeit uncontrolled). Also, items to-be-attended within an experimental context are by nature rewarding because attending to them results in correct performance. From the results of the emotional context N170 experiments I predicted that if EV can modulate the N170 there would be larger amplitudes following gain-associated faces than faces associated with loss or no outcome. One might conclude that the results from Righart and de Gelder's (2006) experiment with fearful contexts fall under the negative context category. However, our society consistently seeks out "blood, guts, and gory" as a source of entertainment and enjoyment. While not many people would voluntarily choose to put themselves in the fearful contexts (e.g., crashed car), the desire to observe them as an outsider is behavior on which businesses such as the film industry thrive. Thus, even though fearful contexts might be negative they can be associated with reward.

P3

The P3 was first reported in 1965 (Sutton, Braren, Zubin, & John, 1965) and it is possibly the most studied component of the ERP (see Nieuwenhuis, Aston-Jones, & Cohen, 2005, for a review). The P3 is a positive potential with typical peak latency between 300 and 600 ms with largest amplitude at centroparietal scalp sites (Sutton et al., 1965) and is thought reflect stimulus evaluation (Johnson, 1988) and the updating of information in WM (Donchin, 1981; Donchin & Coles, 1988). The P3 has been broken down into two distinct late positive components, each reflecting distinct cognitive processes and scalp distributions. The P3a (or novelty-P3 when elicited by novel stimuli) is more frontally distributed and is elicited by highly deviant or salient task-irrelevant (attention capturing) stimuli. The centroparietal P3b[4], also known as the late positive potential (LPP), is elicited by task relevant stimuli to which active attention is given (Courchesne, Hillyard, & Galambos, 1975; Squires, Squires, & Hillyard, 1975).

P3 amplitude is highly sensitive to the subjective probability of the stimulus, as commonly seen in oddball tasks (Squires, Donchin, Herning, & McCarthy, 1977; see Donchin & Coles, 1988, for a discussion). More relevant to the current experiment, P3b amplitude is also thought to reflect increased attentional resources devoted to motivationally significant stimuli and facilitation in perceptual processing of these stimuli (Schupp et al., 2000; Schupp, Junghöfer, Weike, & Hamm, 2003).

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[4] For the current experiment, I was concerned with the P3b only. Henceforth, I will refer to the P3b/LPP as P3.

According to Nieuwenhuis and colleagues (2005), the P3 component is triggered by the outcome of a decision process for the task at hand (e.g., stimulus categorization), which then facilitates a response based on that decision. Motivational significance includes sensitivity to both the relevance of the stimulus to the current task (Duncan-Johnson & Donchin, 1977; Squires et al., 1977) and the potential for the stimulus to be associated with some form of utility (positive or negative; Nieuwenhius et al., 2005). Often, effects of motivational significance on P3 amplitude are explored using emotionally valenced stimuli. P3 amplitude is usually reported to be enhanced by emotional stimuli (both positive and negative) as compared to neutral stimuli (Junghöfer, Bradley, Elbert, & Lang, 2001; Hajcak & Olvet, 2008; Keil, Bradley, Hauk, Rockstroh, Elbert, & Lang, 2002; Schupp et al., 2003), especially with highly arousing emotional stimuli (Schupp et al., 2003; Schupp, Stockburger, Codispoti, Junghöfer, Weike, & Hamm, 2007).

In addition to emotional stimuli, the P3 is also sensitive to information about monetary reward. Specifically, P3 amplitude has been shown to increase with increasing reward magnitude (e.g., Goldstein, Cottone, Jia, Maloney, Volkow, & Squires, 2006; Ramsey & Finn, 1997; Yeung & Sanfey, 2004). For example, Goldstein and colleagues (2006) used a visual discrimination task where participants were instructed to respond to stimuli designated on "Go" trials and to refrain from responding to "No-go" stimuli. Trials were designated as having the potential to earn the participant a specified monetary reward (0¢, 1¢, or 45¢) contingent on correct response; incorrect responses were not penalized. They found P3 amplitude was graded such that it increased with larger reward magnitudes.

The current study extends the previous investigations of reward processing and P3 amplitude by looking at effects of stable value codes, instead of codes acquired during EEG recording. In addition, I investigate the effects of loss codes as well as reward codes to determine whether previous findings (e.g., Goldstein et al., 2006) are driven by the magnitude of the outcome, the valence, or both.

Experiment 6: Value learning and low-level visual object recognition[5]

Taken together, the results from P3 experiments with emotionally valenced images and with reward suggest that stimuli with high motivational salience would elicit larger P3 amplitudes than would stimuli with low motivational salience. In this experiment, participants learned value associations with faces and then categorized them individually as old or new during EEG recording. I predicted that faces previously associated with a high probability of outcome would elicit a larger P3 than faces previously associated with a low probability or no outcome.

The first goal of this experiment was to investigate the role of value learning in modulating the early perception and the structural encoding of faces, as indicated by changes in the N170. Second, the P3 was measured to highlight any modulation by value learning, reflecting increased attentional resources devoted to and facilitation in perceptual processing of these stimuli.

Method

Participants

Twelve experimentally naïve, healthy undergraduates from the Bangor University student panel (7 females; mean age 21 years; normal or corrected-to-normal vision) participated in exchange for money and course credit. Informed

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[5] For Experiment 6, the testing and data analyses were done in collaboration with Dr. Helena Rutherford. Dr. Brian Goolsby and Julia Gomez assisted in the running of participants. I presented the results as a poster at the VSS conference in May 2008. [O'Brien, J. L., Rutherford, H. J. V., & Raymond, J. E. (2008). Can value learning modulate low-level visual object recognition? An ERP study [Abstract]. *Journal of Vision*, *8*(6):36, 36a.]

consent was given prior to participation. Data from two participants were excluded for face recognition accuracy below three SD from the mean.

Stimuli

Learned face stimuli were six male faces from the set of 12 used in Experiment 1 plus six additional computer-generated female faces (GenHead 1.2; Genemation, Inc.). Novel faces (30 male, 30 female) were also computer generated. All stimuli were of equal luminance. Allocation of stimuli to category was balanced.

Apparatus

Stimuli and behavioural responses were designed, controlled and recorded by E-prime software running on an IBM-compatible PC. An elastic electrode-cap (Easy cap) with sintered-silver chloride electrodes was used to collect EEGs. The continuous EEG was recorded using Neuroscan Acquire software on an IBM-compatible PC.

Procedure

The participants were seated comfortably approximately 70 cm in front of a computer screen in an electromagnetically shielded room. They completed both the value learning and the face recognition tasks wearing the EEG cap; EEG was recorded during the face recognition task only.

Value learning. The learning procedure was the same as used in Experiment 1.

Face recognition task. A few minutes after completing the choice game, participation in the face recognition task began. Each experimental trial began with a 1000 ms central fixation cross, and then a face presented in the center of the screen for 300 ms. On half of the trials, the target face was randomly selected from the 12 value-laden faces used in the choice game; on the other half, it was randomly selected from a set of 24 novel faces. After the target face was presented, it was replaced by a blank screen for 400 ms followed by a 1000 ms central question mark indicating a response was necessary, which was on the screen for the entire second irrespective of RT. Participants were instructed to respond as fast and as accurate as possible as to whether the target face was "old" (previously seen in learning task) or "new" (not seen in learning task) by pressing corresponding keys on a keyboard using both hands (hand-to-key relationship counterbalanced across subjects) as soon as they saw the question mark. Within this design, each value-laden face appeared as a target 60 times, randomized across trials. Twenty-four novel faces were presented one time each, with six novel faces presented during each block, randomized across trials. There were a total of 780 trials, broken up into 10 blocks of 78 trials with a two or three minute break in between each block. Each block took approximately three minutes to complete.

EEG acquisition and analyses.

EEG was recorded continuously from 64 Ag/AgCl electrodes (placed according to the extended International 10–20 system) at a sampling rate of 1000 Hz using supraorbital and infraorbital electrodes connected to a bipolar channel. Impedances were kept below 7 kΩ. The electrodes output-signal was amplified with a 16-bit amplifier (Synamp) with a band-pass filter from 0.15 to

100 Hz. EEG was transferred off-line with a 30 Hz low-pass filter, referenced to Cz, and epoched. Epochs ranged from -100 to 900 ms after the onset the target. Eye-blink artifacts were mathematically corrected and any remaining epochs containing artifacts were manually dismissed. Epochs were also eliminated if they contained excessive noise or drift. Trials with response errors were excluded prior to all analyses of EEG and behavioral data. After baseline correction relative to pre-stimulus activity and rejection of errors, there were at least 45 epochs per condition in all participants. Individual difference waveforms and grand-average waveforms were then derived from individual ERPs. Before averaging, trials were classified with respect to the EV associated with the target face during the learning phase.

Data analysis

Face recognition task. Recognition performance was measured using *d'*. Two ANOVAs of recognition performance for value-laden faces were conducted; the first used EV (-.8, -.2, 0, .2, .8) as a factor, and the second used valence (win/loss), and motivational salience (high/low) as factors (and excluded data for EV = 0). Planned paired-sample, 2-tailed *t*-tests (with Bonferroni corrections where applicable) were used to compare means. Alpha levels were set at .05.

ERP analysis. ERP components were determined on the basis of the mean global field power measured across the scalp, which summarizes the contribution of all electrodes in the form of a single vector norm. The N170 component was quantified by computing ERP mean amplitudes within a 160-235 ms post-stimulus latency window, and the P3 component within a 400-600 ms latency window. N170 was studied over the occipitotemporal region (P7, PO7, P8, PO8). P3 was studied over centroparietal sites (CPz, Pz). Mean amplitude values were then analyzed using

ANOVAs conducted separately for P3 and N170 electrodes, using electrode site and EV as within-subject factors.

Results

Learning task

Learning approximated the outcome contingencies significantly more for win pairs than loss pairs, $F(1,9) = 53.58, p < .001$. For win pairs, the high-probability win face (EV = $0.8x$) was chosen on average on 89% (SE = 2%) of trials; for loss pairs, the low-probability loss face (EV = $-0.2x$) was chosen on 75% (SE = 3%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 56% of trials (SE = 7%).

Face Recognition

Behavioral results. Figure 20 shows mean target recognition[6] (old/new; *d*') for stimuli of each EV. I first examined the effects of target EV on recognition accuracy repeated measures ANOVA. Accuracy was well above chance (EV hits M = .86, SE = .04; EV false alarms M = .11, SE = .03) and was almost identical for loss and no outcome associated faces. There was a significant main effect of target EV, $F(4,36) = 3.65, p < .05$, however there was no significant effect of valence or probability, p's > .05. There was a significant interaction between target valence and probability, $F(1,9) = 10.282, p < .05$. Paired-sample *t*-tests revealed significantly better target recognition accuracy for high probability gain faces as compared to low probability gain faces, $t(9) = 2.86, p < .05$. No other differences were significant. A lack of strong behavioral effects contrasts with results from Experiments 2 and 4, which both show a robust

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[6] As RTs were force-delayed for 400 ms, RT was not used as a measure of performance. Analysis of RTs revealed no significant effect of EV, $F < 1$.

advantage for high probability stimuli during brief masked face presentations without dual-task attentional demands. It also provides a strong rationale for investigating the electrophysiological events that occur after recognition of value-laden stimuli. This discrepancy in results between experiments is because target exposure was 300 ms in this experiment and only 85 ms (or less) in Experiments 2 and 4. A long target duration was used in the current experiment to ensure maximal correct response trials for analyses. ERP analyses (before error correction) included the same number of trial events in each EV condition except for low probability gain.

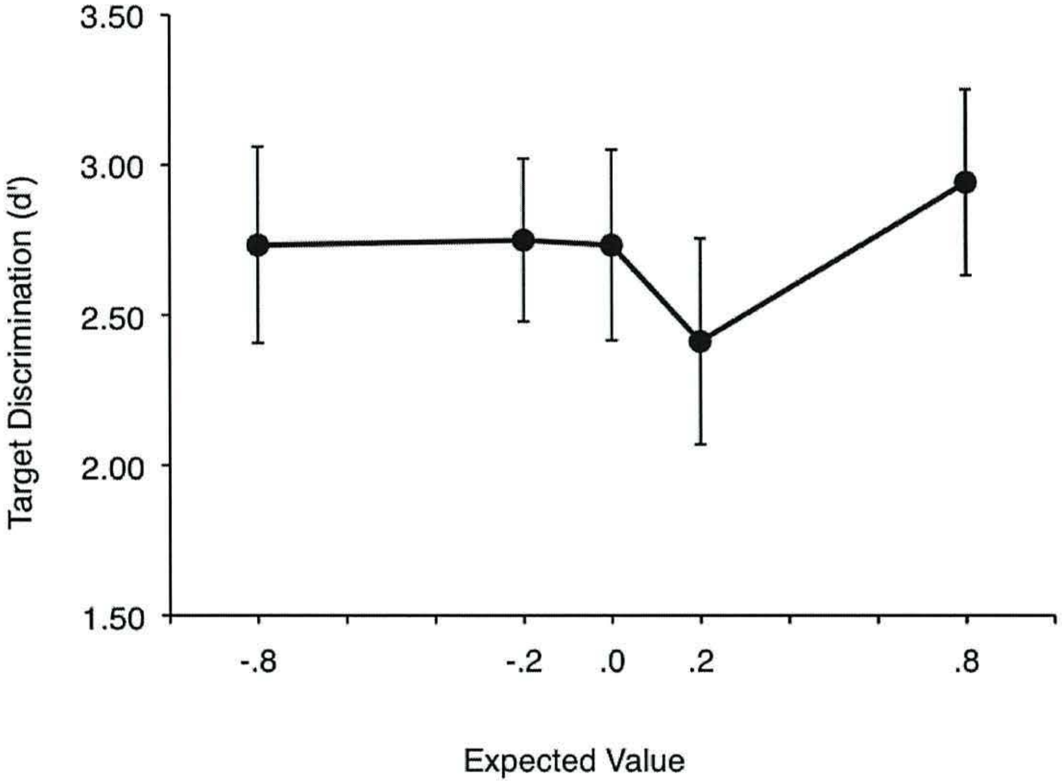

Figure 20. Mean target discrimination accuracy (*d'*) for each target EV. Error bars represent ± 1 SE.

ERP results – N170. Figures 21 and 22 show ERPs obtained at occipitotemporal electrodes in response to value-laden faces in the recognition task, separated by EV. Within the N170 time window, there was no significant modulation of N170 by target EV at any of the sites, $F < 1$, and mean amplitude did not differ across electrode sites (P7, P8, PO7, PO8), $F(1,13) = 1.27, p > .25$. Moreover, electrode site did not significantly interact with target EV, $F < 1$. Additional analyses with all trials included (correct and incorrect) also failed to reveal N170 modulation by target EV, $F < 1$. Thus, there is no conclusive evidence of EV modulating the N170 in this task.

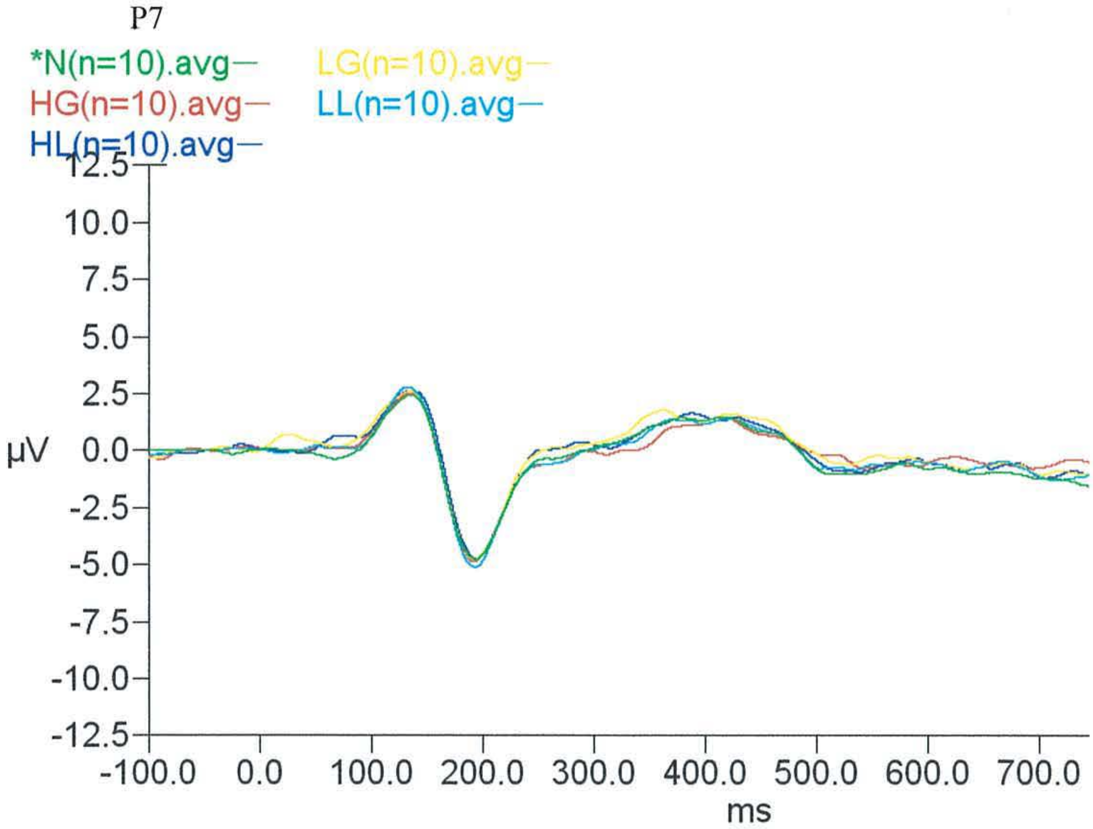

Figure 21. Average ERPs at P7 for each target EV. Green indicates neutral, red indicates high probability gain, blue indicates high probability loss, yellow indicates low probability gain, and light blue indicates low probability loss.

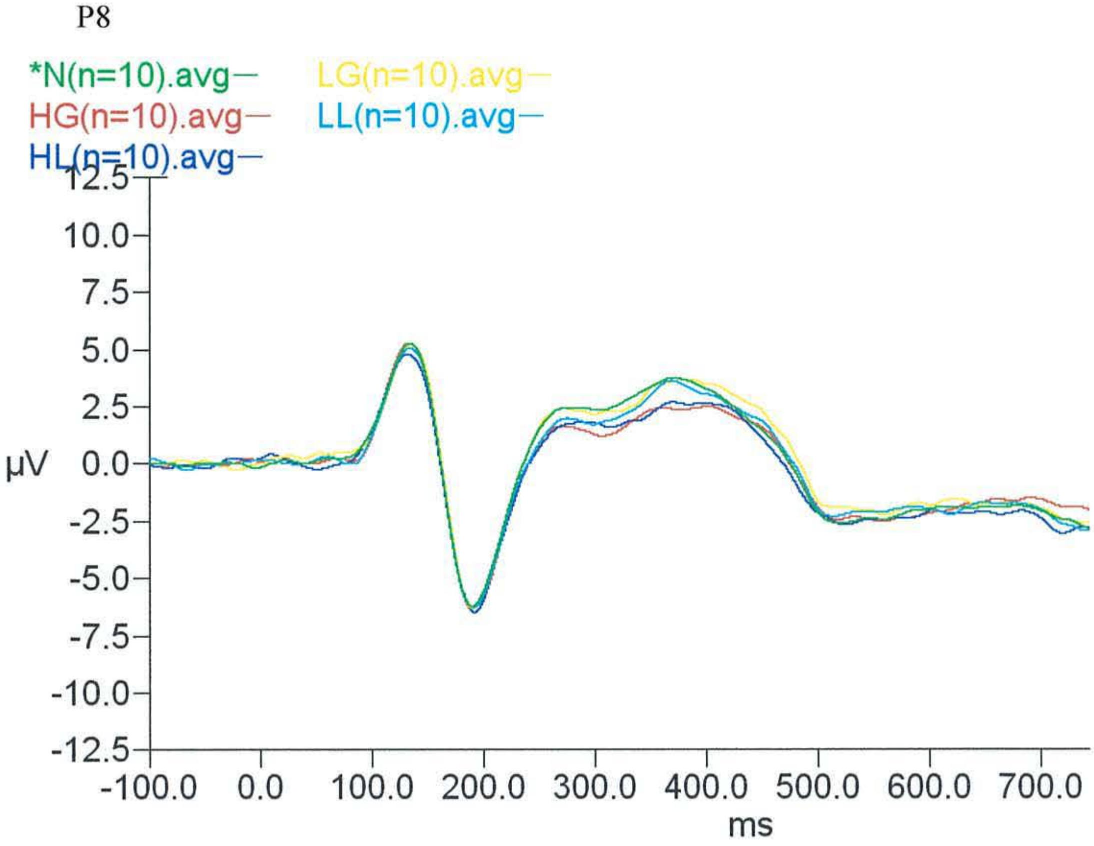

Figure 22. Average ERPs at P8 for each target EV. Green indicates neutral, red indicates high probability gain, blue indicates high probability loss, yellow indicates low probability gain, and light blue indicates low probability loss.

ERP results – P3. Figures 23 and 24 show ERPs obtained at CPz and Pz electrodes in response to value-laden faces in the recognition task, separated by EV. In contrast to N170, within the P3 time window there was a marginally significant modulation of P3 by target EV, $F(4,36) = 2.34$, $p = .073$. Planned comparisons revealed that high probability gain stimuli produced significantly greater P3 amplitude than EV neutral stimuli at both Pz, $t(9) = 5.67$, $p < .001$, and CPz, $t(9) = 3.74$, $p < .01$. Stimuli associated with a high probability of loss did not produce significantly greater P3 amplitude than EV neutral stimuli, $p > .30$. Mean amplitude marginally differed across electrode sites, $F(1,9) = 5.14$, $p = .050$, with larger amplitudes observed at Pz. However, electrode site did not significantly interact with target EV, $F < 1$.

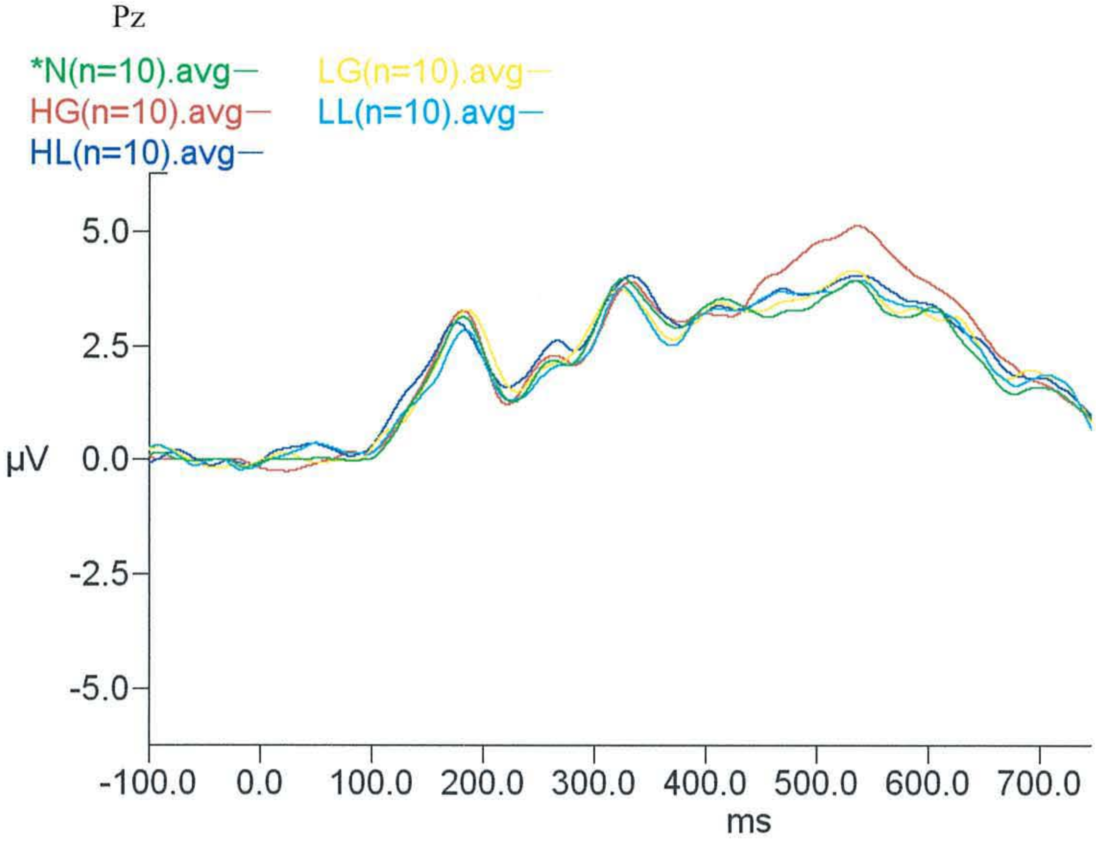

Figure 23. Average ERPs at Pz for each target EV. Green indicates neutral, red indicates high probability gain, blue indicates high probability loss, yellow indicates low probability gain, and light blue indicates low probability loss.

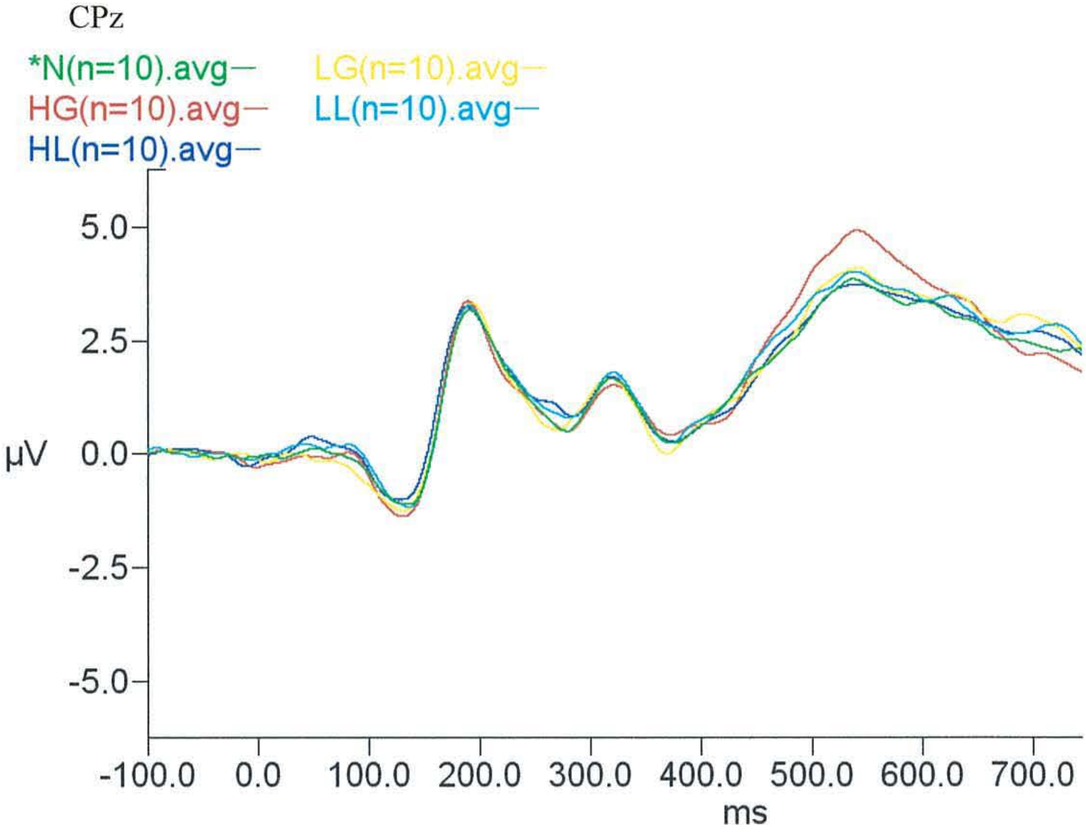

Figure 24. Average ERPs at CPz for each target EV. Green indicates neutral, red indicates high probability gain, blue indicates high probability loss, yellow indicates low probability gain, and light blue indicates low probability loss.

Chapter Discussion – Experiment 6

Experiment 6 provides electrophysiological evidence for the hypothesis that associations with gains enhance the attentional competitiveness of stimuli as well as processes linked to awareness. Faces that had previously been associated with a high probability of reward elicited a larger P3, reflecting increased attentional resources and a facilitation in perceptual processing of these faces as compared to other familiar stimuli with no EV (Schupp et al., 2000; Schupp et al., 2003). This is consistent with the proposal that P3 is sensitive to the motivational significance of stimuli (Nieuwenhuis et al., 2005). It is also consistent with evidence that P3 amplitude is greater for greater reward magnitudes (e.g., Goldstein et al., 2006; Ramsey & Finn, 1997; Yeung & Sanfey, 2004).

Schupp and colleagues (2007), who found a larger P3 for highly arousing emotional pictures (+/-) as compared to low arousing emotional pictures, hypothesized that increased P3 amplitudes to motivationally significant stimuli may reflect consolidation of stimuli in a capacity-limited second stage processing (Chun & Potter, 1995) related to conscious recognition and evaluation of significant stimuli. Indeed, as shown in AB studies measuring ERPs, seen T2 stimuli elicit P3 waves whereas unseen T2 stimuli do not (Kranczioch, Debener, & Engel, 2003; Vogel et al., 1998). According to the proposal that the P3 reflects the updating of WM (Donchin, 1981; Donchin & Coles, 1988), unseen T2 stimuli in an AB task do not elicit a P3 wave because they are never selected for further processing and consolidation into WM (see Chapter 2 for review of the two-stage model of the AB and revised version).

In the current experiment, participants view the target stimulus for 300 ms followed by a 400 ms blank screen before response. During the time window of the elicited P3 wave, the target stimulus is being consolidated into WM for subsequent recognition response. While the behavioral results showed no advantage for stimuli associated with high probability gain outcomes (except over low probability gain stimuli), they appear to have the advantage of facilitated consolidation into WM as reflected by larger P3 amplitude for these stimuli compared to other value-laden stimuli. This also suggests that high probability gain stimuli receive increased attentional resources and facilitation in perceptual processing, consistent with the behavioral results from Experiments 2 and 5 that show enhanced perception of gain stimuli under conditions of constrained attention.

Larger P3 amplitude for high probability gain stimuli is not likely to be a result of stimulus probability (i.e., oddball effect) or the frequency of target occurrence (Courchesne et al., 1975) because all value-associated faces were task relevant and seen the same number of trials during EEG recording as well as during learning. This result is also not likely to be an effect of better gain learning than loss learning in the learning task. If larger P3 amplitudes were a consequence of learning performance, we would expect to see increased amplitude for stimuli associated with low probability gain in addition to high probability gain stimuli as both of these associations are learned together within each pair.

What is surprising, in light of previous results using emotional stimuli, is the absence of P3 modulation by high probability loss faces. The aforementioned studies that found larger P3 amplitude following both positive and negative emotional stimuli, although they did not control for the EV of stimuli. In the current study, both high probability gain and high probability loss stimuli are equated for motivational saliency, so one might expect to find a similar P3 enhancement by high probability loss stimuli. In previous studies, the negative stimuli used included scenes of mutilation and threat (both by human and animal). While these images are rated as highly arousing, participants are still passive observers of them. In contrast, participants were directly affected by occurrences of monetary loss in the learning task utilized within this thesis – *they* lost money instead of watching someone else lose money. As briefly mentioned in the introduction, stimuli and events deemed "negative", including anger and threat stimuli, do not always mean loss in terms of utility. Scenes like these are sought after by millions of people, who pay money to be entertained by them in the form of movies, television, and books. Also, anyone who has been stuck in a traffic jam as a result of an accident on the opposite side of the motorway knows that most people cannot (or do not want to) prevent themselves from viewing negative scenes. It is possible that these experiences are rewarding due to enhanced arousal, and P3 amplitude is increased as a result of their association with reward.

Early visual processing, as reflected by N170, was similarly unaffected by all EVs, suggesting that stimulus value is processed after structural encoding. This is consistent with previous findings that the N170 is unaffected by face identity and emotion (e.g., Bentin & Deouell, 2000; Eimer, 2000; Eimer & Holmes, 2002; Eimer et al., 2003). It is unclear why some studies do show effects of familiarity and emotional context (e.g., Caharel et al., 2005; Galli et al., 2006; Righart & de Gelder, 2006), but these effects may be driven by stimulus properties unrelated to value codes.

In summary, the central finding of the present experiment is that stimuli highly predictive of reward trigger larger P3 amplitudes than stimuli predictive of other outcomes while the N170 is unaffected by stimulus value. Reward associations contribute to P3 generation, reflecting both heightened attention to and enhanced encoding and maintenance of reward information in memory.

SECTION 3

VALUE LEARNING AND VISUAL SEARCH: EFFECTS ON SPATIAL VISUAL ATTENTION, MOTIVATION, AND PERCEPTION[7]

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[7] The results of the experiments in this section were presented as a talk at the 49th annual meeting of the Psychonomic Society in November 2008 [Raymond, J. E., O'Brien, J. L., & Rutherford, H. J. V. (2008). When attention and motivation collide: How value learning modulates visual selection. (Abstract)]

CHAPTER 7

VISUAL SEARCH FOR EMOTIONAL FACES THAT ARE ASSOCIATED WITH VALUE: EXPERIMENTS 7 & 8

The experiments in the previous chapters used temporal attention tasks to demonstrate how value learning effects visual perception and attentional demands of learned stimuli. Regardless of attentional demands, motivational salience can facilitate recognition when this information is task relevant and create larger distractor interference when it is task irrelevant. This can be seen in both the AB and backward masking tasks. Under conditions of constrained attention, stimulus valence can determine ability to perceive a visual stimulus. An association with reward facilitates recognition when this information is task relevant and it creates larger distractor interference when it is task irrelevant, but only when attentional resources are limited.

In this section, I switch from temporal attention tasks to spatial visual search tasks investigating the relationships between value associations, perception, and selective attention. Visual search is an important method for investigating the effects of value learning on stimuli processing. We do visual search tasks all the time, every day. Some searches for items in our crowded visual world are easy; others take more effort. We are aided both by bottom-up information, such as finding a red coffee mug in a cupboard of green glasses, and by top-down knowledge of search parameters, such as looking for a mug with a large handle instead of smaller one. But what happens when this mug is also your favorite mug? Can you find it more quickly because it has motivational relevance, and does it catch your eye even when you are not looking for it?

In the next two chapters, I report a series of visual search experiments investigating the relationships between value associations, perception, and selective attention. Visual search is thought to measure efficiency of perceptual coding and object recognition. It is also a useful way to investigate the allocation of attention and the mechanisms of top-down and bottom-up attentional control. A typical search task involves speeded search for a predefined target among an array of distractor items. The total number of items in the display is referred to as the set size. Once the target has been located, its presence, location, or identity is usually reported. RTs are commonly used as a measure of search performance, in which case the display remains visible until response. RTs are usually faster when a target item is present in the search array compared to absent.

When a target item does not require focal attention to be located, it will be spotted with great ease regardless of the amount of distractors within the search array. Search for target items that do require focal attention is less efficient, with RTs increasing linearly as the set size increases. This type of search is considered to be serial where each item in a search array is checked against an internal representation of the target until the actual target has been located or determined to be absent from the array (e.g. Treisman & Gelade, 1980). Search is considered parallel when the time it takes to locate a target is independent of set size. When less attention is needed to reject distractors and identify a target, each item is individually processed faster and search is more efficient.

Efficiency within visual search is quantified as the slope of the function relating RT to set size (Duncan & Humphreys, 1989; Triesman & Gelade, 1980; Wolfe, 1998). The amount of time each additional distractor slows search for a target item determines the search slope. When the search rate per item is slow, additional items added to the array will result in a steeper search slope. Increasing set size when there is a fast search rate per item has less of an impact on search, resulting in a shallower search slope. Search falls along a continuum of efficiency, ranging from efficient search with shallow slopes (0 – 10 ms/item) to effortful search with steep slopes (20 ms/item and beyond) (Duncan & Humphreys, 1989; Wolfe, 1998).

Search efficiency is determined by the similarity of a target to nontargets (distractors) and of nontargets to each other (Duncan & Humphreys, 1989). When a target is dissimilar to nontargets, search is always highly efficient regardless of the similarity of nontargets to each other. Also, when nontargets are very similar to each other, they can be viewed as a group and disregarded as nontargets with greater ease. However, when the similarity between nontargets is reduced, target-nontarget similarity becomes very important.

According to the Guided Search model of visual search (Wolfe, 1994a; Wolfe & Cave, 1989; Wolfe, Cave, & Franzel, 1989), attention during visual search is guided to items that have high attentional priority as determined by information from top-down and bottom-up analyses of the stimuli. Bottom-up activation is based on how unusual an item is compared to its neighbors in the search array, guiding attention toward distinctive items. Top-down activation guides attention to items that match the perceptual set of a target. Bottom-up activation will guide attention toward a target if it is distinctive, but top-down activation is needed when it is not an unusual item. Attentional priority is thus determined by the interactions between bottom-up activation and how closely examined items match the top-down perceptual set.

In the next two experiments, participants were asked to search for a happy (Experiment 7) or angry (Experiment 8) face among an array of neutral faces. Like in Experiment 5, the target was identified by information unrelated to prior value associations and the task could be completed without previous knowledge of the faces. The target face when present was always a person that participants had learned to associate with a value in the learning task. Therefore, target faces were distinctive from distractor faces owing to their emotional expression, their familiarity as known faces, and their associations with value outcomes.

Familiar stimuli are known to enhance or facilitate performance in many visual perception tasks, such as discrimination amongst highly similar objects (e.g., Diamond & Carey, 1986; Gauthier & Tarr, 1997; Tanaka & Taylor, 1991), object identification (e.g., Bar & Biederman, 1998), object recognition in old/new discrimination tasks (e.g., Jackson & Raymond, 2006) and visual search tasks (e.g., Tong & Nakayama, 1999), and change detection (Buttle & Raymond, 2003). Generally, these studies suggest that high familiarity with a stimulus promotes speeded or more efficient processing. From the results of previous experiment in this thesis, it is clear that value codes can also aid in perception of stimuli as well as attract attention to their presence. It is possible that information about valence could aid in target detection, as happy faces could be intrinsically associated with positive valence (reward). Faces containing information about both happy emotion and reward may be located quicker than faces containing possibly contradictory information about punishment due to a match in top-down perceptual set. However, as there are no dual-task constraints on attention, it is possible that associations with motivational saliency will drive performance. Finally, information about value associations is irrelevant to the current task and could possibly act as a distraction during search for an emotion. Emotion processing per se was not of interest in these experiments as was used as a defining face dimension unrelated to face value. However, interesting effects of face emotion occurred that will be discussed in both this chapter and the next.

Experiment 7: Visual search for a happy value-laden face

The goal of this experiment was to explore the ability of value-laden stimuli to compete for attention within a spatial attention task. In Experiment 7, participants searched for happy target among neutral faces. Happy targets were first seen as neutral expression faces within the learning task. After participants acquired different predicted value codes for learned faces, I measured accuracy and reaction time (RT) to find these faces as happy face targets among an array of neutral faces.

Method

Participants

Nineteen experimentally naïve, healthy undergraduates from the Bangor University student panel (9 females; mean age 23 years; normal or corrected-to-normal vision) participated in exchange for money and course credit. Informed consent was given prior to participation. All achieved learning significantly above chance in the choice game for both win and loss pairs. Data from one participant were excluded due to accuracy below three standard deviations (SD) from the mean.

Stimuli

Face stimuli used in both phases were static grayscale faces of young Caucasian adult males and females (hair and neck not visible) taken from the KDEF database (same as Experiment 5; Lundqvist, Flykt, & Öhman, 1998). Faces were learned with a neutral expression and then seen as targets in the visual search phase with a happy expression. Distractors were neutral in expression. Allocation of stimuli to category was balanced.

Procedure

Value learning. The learning procedure was the same as used in Experiment 1.

Visual search task. A few minutes after completing the choice game, participation in the visual search task began, starting with a short practice session (26 trials). In each experimental trial, four, seven, or 10 faces (target and distractors) were presented at random locations within a white region (approximately 17.0° x 14.4°), with the constraint that each was separated by at least 2.9° on the horizontal axis and 3.4° on the vertical axis. A target was present on half of the trials. The target face expressed a happy emotion and was randomly selected on each target-present trial from the 12 possible value-laden faces. Neutral expression distractors were randomly selected from a set of 54 possible novel faces. Half of the trials were composed of female faces, the other half male, counterbalanced across set size. After a 1000 ms central fixation cross, the search array was presented until the participant responded to the presence or absence of a happy face. Participants were instructed to respond as quickly and accurately as possible. Trials were self-paced, and feedback on response speed and accuracy was provided after each response. Within this design, each value-laden face appeared as a target 18 times, randomized across trials. Participants completed two experimental blocks of 216 trials, each containing the same trials in a random order.

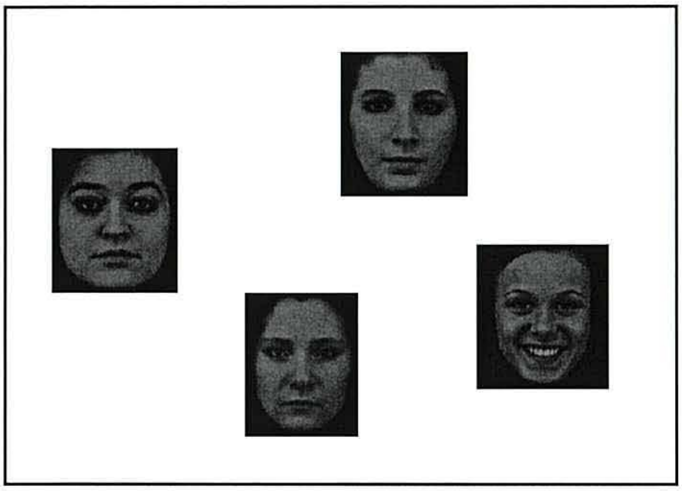

Figure 25. Example of a visual search display (set size 4), displayed until response (present/absent).

Data analysis

For the visual search task, error trials were excluded from reaction time (RT) analysis. Anticipation responses (< 200 ms) and exceedingly slow responses (>2500 ms) were removed (1% of all trials). A mean RT and standard deviation (SD) were then calculated for each condition, and any RTs that exceeded the mean of its condition by more than 2.5 SDs were removed (0.9% of trials). Two ANOVAs of recognition performance for value-laden faces were conducted; the first used EV (-.8, -.2, 0, .2, .8) as a factor, and the second used valence (win/loss) and motivational salience (high/low) as factors (and excluded data for EV = 0). Additional corresponding ANOVAs using set size and target presence were also conducted. Planned paired-sample, 2-tailed *t*-tests (with Bonferroni corrections where applicable) were used to compare means. Alpha levels were set at .05.

Results

Learning task

Learning approximated the outcome contingencies significantly more for win pairs than loss pairs, $F(1,17) = 38.24, p < .001$. For win pairs, the high-probability win face (EV = $0.8x$) was chosen on average on 88% (SE = 3%) of trials; for loss pairs, the low-probability loss face (EV = $-0.2x$) was chosen on 74% (SE = 3%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 45% of trials (SE = 5%).

Visual search

RTs. I first examined the effects of set size and target EV when the target was present[8]. When a happy target face was present in the search array, search RT increased with increasing set size, $F(2,34) = 53.45, p < .001$. Critically, RTs were also significantly modulated by the EV of the target, $F(3,44) = 3.18, p < .05$, independent of set size, $p > .20$. Search was unaffected by the previously associated valence of the target face, $F < 1$. Instead, the motivational saliency of the target EV determined search RT, $F(1,17) = 14.44, p = .001$, and the interaction between motivational salience and set size was marginally significant, $F(2,34) = 3.11, p = .058$. As can be seen in Figure 26, search for happy face targets that were previously associated with low-probability outcomes was quicker than for faces associated with high-probability outcomes at both set size 7, (M = 863 ms vs. 933 ms respectively) $t(17) = 2.90, p = .01$, and at set size 10, (M = 920 ms vs. 1019 ms respectively) $t(17) = 3.96, p = .001$. Performance for high-probability outcome faces was slower at set size 10 than performance for faces associated with no outcome, $t(17) = 2.21, p < .05$, indicating a distracting effect of high probability associations as opposed to low-probability

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[8] When the target was absent, no value-laden face was present in the display. Therefore, I only analyze target present data here.

outcome stimuli lowering RTs. To be sure that there were no effects of visual field, I analyzed the data according to the visual field in which the target appeared. The slowing of response for high-probability faces at set sizes 7 and 10 was also present when analyzing the data separately by visual field, *p*'s < .05 for both visual fields.

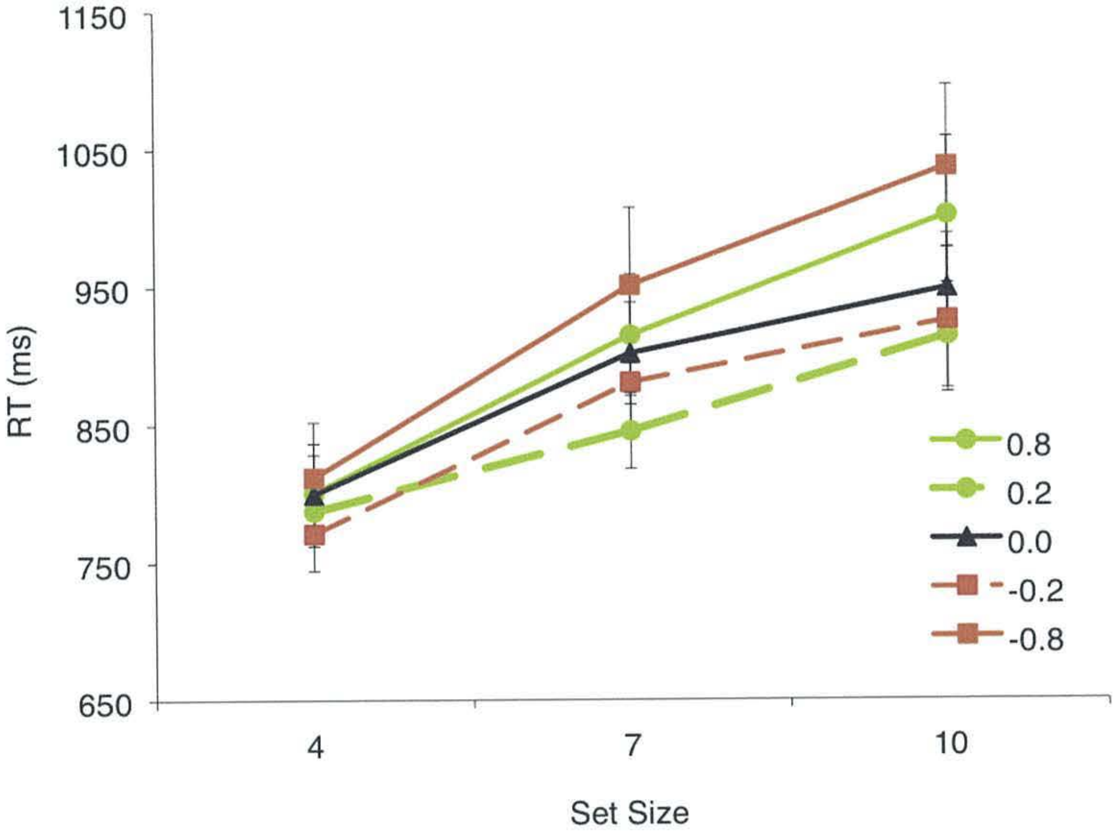

Figure 26. Mean RT (ms) to find a present happy target among neutral distractors per target EV per set size (4, 7, 10). Error bars represent ± 1 SE.

Distractor-rejection search rates. Further evidence for the importance of target probability on visual search is found when examining search slopes, defined as a measure of search efficiency. The slope of a search, calculated for each participant, is a measure of how efficient the searcher is at rejecting an additional distractor added to the search array (Duncan & Humphreys, 1989; Wolfe, 1998). Here, distractor rejection rates also depended on the probability of outcome previously associated with the target. Search rates were significantly slower when a high probability-associated face rather than a low probability-associated face was the target (39 vs. 22 ms/item), as evidenced by steeper search slopes, $F(1,17) = 25.23, p < .001$.

Accuracy. Mean accuracy was 94% (SE = 1%), with performance greater than 85% in all conditions. Performance did not differ by trial block, $p > .10$. A set size x target EV ANOVA revealed a significant main effect of set size, $F(2,34) = 8.01, p = .001$, such that more errors were made with increasing set size. Accuracy was also marginally influenced by target EV, $F(2,33) = 3.16, p = .056$, which did not significantly interact with set size, $F = 1$. Participants were more accurate when the target face was previously associated with a low-probability outcome (M = 94%) than a high-probability outcome (M = 88%), $t(17) = 4.49, p < .001$. Thus, the effects of motivational salience at set size 7 and 10 in the RT data cannot be attributed to speed/accuracy tradeoffs.

Discussion

Results from Experiment 4 suggest that value learning may guide visual search, even when it is irrelevant to the search task. Effects of learned valence were absent; previous associations with reward and loss did not interfere or aid in target detection. Instead, learned motivational salience determined search efficiency. Search for a happy face was quicker when it was associated with low-probability value outcomes than when it was associated with high-probability value outcomes. This was true for search within arrays containing more than three nontarget faces. Stimuli associated with high motivational salience were more distinctive than other items in the search displays and received higher attentional priority as a result, even though this value information was irrelevant to the task. Motivational salience thus interfered with emotion processing such that it took longer to respond to the presence of an emotional face when it was also highly motivationally salient.

Experiment 8: Visual search for a angry value-laden face

It is possible that the effects seen in the previous experiment could be due to an intrinsic relationship between motivational salience and the perceptual set evoked when searching for a happy face. Therefore, Experiment 8 was a repetition of Experiment 7 using angry faces instead of happy faces as targets. The goal of this experiment was to replicate the results in the previous search experiment while eliminating the possibility that the previous results could be explained by an interaction between target value and emotional expression.

Method

Participants

Nineteen different undergraduates from the Bangor University student panel (12 females; mean age 21 years; normal or corrected-to-normal vision) participated. Data from one participant were excluded due to accuracy below three standard deviations (SD) from the mean

Stimuli

The learned faces were the same as used in Experiment 7. These faces were then seen with an angry expression as targets in the visual search task. All distractor faces were the same as used in Experiment 7. Allocation of stimuli to category was balanced.

Procedure

The learning procedure and visual search procedure were identical to that used in Experiment 7, except now participants searched for an angry face.

Data analysis

Anticipation responses (< 200 ms) and exceedingly slow responses (>2500 ms) were removed (6.9% of all trials). A mean RT and standard deviation (SD) were then calculated for each condition, and any RTs that exceeded the mean of its condition by more than 2.5 SDs were removed (0.4% of trials).

Remaining analyses were conducted as in Experiment 7.

Results

Learning Task

For win pairs, the high-probability win face (EV = 0.8x) was chosen on average on 84% (SE = 3%) of trials; for loss pairs, the low-probability loss face (EV = -0.2x) was chosen on 74% (SE = 3%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 52% of trials (SE = 5%). As in Experiment 1, high-probability gain faces were chosen on more gain pair trials than low-probability loss faces on loss pair trials, $F(1,17) = 7.85, p < .05$.

Visual search

RTs. Examination of the effects of search set size and target EV on RTs when the target was present showed that search RT increased with increasing set size, $F(2,34) = 241.33, p < .001$. RTs were not significantly affected by the EV of the target, $F < 1$, and EV did not significantly interact with set size, $p > .40$. However, further analysis of the valence and motivational salience of the target revealed a marginally significant motivational salience x set size interaction, *F*(2,34) = 2.60, *p* = .089. As can be seen in Figure 27, search at set size 4 and 10 was unaffected by target EV, *p*'s > .40. At set size 7, however, search was faster when the target was previously associated with low-probability outcomes (M = 1210 ms) than with high-probability outcomes (M = 1270 ms), *t*(17) = 2.83, *p* < .05. When analyzing data separately by visual field in which the target appeared, RTs were faster for low-probability faces when presented in the right visual field (RVF), *t*(17) = 3.12, *p* < .01, but not the left visual field (LVF), *p* > .60.

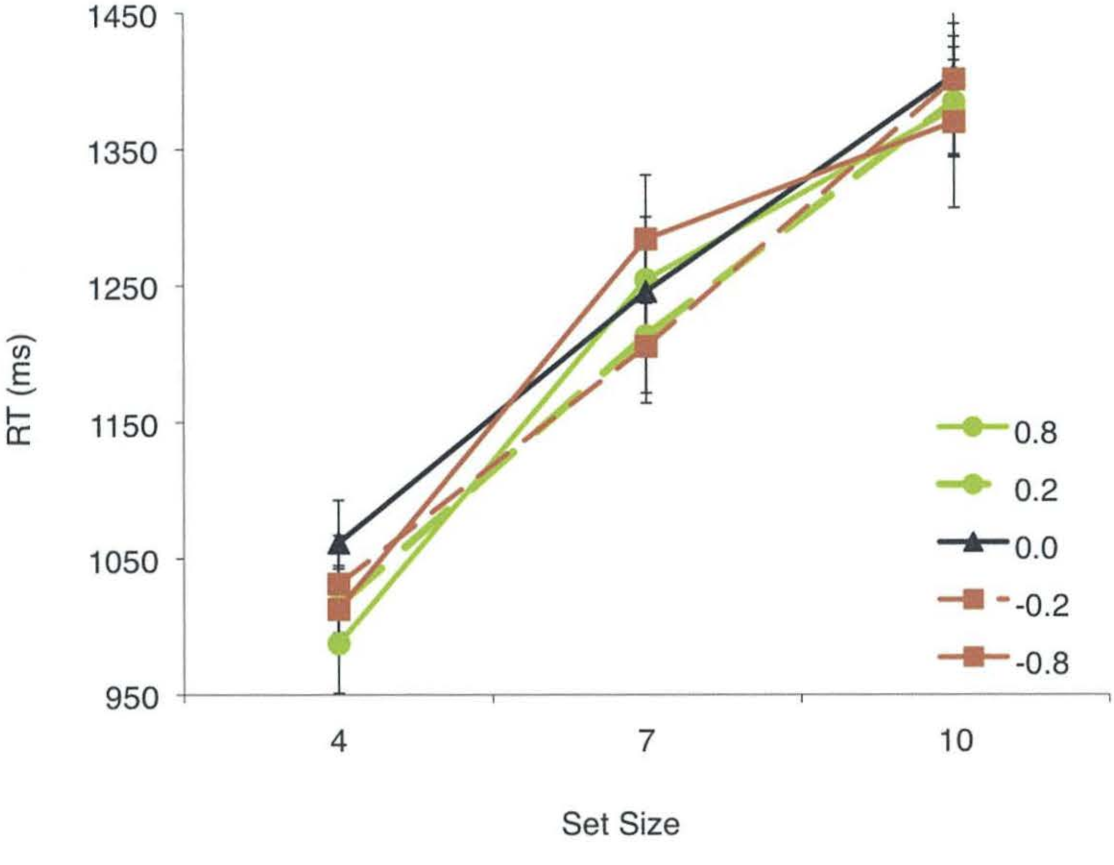

Figure 27. Mean RT (ms) to find a present angry target among neutral distractors per target EV per set size (4, 7, 10). Error bars represent ± 1 SE.

Distractor-rejection search rates. Analysis of target present search rates revealed no significant effects of target EV, *F*'s < 1.

Accuracy. Mean accuracy was 91% (SE = 1%), with performance greater than 90% in all conditions. Performance marginally differed by trial block, *t*(17) = 2.06, *p* = .055, with higher accuracy in the second block (M = .89, SE = .01) compared to the first block (M = .92, SE = .01). A set size x target EV ANOVA revealed a significant main effect of set size, *F*(2,34) = 4.70, *p* < .05, such that more errors were made with increasing set size. There was no significant effect of target EV on accuracy or interaction with set size, *F*'s < 1.

Discussion

Like Experiment 7, the current experiment showed an effect of the target's associated probability on search RTs when an angry target was present. Specifically, at set size 7, search RTs were faster when the target was associated with a low-probability outcome than with a high-probability outcome. This effect (60 ms) was similar in size to the effect found at set size 7 with a happy target (70 ms). However, since search rates were significantly slower for an angry target than a happy target (see below), the effect of motivational salience should be proportionally bigger in this experiment, but it is not. In addition, the distracting effect of motivationally salient stimuli on search RTs only occurred when the value-laden target appeared in the RVF. This is consistent with some theories of lateralization of emotional processing (e.g. approach-withdrawal model of frontal asymmetry, see Davidson, 1992; Davidson, 2004; Harmon-Jones, 2004), which propose that the left hemisphere is dominant in processing approach-related emotions including anger.

A comparison of search performance for happy and angry value-laden faces clearly shows that the probability of outcome associated with a stimulus determines the time it takes to respond to its presence (Figure 28). A between-subjects ANOVA of RTs confirm this main effect, $F(1,34) = 8.62, p < .01$. As can be seen in Figure 28, there is also a large difference in performance for search for a happy compared to angry face, $F(1,34) = 52.08, p < .001$. Happy faces were found more quickly than angry faces, regardless of their value associations, *p*'s < .05. This is consistent with a growing body of research suggesting that happy faces are detected more quickly and accurately than angry faces in visual search (e.g., Calvo, Nummenmaa, & Avero, 2008; Juth et al., 2005; see Frischen, Eastwood, & Smilek, 2008, for review). However, this is contradictory to a large body of evidence supporting an anger superiority effect in visual search (Eastwood, Smilek, & Merikle, 2001; Fox, Lester, Russo, Bowles, Pichler, & Dutton, 2000; Hansen & Hansen, 1998; Hahn, Carlson, Singer, & Gronlund, 2006; Öhman, Lundqvist, & Esteves, 2001). This discrepancy will be discussed in Chapter 8.

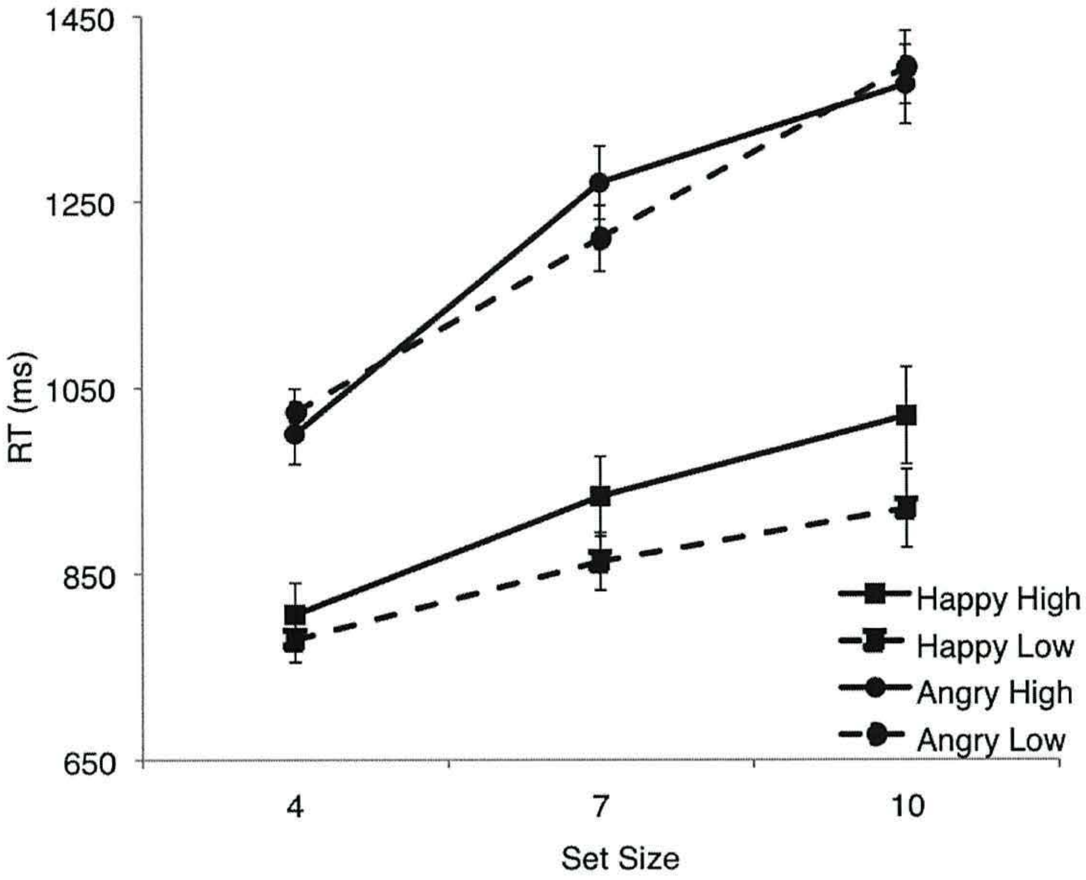

Figure 28. Mean RT (ms) to find a present emotional target among neutral distractors at each set size (4, 7, 10), plotted according to associated motivational salience with the target. Squares represent search for a happy face; circles represent search for an angry face. Solid lines represent targets associated with a high probability of outcome; dotted lines represent targets associated with a low probability of outcome. Error bars represent ± 1 SE.

Chapter Discussion – Experiment 7 & 8

The two visual search experiments reported in this chapter revealed further evidence for the important role of motivational salience in the processing of visual stimuli. Participants were able to find a happy face faster when it was previously associated with low-probability outcomes or no outcome compared to faces previously associated with high-probability outcomes, even though value information was orthogonal to the task. This effect was weaker when participants were searching for an angry face, yet still present at set size 7. Motivational salience acted as a distractor, impeding visual search performance.

Another interesting aspect of these results is that the value-laden faces were learned with a neutral expression and then seen as happy or angry in the visual search task. In the learning task, each face was seen 100 times. According to the defining properties of a robust visual representation, a visual item typically requires extensive visual experience to develop including encounters under a variety of conditions and contexts (Tong & Nakayama, 1999). Seeing a face 100 times does not usually result in a robust representation; true rapid asymptotic visual processing occurs after thousands of exposures. In these experiments, however, this limited exposure coupled with value learning resulted in rapid recognition and effective generalization to novel images – signatures of a robust representation – at least for stimuli associated with high motivational salience. Information about motivational salience drew attention to essentially novel images because they contained this abstract information, which helped participants generalize the identity across emotional expressions.

Current research on how facial affect influences attention allocation suggests that attention is widely distributed when dealing with happy faces, but more narrowly focused when processing faces with negative expressions such as angry (e.g., Fenske & Eastwood, 2003; Fox et al., 2001; Fredrickson, 2004; Fredrickson & Branigan, 2005). A global focus of attention with happy expressions makes search unfocused and more susceptible to capture by irrelevant stimuli, whereas constricted attention toward angry faces makes them resistant to the effects of peripheral information (Fenske & Eastwood, 2003). The results of Experiment 8 are consistent with this proposal: While search overall was slower for angry KDEF faces than happy ones, happy-face search was more susceptible to interference by a value-laden distractor face. It would be interesting to investigate the differences in value effects when happy and angry target search is blocked within a single experiment.

I did not examine the efficiency of search for a value-laden face when value codes were task relevant, so I cannot say for certain if search would be aided by motivational salience in this condition. However, I would predict that search for faces on a dimension relevant to value learning (e.g., locating the presence of a previously learned face amongst novel faces) would result in faster RTs for faces with high motivational salience compared to low motivational salience or associations with no outcome.

CHAPTER 8

VISUAL SEARCH FOR EMOTIONAL FACES WITH A VALUE-LADEN DISTRACTOR: EXPERIMENTS 9 - 11

In the previous two visual search experiments, targets provided information about emotional expression (task relevant) and information about previous but now task-irrelevant value associations. I found slower RTs for targets that had previously been associated with high motivational salience, suggesting that value codes were interfering with emotion processing. To find the target quickly, participants needed to prioritize emotion processing and ignore irrelevant information about face identity (value). However, when the face was motivationally salient, these value codes were processed and slowed RT to the emotion of the face. This was especially prevalent when the search was for happy faces. Angry face search was not as susceptible to interference by value information, but still showed an effect of motivational salience.

In those experiments, attention was captured by motivational salience in a non-contingent manner. What remains unclear from these experiments is whether attention was captured by the emotional expression of the target face followed by a slowing of response due to processing of value associations, or if attention was first captured by the motivational salience of the target stimulus. The final series of experiments attempts to answer this question by introducing a value-laden stimulus into the search array as a non-target, distractor image separate from the predefined target.

Visual selective attention allows privileged processing of task-relevant information while inhibiting distracting information. Normally, distractors capture attention contingent upon whether they are related to the task at hand. Attentional capture is mediated by the top-down task set – whether or not the distractor stimulus (or event) shares a feature property that is critical to the performance of the task at hand (Folk, Remington, & Johnston, 1992; Folk & Remington, 1998; Leblanc, Prime, & Jolicoeur, 2006; Leblanc & Jolicoeur, 2007; Eimer & Kiss, 2008). In other words, the specific needs of the task determine what captures attention, an effect called contingent capture.

However, some studies say that bottom-up saliency of distractors (stimulus driven features) can automatically capture attention, regardless of top-down goals (e.g., Hickey, McDonald, & Theeuwes, 2006; Theeuwes, 1991; 1992). Emotional faces, for example, have been shown to bias the spatial distribution of attention even when they are entirely task-irrelevant and attention is narrowly focused on another demanding visual monitoring task (e.g., N2pc to fearful faces next to the object monitored, Eimer & Kiss, 2007).

The question addressed here is whether value-laden stimuli, which are salient due to the top-down knowledge of prior experience, can bias visual selective attention. We know from the previous AB and masking experiments (2 & 5) that visual processing is biased in favor of reward-associated stimuli when attention is limited. It is possible that this bias will also exert influence in a visual search situation, where attention is used to locate a predefined target among nontargets including a value-laden stimulus. Contingent capture theory predicts that when a value-laden distractor shares a defining feature with the target (task relevant), it should capture attention and slow RT to the target. Value-laden distractors that do not share the target-defining feature (task irrelevant) should not capture attention and RTs should remain unaffected by the presence of the known distractor.

The goal in the present series of experiments was to establish whether value associations in distractor items capture attention in a spatial attention task, and if so, whether attention capture depends on the task-relevance of the value association. The first two experiments used emotional faces as targets, which could share a defining feature with value-laden distractor faces. More specifically, it is possible that a gain-associated stimulus shares a target-defining feature with a happy face, perhaps the quality of being a "positive" stimulus. Conversely, a loss-associated stimulus and an angry face may both be considered "negative." If these contingent relationships are valid, then contingent capture theory would predict that performance when searching for a happy face (Experiment 9) would be slowed by the presence of a gain-associated face due to the shared attentional set of a positive-valenced stimulus, and the same for angry face search when a loss-associated face is present due to the shared attentional set of a negative-valenced stimulus.

However, while anger is negative in valence it often elicits approach motivation (see Harmon-Jones, 2004, for review) while loss most likely does not. In fact, anger is sometimes viewed as a positive when evaluated subjectively as an emotion. Indeed, Ekman and Friesen (1975) even suggested that some individuals take pleasure in experiencing anger. Thus, anger may not equal loss in terms of shared utility, in which case loss-associated faces may not capture attention when searching for an angry target.

Targets in the third experiment were inverted faces, which did not share a defining feature with value-laden distractor faces. In this experiment, I predicted that motivational salience would once again determine search RTs.

Experiment 9: Visual search for a happy target with a value-laden distractor

In Experiment 9, like in Experiment 7, participants searched for a target with a happy expression among neutral faces. However, this time happy targets were novel and had not been previously associated with winning or losing money. Instead, after participants acquired different predicted value codes for learned faces, they saw these faces as neutral distractors within the visual search array. I measured accuracy and reaction time (RT) to find a happy face target among an array of neutral faces including one critical value-laden distractor.

Method

Participants

Thirty-three experimentally naïve, healthy undergraduates from the Bangor University student panel (17 females; mean age 21 years; normal or corrected-to-normal vision) participated in exchange for money and course credit. Informed consent was given prior to participation. Data from three participants were excluded due to accuracy below three standard deviations (SD) from the mean.

Stimuli

Learned faces were the same computer-generated male faces used in Experiment 1. Novel distractor faces and happy target faces were also computer generated. Allocation of stimuli to category was balanced.

Procedure

Value learning. The learning procedure was the same as that used in Experiment 1.

Visual search task. The visual search procedure was the same as that used in Experiment 7, with a happy target was present on half of the trials, randomly selected on each target-present trial from a set of 50 possible novel faces. Neutral expression distractors were randomly selected from a set of 150 possible novel faces. The critical distractor was either selected from the 12 value-laden faces used in the choice game or from the set of neutral expression novel faces.

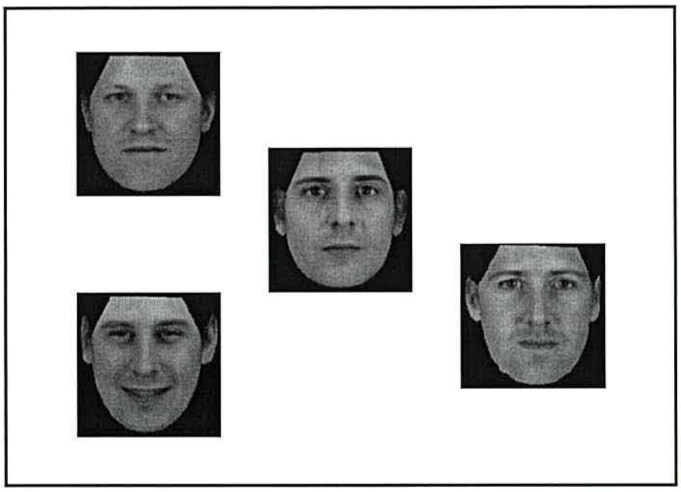

Figure 28. Example of a visual search display for a happy face target (set size 4), displayed until response (present/absent).

Data analysis

For the visual search task, error trials were excluded from reaction time (RT) analysis. Anticipation responses (< 200 ms) and exceedingly slow responses (>2500 ms) were removed (7.5% of all trials). A mean RT and standard deviation (SD) were then calculated for each condition, and any RTs that exceeded the mean of its condition by more than 2.5 SDs were removed (0.1% of trials). Two ANOVAs of recognition performance for value-laden faces were conducted; the first used EV (-.8, -.2, 0, .2, .8) as a factor, and the second used valence (win/loss) and motivational salience (high/low) as factors (and excluded data for EV = 0). Additional corresponding ANOVAs using set size and target presence were also conducted.

Planned paired-sample, 2-tailed *t*-tests (with Bonferroni corrections where applicable) were used to compare means. Alpha levels were set at .05.

Results

Learning task

Learning approximated the outcome contingencies marginally greater for win pairs than loss pairs, $F(1,29) = 3.56$, $p = .062$. For win pairs, the high-probability win face (EV = $0.8x$) was chosen on average on 76% (SE = 2%) of trials; for loss pairs, the low-probability loss face (EV = $-0.2x$) was chosen on 70% (SE = 3%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 42% of trials (SE = 3%).

Visual search

RTs. I first examined the effects of set size and and EV of the critical distractor on search RTs when the target was either present or absent using a repeated measures ANOVA. Search for a happy target was remarkably slower when the target was absent than present (1144 ms vs. 1704 ms), $F(1,29) = 269.39$, $p < .001$. When the target was absent, RTs were slowed more so by the increase in set size than when the target was present, $F(1,34) = 429.52$, $p < .001$. There was also a marginally significant main effect of critical distractor EV, $F(4,116) = 2.07$, $p = .089$.

I then examined the effects of set size and distractor EV for target-absent and target-present conditions separately. When the target was absent, the EV of distractors did not significantly affect search, $p > .30$, and did not significantly interact with set size, $F < 1$. All subsequent analyses focus on target-present data only.

When a happy target was present in the search array, search RT increased with increasing set size, *F*(2,58) = 230.49, *p* < .001. Critically, RTs were also significantly affected by the EV of the critical distractor depending on the set size, as shown by a significant interaction between the two, *F*(8,232) = 1.99, *p* < .05. As is readily apparent in Figure 29, the EV of the critical distractor significantly influenced search at set size 10 but not at the other set sizes. Search was significantly slower when a gain-associated distractor was present than when a loss-associated distractor was present, *F*(1,29) = 13.99, *p* = .001, regardless of the motivational salience of the distractor, *F* < 1. Search was also significantly slower when a gain-associated distractor was present than when a learned distractor associated with no outcome was present (1339 ms vs. 1245 ms), *t*(29) = 2.61, *p* < .05.

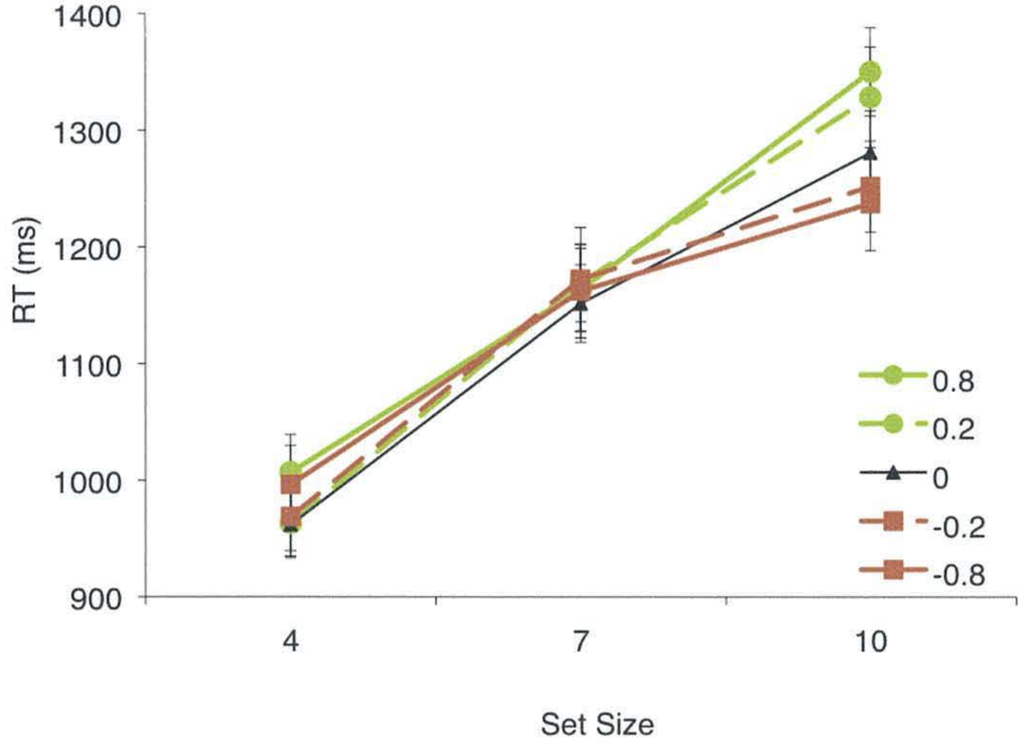

Figure 29. Mean RT (ms) to find a present happy target among neutral distractors per distractor EV per set size (4, 7, 10). Error bars represent ± 1 SE.

Distractor-rejection search rates. Further evidence for the importance of distractor valence on visual search is found when examining search slopes. Distractor rejection rates depended on the valence of the critical distractor. Search rates were significantly slower when a gain-associated distractor rather than a loss-associated one was present (59 vs. 44 ms/item), as evidenced by steeper search slopes, $F(1,29) = 10.62$, $p < .01$. Search rates were also significantly slower when a gain-associated distractor rather than a learned distractor associated with no outcome was present (59 vs. 50 ms/item), as evidenced by steeper search slopes, $t(29) = 2.22$, $p < .05$.

Accuracy. Mean accuracy was 93% (SE = 1%), with performance greater than 88% in all conditions. A set size x distractor EV ANOVA revealed a significant main effect of set size, $F(2,58) = 28.51$, $p < .001$, such that more errors were made with increasing set size. However, accuracy was not significantly influenced by distractor EV, $F(3,83) = 2.26$, $p = .091$, and distractor EV did not significantly interact with set size, $F < 1$. Thus, the effects of valence at set size 10 in the RT data cannot be attributed to speed/accuracy tradeoffs.

Discussion

The present experiment showed significant effects of distractor valence on search RTs. The interference was due to the presence of gain-associated distractors; search was unaffected by the presence of distractors associated with loss or no outcome. This is consistent with a contingent capture hypothesis: gain-associated faces captured attention because they contained a target-defining feature (positive valence) and therefore matched the current top-down attentional set. This finding is also consistent with results from Chapter 4 suggesting that gain-associated stimuli have a processing advantage when stimuli are competing for attention. It is possible that gain-associated stimuli captured attention away from the target due to enhanced attentional competitiveness afforded to gain stimuli. If this is true, then gain-associated stimuli should capture attention and increase RTs in the same manner when the feature that defines the target is not shared with gain stimuli.

Experiment 10: Visual search for an angry target with a value-laden distractor

One possible explanation of the modulation of search RTs by gain-associated distractors found in Experiment 9 is that these distractors were more similar to the targets and thus increased search difficulty (Duncan & Humphreys, 1989). A contingent capture hypothesis would suggest that involuntary orienting of attention to the gain-associated distractors occurred because they shared a feature property that is critical to locating the target (Folk et al., 1992). A top-down goal of searching for a positive face thus might increase the salience of the value-laden distractors containing this task-relevant property (Cave & Wolfe, 1990). Since the loss-associated distractors did not share this feature with happy targets, they were suppressed, resulting in fewer distractors and speedier search. If this were the case, then the same RT modulation by value-laden distractors should occur with loss-associated distractors when the target face is negative. However, if the valence effects are a result of the attentional competitiveness of gain stimuli, then the same results should be seen when the target expresses a different emotion. To test this, I repeated Experiment 9 using angry targets instead of happy.

Method

Participants

Thirty-three different undergraduates from the Bangor University student panel (22 females; mean age 20 years; normal or corrected-to-normal vision) participated. Data from five participants were excluded due to accuracy below three standard deviations (SD) from the mean.

Stimuli

Targets were computer-generated angry male faces. All distractor faces (novel and learned) were the same as used in Experiment 9. Allocation of stimuli to category was almost balanced, with four people in learning version 1 and 4, and five people in version 2, 3, 5, and 6.

Procedure

The learning procedure and visual search procedure were identical to that used in Experiment 9, except now participants searched for an angry face.

Data analysis

Anticipation responses (< 200 ms) and exceedingly slow responses (>2500 ms) were removed (3.1% of all trials). A mean RT and standard deviation (SD) were then calculated for each condition, and any RTs that exceeded the mean of its condition by more than 2.5 SDs were removed (0.1% of trials). Remaining analyses were conducted as in Experiment 9.

Results

Learning Task

For win pairs, the high-probability win face (EV = 0.8*x*) was chosen on average on 81% (SE = 2%) of trials; for loss pairs, the low-probability loss face (EV = -0.2*x*) was chosen on 70% (SE = 2%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 44% of trials (SE = 4%). High-probability gain faces were chosen on more gain pair trials than low-probability loss faces on loss pair trials, $F(1,27) = 19.15, p < .001$.

Visual search

RTs. Examination of the effects of search set size and critical distractor EV on RTs showed that search for an angry target was remarkably slower when the target was absent than present (1367 ms vs. 960 ms), $F(1,27) = 201.28, p < .001$. As in Experiment 9, there was a significant target presence x set size interaction, $F(1,37) = 90.60, p < .001$. Unlike Experiment 9, however, the main effect of critical distractor EV was not significant, $F(3,84) = 1.53, p = .211$.

A two-way ANOVA of target absent data using distractor EV and set size as factors revealed a surprising significant main effect of distractor EV, $F(4,108) = 3.26, p < .05$, which did not interact with set size, $F < 1$. When the data were reanalyzed for valence and motivational salience effects, RTs for search when a gain-associated distractor was present were significantly slower than when a loss-associated distractor was present (1381 ms vs. 1354 ms), $F(1,27) = 6.50, p < .05$. Also, the effect of motivational salience was marginally significant, $F(1,27) = 3.73, p = .064$; highly predictable distractors slowed search more than less predictable distractors. More specifically, search was marginally quicker with the presence of a distractor associated with low-probability loss (1340 ms) than when any of the other value-laden distractors were present, *p*'s < .07.

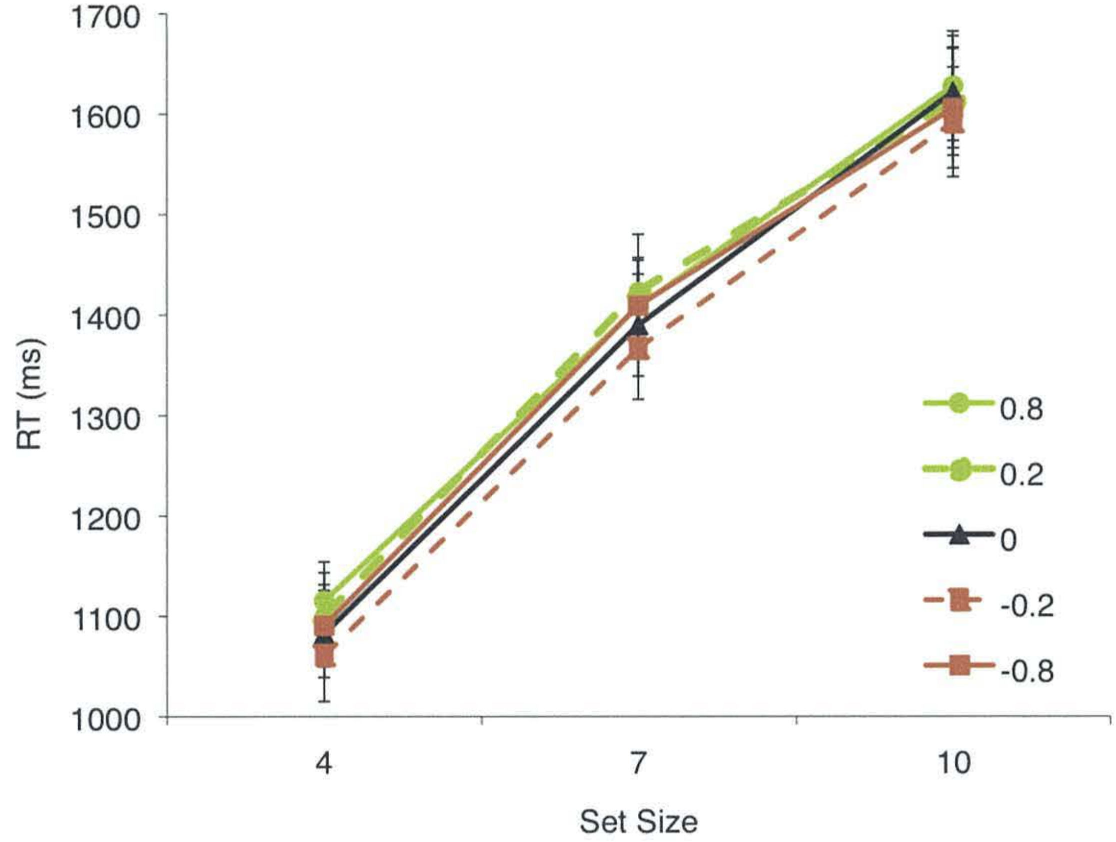

Figure 30. Mean RT (ms) to determine that an angry target is absent among neutral distractors per distractor EV per set size (4, 7, 10). Error bars represent ± 1 SE.

When an angry target was present in the search array, search RT increased with increasing set size, *F*(2,54) = 108.74, *p* < .001 (Figure 31). RTs were not significantly affected by the EV of the critical distractor, *F* < 1, and EV did not significantly interact with set size, *F*(5,145) = 1.07, *p* = .386.

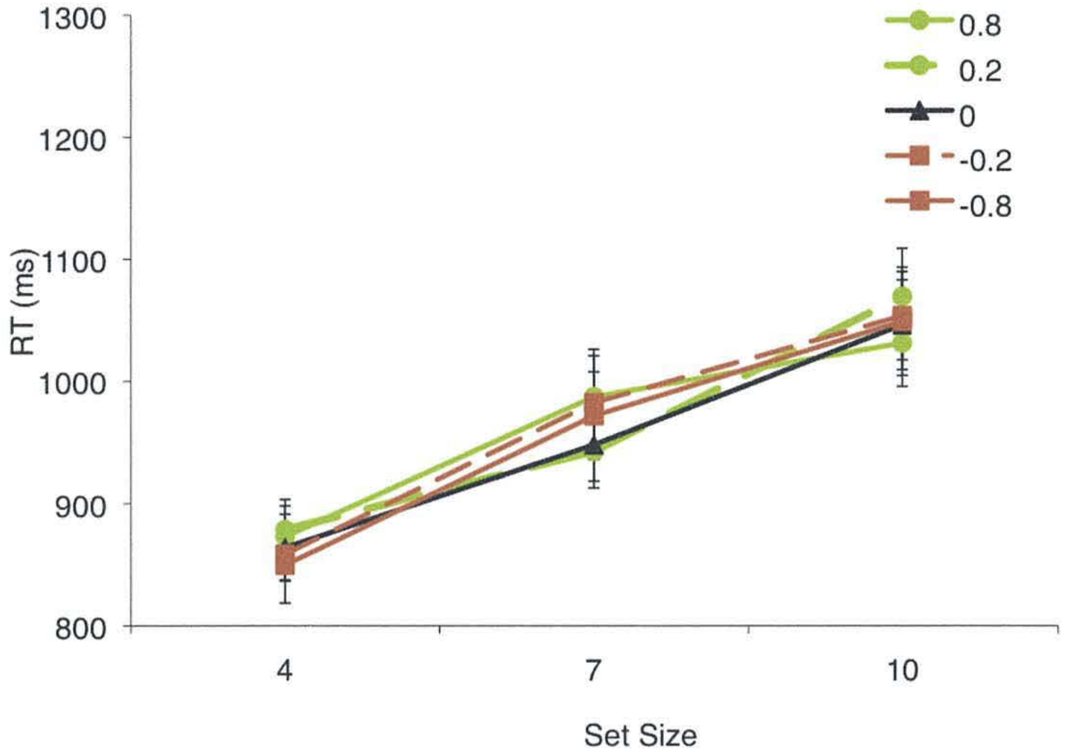

Figure 31. Mean RT (ms) to find a present angry target among neutral distractors per distractor EV per set size (4, 7, 10). Error bars represent ± 1 SE.

Target – critical distractor proximity. To further examine the lack of distractor EV modulation on search RT when the target was present, I analyzed RTs based on the proximity of the critical distractor to the target. Trials were grouped into two groups: close (fewer than half the available screen pixels separating both the x and y coordinates of the target and critical distractor) or far (more than half of the available screen pixels separating either the x or the y coordinates of the target and critical distractor). Separate analysis of close and far RTs revealed no significant effects of distractor EV in either case, *p*'s > .20.

Distractor-rejection search rates. Analysis of target present search rates revealed no significant effects of distractor EV, *F*'s < 1.

Table 5. Search slopes for correct angry face search when target was present.

EV	Slope
0.8	26
0.2	32
0	30
-0.2	33
-0.8	33

Accuracy. Mean accuracy was 93% (SE = 0%), with performance greater than 90% in all conditions. A set size x distractor EV ANOVA revealed a significant main effect of set size, $F(2,54) = 6.71, p < .01$, such that more errors were made with increasing set size. The effect of distractor EV on accuracy was marginally significant, $F(4,108) = 2.40, p = .054$, and its interaction with set size was also marginally significant, $F(8,216) = 1.77, p = .084$. Reanalyzing the accuracy data for effects of valence and motivational salience revealed a significant three-way interaction of set size, valence, and probability, $F(2,54) = 3.36, p < .05$. I analyzed accuracy for each set size separately, and found significant effects of distractor EV only in set size 4, with nonsignificant distractor effects at larger set sizes, *p*'s > .10. More specifically, at set size 4 the valence of the critical distractor significantly interacted with its probability, $F(1,27) = 13.25, p = .001$. Paired samples *t*-tests showed that, at set size 4, accuracy was significantly higher when a search array contained a distractor associated with high-probability loss outcomes (96%) than any other value-laden distractor, *p*'s < .058.

Discussion

Unlike Experiment 9, the current experiment showed no effects of critical distractor EV on search RTs when an angry target was present. When the target was absent, however, distractor EV did produce marginal interference. Specifically, search RTs were faster when a distractor associated with low-probability loss was included in the search array than any other value-laden stimuli. It is possible that the results in Experiment 9 are not due to compatibility between critical distractor and target, and instead are value specific. This idea is supported by the fact that, when the target was present, there were fewer errors (at set size 4) when the search array contained a high-probability loss distractor than any other value-laden distractors. In other words, the compatibility of loss-associated distractors with an angry target did not affect search RTs. On the contrary, loss-associated distractors aided search RTs and accuracy.

If the gain effects in Experiment 9 are due to preferential processing of gain-associated stimuli, then why do we not see these same effects in this experiment? Many studies have shown that anger information is available preattentively and angry faces have been shown to guide focal attention more effectively in visual search than happy faces (e.g., Eastwood et al., 2001; Fox et al., 2000; Gerritsen, Frischen, Blake, Smilek, & Eastwood, 2008), a well-documented occurrence known as the "anger superiority effect" (Hansen & Hansen, 1988). It is possible that angry face targets guided focal attention (narrowing of attention) to their location before a value-laden distractor could have an effect; whereas, in Experiment 9, happy face targets were less efficient in guiding focal attention (broadening of attention) and were thus subject to more interference by a meaningful distractor. In support of this, a comparison of search slopes of Experiments 9 and 10 using a mixed factors ANOVA with target type as a between-participants variable and distractor EV as a within-participants variable revealed considerably steeper slopes for happy targets (M = 51.66) than for angry targets (M = 31.20), *F*(1,56) = 34.18, $p < .001$[9].

Another possibility is that searching for an emotional face among distractor faces places constraints on attention similar to the reduced attention condition in an AB task. While searching for an emotional face, participants have to attend to task relevant information while ignoring irrelevant information. Faces associated with gain outcomes capture attention, like in an AB task, but here this face is not the target and performance is slowed (Experiment 9). Loss associations do not enhance the attentional competitiveness of stimuli; thus, these distractors do not capture attention in either task.

Finally, the results of both experiments could be due to contingent capture. Critical distractors that did not share the target-defining feature were ignored in both experiments: loss-associated faces in happy search and gain-associated faces in angry search. In addition, loss-associated faces may not have shared a target-defining feature with angry faces and were ignored as well. In this case, lack of effects on performance by distractor EV could be due to lack of contingent attentional capture by value-laden stimuli. To address these issues, none of the distractors shared the target-defining feature in Experiment 11.

An additional point of interest in the results of the aforementioned visual search experiments (7 – 10) is the difference in search efficiency for emotional faces. In Experiments 7 and 8, search was quicker and more efficient for happy faces compared to angry faces. In Experiments 9 and 10, the opposite result occurred. In all four experiments, the procedure was identical and the only thing that changed was the

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[9] It is also possible that differences in search efficiency result from featural differences between the positive and negative faces used in these experiments, and not the emotional valence (see Wolfe & Horowitz, 2004).

face set used. Happy faces were found more quickly and easily when they were from the KDEF database than computer generated, and vice versa for angry faces.

There were some featural differences between the sets. All happy faces in both face sets were showing teeth, but only some angry faces in the computer-generated set and no faces in the KDEF set showed teeth. However, if differences in search rates were due to the presence of teeth, then we would expect happy computer-generated faces to show the same search RTs as happy KDEF faces and angry computer-generated faces. In fact, analysis of RTs from all four experiments using emotional targets revealed a significant interaction between the emotion of the face and the face set from which it came, $F(1,90) = 72.26$, $p < .001$. As established earlier, performance within a face set significantly differed by emotional expression, *p*'s $< .001$. In contrast, fast and efficient search for angry computer-generated faces did not significantly differ from search for happy KDEF faces, $p = .10$. Slower and less efficient search for happy computer-generated faces also did not significantly differ from search for angry KDEF faces, $p > .35$. While differences in overall search performance could still be attributed to low-level visual features, it is an interesting discovery to find that search for an angry or happy face among neutral distractors can be equivalent, depending on the face set used.

Experiment 11:

Visual search for an inverted neutral target with a value-laden distractor

The primary focus of the present series of experiments is to investigate how the EV of a stimulus captures attention during visual search as well as how effective the searcher is at inhibiting them. Therefore, I was not specifically concerned with differences in emotion processing when searching for a happy versus an angry face.

In this experiment, the emotion variable was removed and participants searched for an inverted face among upright faces instead.

Method

Participants

Twenty-five experimentally naïve, healthy undergraduates from the Bangor University student panel (17 females; mean age 20 years; normal or corrected-to-normal vision) participated in exchange for money and course credit. Informed consent was given prior to participation. Data from three participants were excluded due to accuracy below three standard deviations (SD) from the mean. Data from an additional participant were excluded due to ceiling performance

Stimuli

Learned faces were the same computer-generated male faces used in Experiment 2. Novel distractor faces were the same used in Experiments 9 and 10. Inverted faces were additional novel faces not seen as distractors. All faces were cropped such that the ears and top of the forehead were not shown (Figure 32). Allocation of stimuli to category was almost balanced, with two people in learning version 2, three people in version 5, and four people in versions 1, 3, 4, and 6.

Procedure

Value learning. The learning procedure was the same as used in Experiment 1.

Visual search task. The visual search procedure was the same as used in Experiments 9 and 10, except participants now searched for an inverted face among upright faces. An inverted target face was present on half of the trials, randomly selected on each target-present trial from a set of 50 possible novel faces. Neutral expression distractors were randomly selected from a set of 100 possible novel faces. The critical distractor was either selected from the 12 value-laden faces used in the choice game or from the set of neutral expression novel faces.

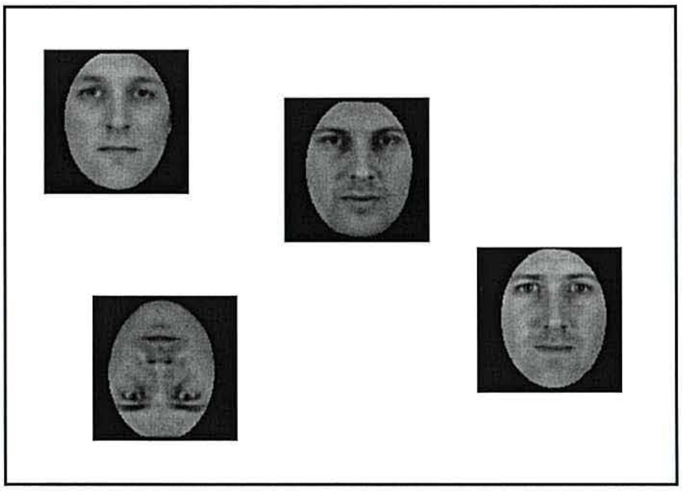

Figure 32. Example of a visual search display for an inverted face target (set size 4), displayed until response (present/absent).

Data analysis

For the visual search task, error trials were excluded from reaction time (RT) analysis. Anticipation responses (< 200 ms) and exceedingly slow responses (>2500 ms) were removed (2.1% of all trials). A mean RT and standard deviation (SD) were then calculated for each condition, and any RTs that exceeded the mean of its condition by more than 2.5 SDs were removed (1.2% of trials). Remaining analyses were conducted as in Experiment 9.

Results

Learning task

Learning approximated the outcome contingencies greater for win pairs than loss pairs, $F(1,21) = 4.70$, $p < .05$. For win pairs, the high-probability win face (EV = $0.8x$) was chosen on average on 77% (SE = 3%) of trials; for loss pairs, the low-probability loss face (EV = $-0.2x$) was chosen on 70% (SE = 3%) of trials; and for no-outcome control pairs (EV = 0), an arbitrarily selected face in each pair was chosen on 49% of trials (SE = 3%).

Visual search

RTs. I first examined the effects of set size and and EV of the critical distractor on search RTs when the target was either present or absent using a repeated measures ANOVA. Search for an inverted target was remarkably slower when the target was absent than present, $F(1,20) = 64.57$, $p < .001$. When the target was absent, RTs were slowed more so by the increase in set size than when the target was present (1037 ms vs. 1324 ms), $F(2,30) = 24.13$, $p < .001$.

I then examined the effects of set size and distractor EV for target-absent and target-present conditions separately. When the target was absent, the EV of distractors did not significantly affect search, $p > .20$, and did not significantly interact with set size, $F < 1$. All subsequent analyses focus on target-present data only.

When an inverted target was present in the search array, search RT increased with increasing set size, $F(2,40) = 113.52$, $p < .001$. RTs were not significantly affected by the EV of the critical distractor, $F < 1$. However, analysis of effects of distractor valence and motivational salience on RTs revealed a significant interaction between distractor motivational salience and set size, $F(2,40) = 4.94$, $p < .05$. At set size 10, search was significantly slower when a motivationally salient distractor was present (1169 ms) than when a distractor with low motivational saliency was present (1117 ms), *F*(1,20) = 5.11, $p < .05$, regardless of the valence of the critical distractor, $F < 1$. Additionally, performance at set size 4 was also affected by the motivational salience of the critical distractor, but in the opposite way: RTs were marginally faster when a motivationally salient distractor was present (887 ms) than when a distractor with low motivational saliency was present (924 ms), *F*(1,20) = 3.93, $p = .061$.

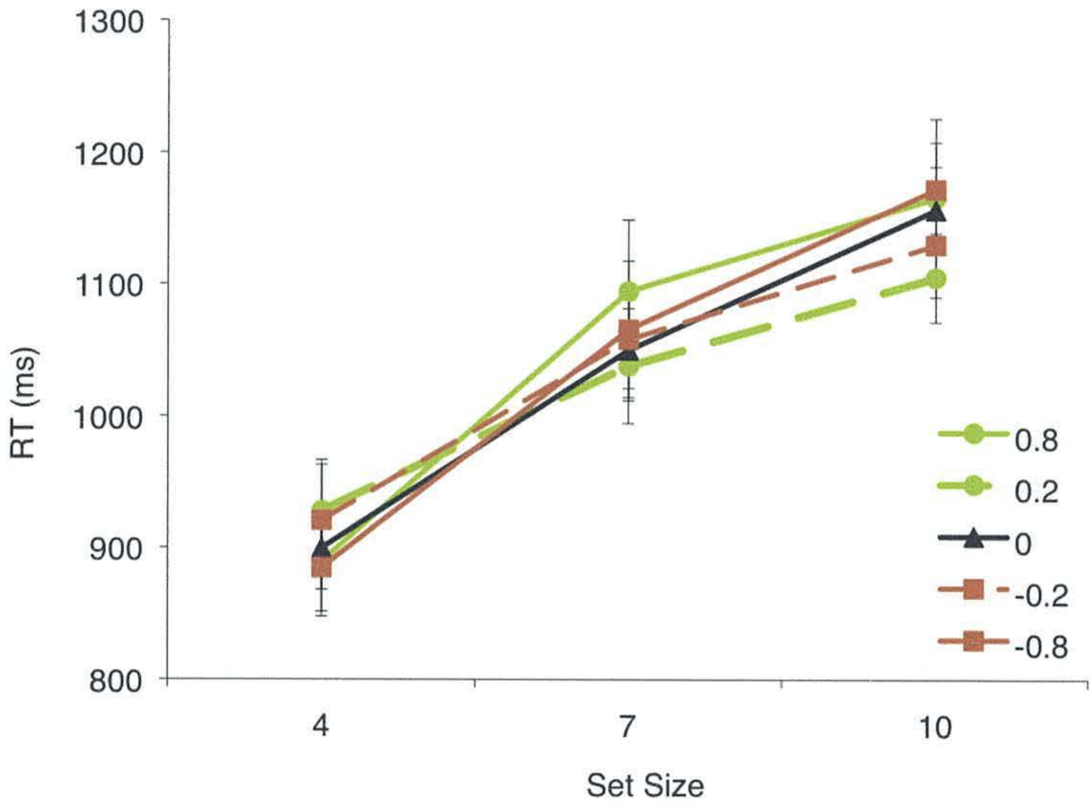

Figure 33. Mean RT (ms) to find a present inverted face target among upright distractors per distractor EV per set size (4, 7, 10). Error bars represent ± 1 SE.

Distractor-rejection search rates. Distractor rejection rates also depended on the motivational salience of the critical distractor. Search rates were significantly slower when a motivationally salient distractor rather than a distractor associated with a low probability of outcome was present (47 vs. 32 ms/item), as evidenced by steeper search slopes, $F(1,20) = 10.27, p < .01$. Search rates when a high or low motivationally salient distractor was present were not significantly different from when a learned distractor associated with no outcome was present, *p*'s > .05.

Accuracy. Mean accuracy was 96% (SE = 1%), with performance greater than 90% in all conditions. A set size x distractor EV ANOVA revealed no significant effects of set size or distractor EV, *p*'s > .15. Thus, the effects of motivational salience in the RT data cannot be attributed to speed/accuracy tradeoffs.

Discussion

When an inverted face was presented among upright faces, the presence of a non-target face associated with a high probability of outcome significantly slowed search at set size 10 compared to the presence of a face associated with a low probability of outcome. Similar to Experiment 10, the current experiment revealed no effects of distractor valence on search RTs. Unlike Experiment 10, however, recognition was enhanced for stimuli with high motivational salience and interfered with the detection of the target. It is possible that effects of motivational salience were absent in Experiment 10 due to a narrowing of attention when searching for an angry face that successfully inhibited attentional capture by value-associated stimuli.

These results suggest that the gain effect in Experiment 9 is due to contingent capture by a shared feature with the target. When the task set was to search for a happy face, gain-associated faces successfully competed for attention. When the task set was to search for an angry face, loss-associated faces did not compete for attention. The reason for this could be the lack of attentional competitiveness of loss-associated faces, as seen in Experiment 2, or a narrowing of attention when searching for an angry face. It could also be accounted for by a lack of contingency between loss-associated and angry faces. Additional investigation is needed to disentangle this issue.

Chapter Discussion – Experiments 9, 10, & 11

In three experiments, participants were required to locate the presence of a predefined target while ignoring a value-laden distractor. In Experiment 9, the target was defined as a happy face, and gain-associated distractors slowed performance. In Experiment 10, the target was defined as an angry face, and performance was unaffected by the presence of value distractors (when target was present). Finally, in Experiment 11 the target was an inverted face and motivationally salient faces slowed performance.

The pattern of results across these experiments supports three main conclusions. First, gain-associated faces contingently capture attention when they are irrelevant distractors but match the current attentional set; loss-associated faces do not. Second, faces high in motivational salience capture attention when they are outside of the current attentional set. These results are consistent with the idea that associations with gains but not losses enhances the attentional competitiveness of stimuli, whereas outcome probability modulates other processes important for recognition independently of attention. Third, effects of value learning were present for happy search, when attention was more globally focused, and absent for angry search, when attention was more locally focused. This is consistent with hypothesis that happy face search is more susceptible to attention capture by irrelevant stimuli while angry face search is resistant (e.g., Fenske & Eastwood, 2003; Fox et al., 2001; Fredrickson, 2004; Fredrickson & Branigan, 2005).

SECTION 4

GENERAL DISCUSSION

To perceive an object in our visual world, we rely on bottom-up feedforward processing of visual information through the hierarchy of visual processing, along with top-down feedback information. Top-down information helps guide feedforward processing to interpret sensory information more quickly and efficiently than feedforward processing can typically accomplish on its own (except in cases of pop-out) (Bar, 2003; Di Lollo et al., 2000; Kveraga et al., 2007). Top-down facilitation can originate from prior experience with an object (or scene) and from current attention directed at what is being perceived. This information serves to bias competition among representation of visual stimuli so that we can attend to relevant items and ignore irrelevant ones (Desimone & Duncan, 1995; Spratling & Johnson, 2004a).

Once the visual content of a stimulus has been encoded, information about it must be sustained in an active representation to be available for conscious perception. This requires access to WM, where active representations are maintained temporarily until ready for use. WM then uses attention as its selection mechanism to enhance relevant information processing, inhibit irrelevant processing, and maintain representations for additional processing (Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Miller & Cohen, 2001).

One possible form of top-down bias that could influence perception is information about the expected value of a visual stimulus, derived from prior experience with that stimulus. Value prediction codes, learned during instrumental conditioning, are acquired when the outcome of an action (response to an object) produces a reward (gain), punishment (loss or pain), or has no outcome. They encompass information about the magnitude and valence of the outcome (win or loss) (Knutson et al., 2001; O'Doherty et al., 2002), its likelihood of being produced

(O'Doherty et al., 2002), and an estimate of the delay in occurrence after response (McClure et al., 2004). After we learn to associate a certain value with an object, we then use these codes to predict which outcome is most likely, should the same object be encountered again.

The experiments reported in this thesis investigated whether value prediction codes, expressed in terms of expected value, are used as top-down information to bias the processing of visual stimuli and their subsequent percept. To create value-laden visual stimuli, I manipulated the valence and probability of outcome after response to each stimulus seen in a choice game. I then incorporated these learned stimuli in temporal and spatial attention tasks and measured recognition decisions for them or for other concurrently present stimuli. Three different paradigms were used: attentional blink, backward masking, and visual search. I found that the EV of a stimulus determines its recognition.

In the following section, I will outline the main findings of the previous empirical chapters, highlighting the pattern of results that has emerged. I will discuss how these results are informative about the nature of the interaction of value codes with attention, and how they combine to influence perception. I will then discuss a few of the myriad questions that have arisen from these results as well as some potential ways to empirically explore this topic in the future.

The effect of value prediction on recognition in temporal attention tasks

In Chapter 4, I reported two experiments that used the AB paradigm to examine the effect of value prediction on target recognition and attentional demand at two different temporal target positions (T1 & T2). Experiment 2 saw value-laden faces as the second of two targets to be recognized. When the lag between presentations of each target was sufficiently long, thus maximizing available attentional resources, recognition was substantially enhanced for motivationally salient stimuli (highly predictive of outcomes) regardless of valence (win or loss) compared to equally familiar stimuli with weak or no motivational salience. However, when the two targets were presented in close succession and attention was constrained, valence determined recognition of the second target. Targets previously associated with loss or no outcome were less likely to be recognized – an attentional blink. In contrast, targets previously associated with reward were immune to the AB, suggesting that association with gains but not losses enhances attentional competitiveness of stimuli. In addition, motivational salience continued to enhance perception when attention was limited, suggesting that it acts independently of attention to modulate perceptual decisions. In Experiment 3, value-laden faces appeared as the first of two targets to be recognized, and EV did not modulate the AB of the second target.

Chapter 5 presented two experiments in which value-laden faces were used as to-be-recognized targets seen for a brief duration and then backward masked. In Experiment 4, attention was focused on the value-laden target with no additional constraints (e.g., no dual task requirements) and recognition was determined by the motivational salience of the target – participants were consistently better at identifying targets as previously seen (old). They required shorter viewing times when targets were associated with high motivational salience compared to stimuli associated with a low probability of outcome.

The effect of motivational salience was also found in Experiment 5 where the task was orthogonal to identity recognition. In this experiment, value information was irrelevant to the task (gender discrimination) and appear to successfully compete with gender information for processing resources, thereby lowering accuracy to identify the relevant target information. When dual-task processing was again required and access to WM was limited (due to concurrent high WM load), information about a face's reward associations interfered with identifying its gender, further supporting the hypothesis that associations with reward enhances competitiveness for processing resources.

In Experiment 6 (Chapter 6), stimuli associated with a high probability of reward were also shown to elicit a larger P3 ERP component than other familiar stimuli with no EV, reflecting increased attentional resources and a facilitation in perceptual processing of these faces due to enhanced encoding and maintenance of reward information in WM.

The effect of value prediction on recognition in spatial search tasks

The remaining experiments investigated the effect of value associations on the detection of a target in a spatial array of visual stimuli. In Chapter 7, the target face was defined by its emotional expression and its predicted value was irrelevant. Here, attention was directed at the target and the (high) motivational salience of the target successfully competed with emotion information for processing resources, impeding response to face emotion. In Chapter 8, the target face was also defined by its emotional expression or its orientation, but it did not have an associated value. Instead, one of the non-target faces in the search array was associated with a value. In Experiment 9, reward-associated faces captured attention and slowed search when the target was a happy face. In Experiment 10, search for an angry face was unaffected by the presence of a value-laden distractor face within the search array, possibly due to a narrowing of attention by angry faces. Finally, Experiment 11 revealed an effect of highly motivationally salient distractors on search for an inverted face. This suggests that the effect of reward-associated distractors on search performance in Experiment 9 occurred because they shared a defining feature with the target (positive valence). When the value-laden distractor did not share a defining feature with the target, effects of motivational salience occur.

An outline of how value codes cooperate with visual attention

The main two conclusions from the present research are as follows: (1) motivational salience modulates perception independently of attention; (2) reducing attention has differential effects on access to value codes such that reward-related codes are still accessible but loss-related ones are less accessible. In each experiment, all value-laden stimuli were equally familiar and equally task-relevant (or task-irrelevant). However, they did not engage top-down attention similarly. Instead, recognition was determined by the specific predicted value of a stimulus, depending on the task demands and available attentional resources.

Motivational salience provides a top-down signal that can facilitate processes necessary for recognition, such as perception and long-term memory. Recognition of stimuli varies with motivational salience, even when attention is limited. Stimuli that have high motivational salience need less viewing time to be recognized than other stimuli, and this information is preferentially processed even if it is not relevant to current task goals. This is important because it shows that current, task-specific attentional demands do not solely determine the outcome of visual decisions.

When attentional resources are limited, value codes for reward enhance the attentional competitiveness of stimuli, allowing them to be accessible for processing even if task-irrelevant. In contrast, the pattern of results from this thesis suggest that value codes for loss-associated stimuli are less accessible and less available for high-level processing when there are constraints on attention. Thus unlike gain-associated stimuli, loss-associated stimuli do not escape the attentional blink, they do not interfere with an orthogonal recognition task, and they fail to capture attention as a task-irrelevant distractor. This is consistent with neurobiological evidence that different neural networks mediated value coding for gain and loss (Kahn et al., 2002; Yacubian et al., 2006). It is also consistent with studies showing that attention is needed if emotional stimuli are to modulate responding in the amygdala and OFC (Pessoa et al., 2002; Silvert et al., 2007).

WM uses attention to enhance and maintain visual representations; so reduced attention will limit access to these representations in WM. Dopamine plays a major role in the updating of WM with current task representations as well as in the formation of LTM representations (Aalto et al., 2005; Fried et al., 2001; Goldman-Rakic, 1996; Muller et al., 1998; Williams & Goldman-Rakic, 1995). Activation of dopaminergic midbrain regions enhances hippocampus-dependent memory formation (Wittmann et al., 2005), possibly by enhancing consolidation (Schott et al., 2004). Activation of dopamine neurons (in response to reward outcomes) is also crucial to the encoding of reward prediction. Dopamine response to reward prediction enhances and focuses processing of these inputs over others (Schultz, 2002) and improves hippocampus-dependent long-term memory formation (Wittmann et al., 2005). Stimuli associated with reward benefit from enhanced memory formation and subsequent ease of consolidation in WM, possibly giving them competitive access within WM that other stimuli (e.g., loss) do not have.

Implications for current theories

The finding that value codes directly influence recognition processes and can do so independently of attention has a large impact on how results from studies of perception, attention, and motivation should be interpreted. To begin with, many experiments on attention and motivation confound the two. In studies of attention, the tool used to control attention is the manipulation of reward (Maunsell, 2004). The act of directing attention is motivated only by expectations about which stimulus (object, event, action, etc) or location is more likely to be associated with a reward. Often the reward is merely the state of being correct, but this is a reward nonetheless.

Conversely, experiments examining the effects of reward on neural activity or behavioral response can be thought of in terms of attention. Attention is allocated more to stimuli or locations that are more likely to be rewarding. Behavioral responses to stimuli (RTs, detection thresholds, etc) are superior when the stimuli are attended (Posner, 1980) and when they are associated with larger rewards (Kawagoe et al., 1998; Ramnani & Miall, 2003). However, results from experiments in this thesis suggest that attention and motivation provide separable, independent top-down signals for controlling perceptual awareness. Therefore, it is very important to recognize the inability to disentangle effects of attention from motivation (and vice versa) in experiments that do not clearly dissociate the two.

Results from experiments with familiar stimuli can possibly be explained in terms of value prediction. For instance, long-term experience or practice with visual stimuli creates representations of these stimuli in LTM. Extensive visual experience with a stimulus in multiple contexts can create a robust mental representation for it in LTM, which then facilitates a variety of visual and decisional processes and demand less attentional resources needed to do so (Jackson & Raymond, 2006; Tong & Nakayama, 1999). Long-term experience with stimuli biases the guidance of attention to them (Chanon & Hopfinger, 2008; Summerfield et al., 2006) and also makes them harder to ignore when they are subsequently irrelevant in a task (Shiffrin & Schneider, 1977). WM capacity is also enhanced for familiar stimuli compared to unfamiliar stimuli (Jackson & Raymond, 2008).

All of these processing benefits attributed to the familiarity of a stimulus can also be influenced by value prediction. A familiar stimulus by nature has an expected value due to the extensive stimulus-response contingencies experienced with it. In the experiments presented in this thesis, familiarity was held constant yet there were differential effects of value codes on perception and the engagement of top-down attention. While familiarity benefited visual processing as compared to novel stimuli, it could not account for all of the effects observed. Instead, the predicted value stimuli modulated processing in addition to the effects of familiarity.

Effects of emotional stimuli on visual processing can also be attributed in part to the associated values with these stimuli. Typically, studies using stimuli containing emotional content make *a priori* assumptions about stimulus value (valence and motivational salience). The classification of stimuli as positive or negative (e.g., happy vs. angry face) does not always map on to their expected value, however. For instance, evidence from this thesis suggests that emotional stimuli commonly classified as negative in valence do not engage WM and top-down attention in the same manner as stimuli associated with loss outcomes (Experiment 6). Therefore, it is important to control for each participant's actual expected value of stimuli to be able to make conclusions about the role of emotional valence in visual processing.

Future considerations

The research presented in this thesis generates numerous questions and possible follow-up and exploratory experiments. There are four questions in particular that I think are important to answer in the next stage of this research. First, the stimuli used in these experiments were faces, chosen to capitalize on our ability to rapidly learn individual face identities. This leaves open the possibility that the value effects I have found are face specific. It will be necessary to utilize value-laden stimuli from other object categories in future investigations to eliminate this possibility. Currently, we are pursuing several investigations of the effects of value codes on visual processing using stimuli such as Chinese characters and dot arrays.

Second, I have yet to examine how value-laden stimuli vie for processing resources when competing against another value-laden stimulus. It is unknown how attention is prioritized when two stimuli previously associated with value are competing against each other for attention (e.g., a gain- vs. a loss-associated stimulus). Does this lead to irrational biases in decision-making, for instance under conditions of high cognitive load? In a related vein, it would be prudent to determine the time course of processing specific values. For instance, are gain-associated stimuli processed more quickly than loss-associated ones?

Finally, I manipulated stimulus EV using only valence and probability of outcome. Other important future manipulations will include varying the magnitude of outcome and the delay in outcome after response. In addition to this, it would be interesting to change the reward contingencies of stimuli within an experiment to see how stable value codes are in LTM.

In summary, the experiments reported in this thesis have highlighted how associations with value influences visual processing in several ways. Motivationally salient stimuli modulate perception independently of attention. They are more rapidly and efficiently encoded and more effectively maintained in WM compared to stimuli that have low motivational salience. In addition, stimuli associated with reward are more competitive for attentional resources and facilitate perceptual processing in conditions of limited attention compared to stimuli associated with loss. Reward information is also more efficiently maintained in WM than loss information when attentional resources are scarce. This converges with evidence that different networks code the value and subsequent prediction of rewards and punishments.

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APPENDIX

Appendix A: Examples of Stimuli

Value Learning Faces

Computer-Generated Male (Experiment 1, 2, 3, 4, 6, 9, 10, 11)

Computer-Generated Female (Experiment 6)

KDEF Male (Experiment 5, 7, & 8)

KDEF Female (Experiments 5, 7, 8)

Target Faces

Neutral Computer-Generated Male **EV** Target (Old/New: Experiment 2, 3, 4, 6)

Neutral Computer-Generated Female **EV** Target (Old/New: Experiment 6)

Neutral KDEF Male **EV** Target (Male/Female: Experiment 5)

Neutral KDEF Female **EV** Target (Male/Female: Experiment 5)

Happy KDEF Male **EV** Targets (Visual Search for Happy: Experiment 7)

Happy KDEF Female **EV** Targets (Visual Search for Happy: Experiment 7)

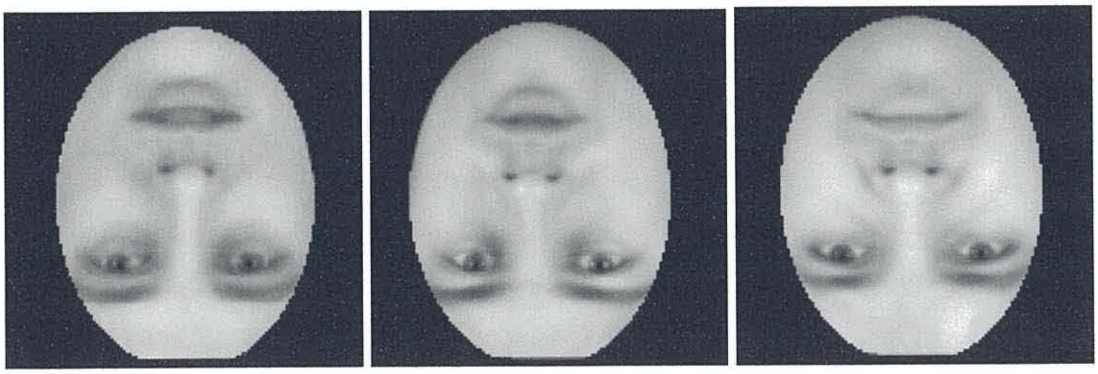
Angry KDEF Male **EV** Targets (Visual Search for Angry: Experiment 8)

Angry KDEF Female **EV** Targets (Visual Search for Angry: Experiment 8)

Happy Computer-Generated Male **Novel** Target (Visual Search for Happy: Experiment 9)

Angry Computer-Generated Male **Novel** Target (Visual Search for Angry: Experiment 10)

Neutral Computer-Generated Inverted Male **Novel** Target (Upright/Inverted: Experiment 11)



Distractor Faces

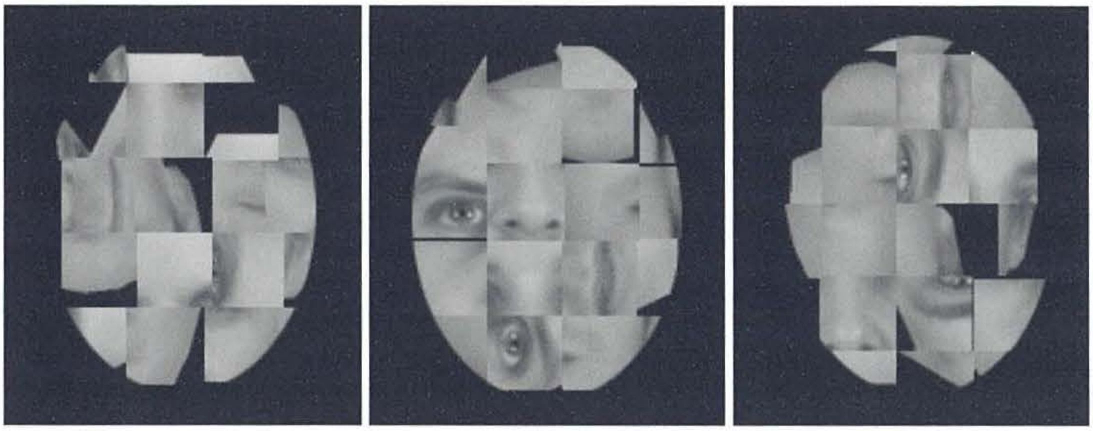
Neutral Computer-Generated Male **EV** Distractor (Visual Search for Happy, Angry, & Inverted: Experiment 9, 10, 11)

Neutral KDEF Male **Novel** Distractor (Visual Search for Happy & Angry: Experiment 7, 8)

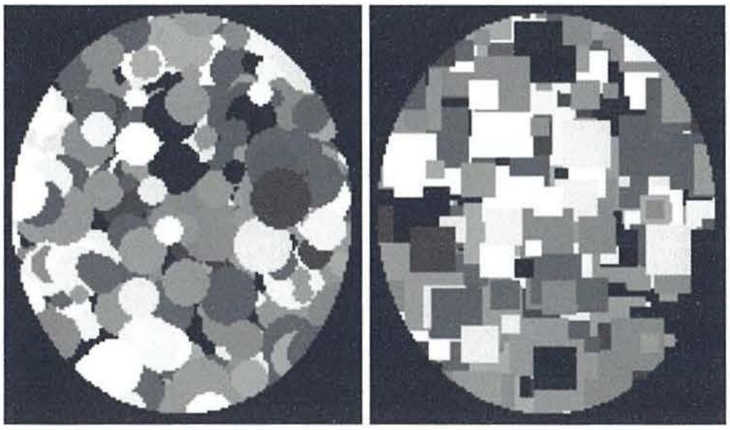
Neutral KDEF Female **Novel** Distractor (Visual Search for Happy & Angry: Experiment 7, 8)

Neutral Computer-Generated Male **Novel** Distractor (Visual Search for Happy, Angry, & Inverted: Experiment 9, 10, 11)

Masks (Experiment 2, 3, 4, 5, 6)



Abstract Elliptical Patterns (Cirlces/Squares: Experment 2, 3)



Working Memory Faces (Remembered/Not in Memory: Experiment 5)

Appendix B: Assignment of Learning Values to Stimuli

This table shows the assignment of EV to each of 12 learned stimuli during the learning task in each experiment. The actual images (e.g., "Image 1") were constant in all the versions of the learning task; only the assigned EV changed.

Image	Learning Version					
	1	2	3	4	5	6
Image 1	0.8 pair 1	-0.8 pair 1	0 pair 1	0.8 pair 1	-0.8 pair 1	0 pair 1
Image 2	0.2 pair 1	-0.2 pair 1	0 pair 1	0.2 pair 1	-0.2 pair 1	0 pair 1
Image 3	0.8 pair 2	-0.8 pair 2	0 pair 2	0.8 pair 2	-0.8 pair 2	0 pair 2
Image 4	0.2 pair 2	-0.2 pair 2	0 pair 2	0.2 pair 2	-0.2 pair 2	0 pair 2
Image 5	-0.8 pair 1	0.8 pair 1	-0.8 pair 1	0 pair 1	0 pair 1	0.8 pair 1
Image 6	-0.2 pair 1	0.2 pair 1	-0.2 pair 1	0 pair 1	0 pair 1	0.2 pair 1
Image 7	-0.8 pair 2	0.8 pair 2	-0.8 pair 2	0 pair 2	0 pair 2	0.8 pair 2
Image 8	-0.2 pair 2	0.2 pair 2	-0.2 pair 2	0 pair 2	0 pair 2	0.2 pair 2
Image 9	0 pair 1	0 pair 1	0.8 pair 1	-0.8 pair 1	0.8 pair 1	-0.8 pair 1
Image 10	0 pair 1	0 pair 1	0.2 pair 1	-0.2 pair 1	0.2 pair 1	-0.2 pair 1
Image 11	0 pair 2	0 pair 2	0.8 pair 2	-0.8 pair 2	0.8 pair 2	-0.8 pair 2
Image 12	0 pair 2	0 pair 2	0.2 pair 2	-0.2 pair 2	0.2 pair 2	-0.2 pair 2