

The nature and organization of object concepts : behavioral evidence for grounded cognition

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The nature and organization of object concepts:
Behavioral evidence for grounded cognition

David Elwin Lewis

A thesis in fulfillment of the requirements for the degree of
Doctor of Philosophy



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THE UNIVERSITY OF NEW SOUTH WALES

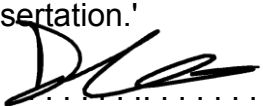
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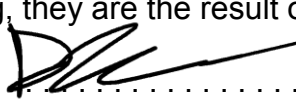
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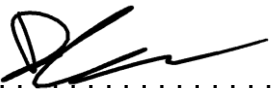
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For my son

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I would like to acknowledge the contributions of numerous individuals and institutions, without which I would not have been able to complete this thesis.

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“Science is nothing but perception.”

- *Plato*

LIST OF RELEVANT PUBLICATIONS AND PRESENTATIONS

Publications

Lewis, D. E., O'Reilly, M. J., Khuu, S. K., & Pearson, J. (2013). Conditioning the mind's eye: Associative learning with voluntary mental imagery. *Clinical Psychological Science*. doi:10.1177/2167702613484716 (see APPENDIX A)

Chang, S., Lewis, D. E., Pearson, J. (in press). The functional effects of colour perception and colour imagery. *Journal of Vision*. (see APPENDIX B)

Lewis, D. E., Pearson, J., & Khuu, S. K. (2013). The color "fruit": Object memories defined by color. *PLoS ONE*, 8(5), e64960. doi: 10.1371/journal.pone.0064960 (see APPENDIX C)

Presentations

Lewis, D., Khuu, S., & Pearson, J. (2013). *The color "fruit": Object memories defined by color*. Poster presentation at Vision Science Society 13th Annual Meeting in Naples, FL.

Chang, S., Lewis, D. E., Pearson, J. *The functional effects of colour perception and colour imagery*. Poster presentation at Vision Science Society 13th Annual Meeting in Naples, FL.

Lewis, D., Khuu, S., & Pearson, J. (2011). *If the tool fits, use it: Response priming for functionally related objects*. Poster presentation at the Australasian Cognitive Neurosciences Conference at Macquarie University.

Lewis, D., & Pearson, J. (2011). *Evaluative Conditioning with Mental Imagery*. Poster presentation at Vision Science Society 11th Annual Meeting in Naples, FL.

Lewis, D., & Pearson, J. (2010). *Evaluative Conditioning with Visual Imagery*. Paper presentation at Sydney Postgraduate Psychology Conference in Sydney, NSW.

LIST OF ABBREVIATIONS

AEC: after-effect cancellation

ANOVA: analysis of variance

cd/m²: candela per square meter

CIE: a color space developed by the International Commission on Illumination

CFS: continuous flash suppression

CR: conditioned response

CS: conditioned stimulus

Hz: hertz

IAPS: International Affective Picture System

ISI: inter-stimulus interval

ITI: inter-trial Interval

ms: milliseconds

PDP: parallel distributed processing

s: seconds

SOA: stimulus onset asynchrony

SEM: standard error of the mean

SF: spatial frequency

UCR: unconditioned response

UCS: unconditioned stimulus

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ABSTRACT

The theory of modality grounded cognition is steadily gaining in popularity as the explanation for the nature and organization of object concepts. This theory, also known as embodied cognition, states that object memories are encoded within the same neural networks that were active during the perception of, or interaction with, that object. Certain aspects of this modality grounding remain unexplained, limiting its widespread acceptance. In particular, it is unknown whether memories are grounded according to all relevant perceptual features, or if only the most diagnostic features are used. Also, the current version of the theory cannot account for abstract concepts, which are those with no inherent perceptual or motion information.

The current thesis addresses these issues by way of four independently conducted studies using varied behavioral techniques. The first study shows that associative links can form between mental imagery and perceptual stimuli. This finding demonstrates that imagery and perception are largely interchangeable within associative learning, indicating that similar patterns of neural activity are likely involved for both kinds of stimuli. The second study shows that color imagery can bias color perception. This finding indicates that the previously demonstrated processing similarity between mental imagery and perception can also involve perceptual color areas. The third study shows that the recognition of highly color-diagnostic objects can be facilitated through the prior presentation of their known color associates. Along with the previous study, this finding provides strong evidence that color plays an important role in the perceptual grounding of memories for certain objects. The fourth study shows evidence suggesting that the

recognition of specific tools may be facilitated through the prior presentation of tool-use pantomimes. While this facilitation was only observed when the prime stimuli contained real visual motion information, not implied motion, this finding indicates that motion is a very important aspect of the grounding of manipulable object concepts. Together these four studies provide novel and diverse behavioral support for the theory of modality grounded cognition by addressing its major criticisms.

1. GENERAL INTRODUCTION

Visual perception is knowledge based. Information gained from prior experience is stored within the mind as collections of memories that together form concept knowledge. Concepts are internal representations of the physical world comprised of the sensory experiences and semantic knowledge associated with a particular category of objects, settings, or ideas (A. Martin, 2007). This concept knowledge allows us to effectively and efficiently operate within our environment. For visual perception, it allows us to quickly interpret the large volume of complex information that is often present within even the simplest of visual scenes (Gibson, 1978; Murphy, 2002). This knowledge can transform seemingly random patterns of light into meaningful objects and their features (Milner & Goodale, 1998).

While it is generally agreed upon that concepts are complex forms of memory that combine information stored within various sensory and motor systems (Allport, 1985; Barsalou, 1999; Gallese & Lakoff, 2005; A. Martin, 1998), the nature of this information and how it is organized within the brain has remained the subject of a great deal of debate. Accumulating evidence suggests that concepts involve the same perceptual and motor processes as the experiences they are based upon (see Barsalou, 2008). This is known as the theory of modality grounded cognition, or embodied cognition, and it has become a widely popular explanation of the nature and organization of object concepts. The purpose of the current thesis is to examine the evidence for and against this theory, and to address some of the contentious issues within the literature. Resolving the debate on what concepts are and the manner in which they are organized in the brain has the potential to produce strong reverberations throughout the fields of

psychological science, cognitive neuroscience, vision science and many others by explaining the very nature of thought itself.

1.1. Concept Organization

Concepts appear to be organized according to a parallel distributed processing (PDP) model (McClelland & Rumelhart, 1987; Rumelhart & McClelland, 1986). Often referred to using the more general term “connectionism”, this model states that the knowledge of a particular concept is coded as a pattern of activity within the brain. This activity may originate within one or more brain areas but will then spread to others within a complex neural network. As these brain areas, often referred to as “units”, become active they will either increase or decrease the activity of their connected brain areas. Additionally, these units tend to be differently weighted, in that some units can have a greater influence on their connected units’ activity than others. Once the neural activity has spread to enough units the resultant concept is then brought to mind.

Parallel distributed processing models also provide an explanation for the mechanisms of learning and generalization. According to what was initially known as the learning rule of PDP, the connections between neurons and their individual weights are altered due to experience (Rumelhart, Hinton, & McClelland, 1986). The corresponding neural changes are best described by Hebbian theory, or Hebb’s rule (Hebb, 1949), wherein new synaptic links will be created and pre-existing links will be strengthened between neurons processing the associated information (see also Geinisman, 2000). Conversely, the learning of a non-

association occurs through the weakening or loss of these same synaptic links. Generalization is also possible within this model as the neural networks for similar concepts tend to overlap (see Section 1.1.1.). Due to this overlap the neural activation of one concept will result in the partial or full activation of related concepts, which was initially called the propagation rule PDP (Rumelhart et al., 1986). This brief overview of PDP greatly simplifies the volumes of evidence that support it. As it is not the aim of the current thesis to fully critique PDP and connectionist theory, perhaps the most efficient way to explain what they entail concerning the nature and organization of concept knowledge is to draw comparisons with its primary alternative theories, localism and computationalism.

Localism argues against the idea that concepts are distributed throughout neural networks within the brain. Localist theory states that each individual concept is stored in a discrete area of the brain, potentially even within a single neuron (Barlow, 1972). This theory is often derided using the term “grandmother cell”, which refers to the localist contention that an individual neuron may in fact be responsible for the processing of a single concept, such as your grandmother (see Gross, 2002). Localism originated as somewhat of a straw-man argument used by proponents of distributed models, but some support for it has been provided (Besner, Twilley, McCann, & Seergobin, 1990; Bowers, 2002; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001).

Quiroga, Fried and others (2008; 2005) have produced particularly strong evidence supporting localist theories. In multiple studies individual neurons within the human temporal lobe were observed to only respond to very specific objects or individuals. This neural activity appears to be indicative of concept activation, as it

is unaffected by even large changes in the preferred object's appearance and is also found for the object's name. While this lends strong support to the presumption that a single cell can be responsible for the processing of a single concept (eg. grandmother), it was not the intention of the authors to do so. Instead they argue that these highly selective neurons are likely responding to individual concept features, and only when combined with other neurons within a sparse neural network will a specific concept become activated (Fried, MacDonald, & Wilson, 1997; Quiroga, Kreiman, Koch, & Fried, 2008; Waydo, Kraskov, Quiroga, Fried, & Koch, 2006). While they concede that it is in fact possible that a single cell may process a single concept their conclusions are more in line with distributed models of concept knowledge. This apparent hesitance to support localist theories and especially the grandmother cell hypothesis seems to be shared by the majority of the scientific community, with some exceptions (Bowers, 2009). Perhaps this hesitance is the result of such theories being unable to explain fundamental neural processes (Plaut & McClelland, 2010). In particular they cannot account for learning and generalization, because if each concept is represented by a single cell – or discrete cluster of cells – then it is unclear how categories or associations between different concepts could possibly form. For such reasons localism has been largely rejected.

Computationalism argues against the idea that concepts include sensory-like information (Fodor, 1988; Fodor & Pylyshyn, 1988). Often referred to as the “classical” or “standard” theory of cognition, computationalist theory states that what is often referred to as a “concept” is actually a set of abstract mental symbols that are combined in a stepwise fashion. These symbols, often referred to as

“mentalese” or “the language of thought” (Fodor, 1975), form a combinatorial syntax that is used to form concepts that are abstract. These concepts do not resemble the things that they represent, in the same way that the word “dog” does not resemble an actual dog. This combinatorial syntax allows for a finite number of neural units to represent a virtually limitless number of different concepts.

Mainstream acceptance of this symbolic language of thought increased greatly with early developments in computer science and the rising popularity of home computing. In fact, computationalist theory was originally based upon the structure and function of Turing and Von Neumann computers (Fodor & Pylyshyn, 1988). Even to this day computer processing remains the predominant metaphor for human thought. Yet metaphors are by definition inaccurate, and their use to understand and describe something as highly complex as human thought can clearly lead to erroneous conclusions about the neural processes that must be involved. For instance, though PDP and computationalism are often contrasted with one another due to their highly different assumptions on the nature and organization of concept knowledge, these theories do not necessarily conflict. Both theories posit that concepts consist of the systematic combination of multiple pieces of information. It may be that concepts are symbolic in nature and the brain areas responsible for their processing are distributed throughout the brain, or it simply may be that some concepts involve symbolic processing while others involve perceptual processing (Mahon & Caramazza, 2008; Pezzulo et al., 2011). These kinds of questions have been addressed by a large body of research on where and how visual information is processed within the brain.

1.1.1. Dorsal versus Ventral Streams.

Incoming visual information is widely known to be processed along two neural pathways, the ventral (“what”) stream and dorsal (“how”) stream (Goodale & Milner, 1992; Milner & Goodale, 1998). Figure 1.1 diagrams this two-streams hypothesis of visual processing, also known as the perception-action model, wherein information undergoes progressively complex neural processing along one of two different pathways based on the nature of the information. A large body of evidence has been produced in support of the two-streams hypothesis (e.g. Dekker, Mareschal, Sereno, & Johnson, 2011; Frey, 2007; Mishkin, Ungerleider, & Macko, 1983; Schneider, 1969), the main findings of which are summarized below.

Ventral stream areas are mostly involved in the processing of form information. Extending from the occipital cortex to the inferior temporal cortex, neural areas along this stream are largely involved in object recognition processing (Goodale & Milner, 1992). Accordingly, multiple sites within the temporal cortex have been identified that are predominantly involved in the recognition of different categories of objects, such as faces, animals, and places (Chao, Haxby, & Martin, 1999; Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997). Recently, specific neural areas have also been identified for the recognition of various body parts (Orlov, Makin, & Zohary, 2010), and even a unique area just for hands (Bracci, Ietswaart, Peelen, & Cavina-Pratesi, 2010). Though the categories that have been identified so far are rather broad, these findings appear to suggest that all parts of the human body, and many other categories of objects, may have specific processing areas within the ventral stream. The imminent development of higher resolution functional magnetic

resonance imaging (fMRI) makes it seem even more likely that neural areas subserving very specific categories may become detectable.

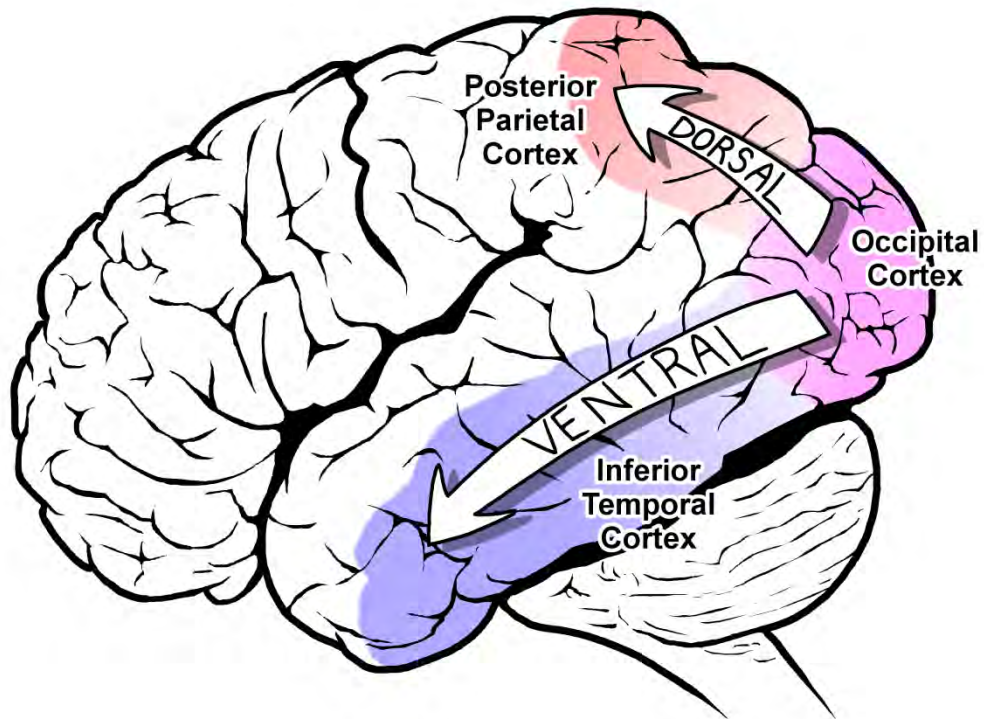


Figure 1.1. Dorsal and ventral processing streams. Ventral “what” stream extends from the occipital cortex to the inferior temporal cortex and is largely involved in object recognition processing. Dorsal “how” stream extends from the occipital cortex to the posterior parietal cortex and is largely involved in motion, action, and spatial processing.

Dorsal stream areas are mostly involved in the processing of motion, action, and spatial information. Extending from the occipital cortex to the posterior parietal cortex, neural areas along this stream are largely involved in maintaining the spatial layout of visual objects within a scene and checking for any discrepancies over time (eg. movement) (Goodale & Milner, 1992). Though object recognition processing occurs predominantly within the temporal cortex, significant parietal

cortex activity has also been observed during the recognition of objects that have strong associations with specific forms of motion or action (Oliver & Thompson-Schill, 2003), such as tools and other manipulable objects (Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2008; Chao & Martin, 2000; Culham et al., 2003; Faillenot, Toni, Decety, Gregoire, & Jeannerod, 1997; Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2012).

Since the seminal work of Goodale and Milner (1992) it has generally been assumed that visual information is segregated between the two processing streams. However, recent reviews of the literature (Farivar, 2009; Farivar, Blanke, & Chaudhuri, 2009; Milner & Goodale, 1998; Oliver & Thompson-Schill, 2003; Young, 2006) and the previously discussed parietal cortex activity during object recognition processing are indicative of a high amount of interaction between the two streams. Additionally, as many of the previously mentioned studies used still images that have no actual motion information, the finding of parietal cortex activity appears to suggest that the recognition of manipulable objects includes a sort of mental simulation of the actions associated with them (see Section 1.2.1.). Despite the high level of interactivity between the dorsal and ventral streams, their specializations in the processing of different forms of visual information remains a basic organizational principle for concept knowledge.

1.1.2. Taxonomic and Thematic Categories

Concepts that have a high degree of similarity tend to be represented within similar neural areas, which drives the creation of categories of concepts (Mahon & Caramazza, 2011). These categories are known to be distributed throughout the

brain within a continuous space (Huth, Nishimoto, Vu, & Gallant, 2012). Within this space related categories show a greater degree of overlap in their patterns of neural activity than unrelated categories. Generally this relatedness is based upon the categories' perceptual similarity, but it can also be based on higher-level information concerning what the object does or is used for.

Taxonomy, or taxonomic categorization, refers to the grouping of items based upon the similarity of their features. When applied to object concepts, this form of categorization most often results in the creation of groups based upon similarities in visual form, but it can also be based on other kinds of visual features such as color, texture, or motion. Though the amount of taxonomic categories a person can generate and utilize is innumerable, the most commonly used and extensively studied categories include faces, animals, places, and tools (for review see Mahon & Caramazza, 2009). Within the temporal cortex different areas are known to be selectively involved in the processing of each one of these categories, and it seems rather likely that many other areas selective for different taxonomic categories will soon be discovered (see Section 1.1.1.). Yet grouping concepts based on their visual similarity is not the only way they can be categorized.

Themes, or thematic categorization, refers to the grouping of items that interact or co-occur in some manner. When applied to object concepts, this form of categorization groups objects that play complementary roles within a specific context, regardless of whether or not they have any visual or conceptual similarities. Commonly used basic thematic categories include those based upon the temporal, spatial, causal, possessive, productive, and functional relationships between concepts (for review see Estes, Golonka, & Jones, 2011).

The primary difference between these two forms of categorization is that thematic categorization requires an understanding of the relationships between concepts (McRae & Boisvert, 1998). As a result, though novel objects can be assigned to a taxonomic category based upon their similarity to previously experienced objects, they cannot be assigned to a thematic category unless their relationships with other objects is made clear. However, because objects are rarely experienced in isolation this kind of relationship-based grouping does appear to be a more natural way for most people to organize their concepts. Young children, adults with no formal education, and older adults with formal education in the distant past are all more likely to group objects according to thematic categories, while adults that recently received a formal education are more likely to group objects according to their taxonomic similarity (Annett, 1959; Lin & Murphy, 2001; S. Simmons & Estes, 2008; Smiley & Brown, 1979). This evidence seems to clearly indicate that categorizing by themes is the preferred method, as people will naturally group together concepts that co-occur or interact in a meaningful way unless pressured to use a different grouping strategy.

Perhaps this thematic preference exists because these kinds of relationships allow an individual to make accurate predictions about the future. The perception of an object or event tends to generate expectations for the subsequent perception of thematically related objects or events (Hare, Jones, Thomson, Kelly, & McRae, 2009; McRae & Matsuki, 2009). In this way, thematic categories can allow an observer to make implicit or explicit predictions about the nature of future stimuli. Additionally, the formation of strong thematic relationships between objects or events has been shown to even increase their perceived taxonomic similarity

(Golonka & Estes, 2009). Along with the predictive nature of these relationships, this perception of similarity where none may actually exist has profound implications for priming research as discussed in Chapter 2.2. In Chapter 6 the predictive power of a similar kind of functionally interactive thematic relationship is tested using pantomime-hands and their corresponding hand-held tools. If priming can be observed using such a method it would suggest that there is significant overlap in the neural processing of these highly dissimilar objects.

1.2. Modality Grounded Cognition

As evidenced by the previously discussed research, concepts appear to be organized based upon the nature of their perceptual and functional information. The ramifications of this manner of concept organization has been described using a unique connectionist model known as the theory of modality grounded cognition, or embodied cognition. This model states that the stored knowledge about an object or event is encoded within the same neural networks that were active during the perception of, or interaction with, that object or event (for reviews see Barsalou, 2008; Barsalou, Simmons, Barbey, & Wilson, 2003; Gibbs Jr, 2005; Jirak, Menz, Buccino, Borghi, & Binkofski, 2010; M. Wilson, 2002).

Grounded cognition rejects the symbolic mentalese of computationalist theory in favor of a more analog explanation of concept knowledge. As concept knowledge is distributed throughout brain's perceptual and motor cortices, the activation of a concept is much like a simulation or re-experiencing of its associated object or event (Barsalou, 2009; Decety & Grèzes, 2006). Simply

stated, thinking about an object or event is largely the same process as perceiving it. Clearly this has profound implications for theories of mental imagery which are discussed in further detail in Section 1.2.1.

Arguments supporting a modality grounded description of concept knowledge date back thousands of years (see Barsalou, 1999). However, only in the last few decades have researchers moved away from computationalist theories and started taking grounded cognition more seriously (Barsalou, 2010). To this day computationalist theories remain dominant in many fields of cognitive science despite a quickly growing amount of evidence supporting grounded cognition. The majority of this evidence comes from a wide range of behavioral and neuroimaging studies focusing on the mechanisms of object recognition (Chapter 2.1).

In recent years this overlap between perceptual and knowledge-based processing has been observed in a wide range of studies using various kinds of methodology and stimuli. Far too many studies have found evidence of this overlap to be able to discuss them all in detail, but certain studies stand out due to their strength of the evidence they have produced. Behavioral research has produced a great deal of support for grounded cognition by showing that memory-based tasks can interfere with concurrent or subsequent perception and action (Glenberg, 1997). Studies have shown that motion words can interfere with the perception of motion (Meteyard, Zokaei, Bahrami, & Vigliocco, 2008), the names of objects that are similarly colored can be used to prime each other (Yee, Ahmed, & Thompson-Schill, 2012), visual objects can alter how subsequently presented objects are interacted with (Craighero, Fadiga, Umiltà, & Rizzolatti, 1996), and action observation can influence the performance of similar actions (Vogt, Taylor, &

Hopkins, 2003). By showing a clear interaction between the processing of memory and perception these behavioral results provide compelling support for grounded cognition. However, neuroscience has been responsible for producing the greatest amount of support.

Neuroscientific studies have supported grounded cognition by showing that cortical areas involved in the processing of perceptual stimuli are also active during memory-based tasks (A. Martin, 2001, 2007; Thompson-Schill, 2003). As this neural activity varies based upon the particular memory being recalled, this activity appears to be based upon the perceptual content of these memories instead of more general memory processing. In accordance with these findings, similar neural activity within the motor cortex has also been found. Studies have shown that the reading and generation of action words can produce activity within motor cortex areas corresponding to those actions (D'Ausilio et al., 2009; A. Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Willems & Hagoort, 2007), with different patterns of activity for actions that require different body parts (Pulvermuller, 2005). This kind of overlap in neural processing appears to even extend to mental imagery, in that the same low-level visual areas have been shown to be involved in both the processing of visual mental imagery and visual perception (Section 1.2.1).

As the evidence supporting grounded cognition has generally been very compelling, many researchers have outright rejected the so-called “classical” theory of cognition. Unfortunately grounded cognition has at least one major problem: it cannot easily explain how the brain represents abstract concepts, which are those with no inherent sensory or motor information (Mahon & Caramazza, 2008). As most functional imaging research has shown differences between the

neural activity involved in perceptual and knowledge-based processing (Schupp, Lutzenberger, Birbaumer, Miltner, & Braun, 1994; Wadsworth & Kana, 2011) it may be the case that this neural activity involves both modal (sensory) and amodal (symbolic) information. Along this line of reasoning, researchers have attempted to reconcile grounded cognition with computationalism by arguing that amodal symbols are used to represent more abstract concepts while sensory and motor information is used to represent more concrete objects, and these two forms of representations can interact (Mahon & Caramazza, 2008; Pezzulo et al., 2011).

This abstract concept problem may however have a simpler solution. The study in Chapter 3 demonstrates that associative learning can occur for sensory stimuli that are not physically present. Consequently, associative learning theory might be able to provide an explanation as to how these inherently non-modal concepts, which have no physical presence, may become grounded within modality specific systems. This possibility and its ramifications for theories of mental imagery, associative learning, and grounded cognition are discussed in Chapter 7.1.3.

1.2.1. Mental Imagery

Mental imagery is based on knowledge gained from prior sensory and motor experiences. The generation of mental imagery therefore produces a perception-like experience that can occur in the absence of any physical stimulation (Kosslyn, Ganis, & Thompson, 2001). Additionally, though mental imagery for any modality is possible, the most commonly experienced and heavily researched is visual imagery or “seeing with the mind’s eye”. As the generation of a mental image

utilizes much of the same perceptual areas as normal perception, mental imagery appears to act like a simulation of the sensory information corresponding to a specific category of objects or events (Barsalou, 2009; Decety & Grèzes, 2006; Grèzes & Decety, 2002).

A large body of research has shown that imagery and perception are similar in many ways (Behrmann, 2000; Kosslyn et al., 2001). Influential studies of mental imagery have shown that early visual areas are active when visualizing objects (Kan, Barsalou, Solomon, Minor, & Thompson-Schill, 2003; Kosslyn, Thompson, Kim, & Alpert, 1995; Slotnick, Thompson, & Kosslyn, 2005), cortical damage to areas which process specific kinds of stimuli will interfere with imagery of the same kind (Barton & Cherkasova, 2003; Farah, 1984; Farah, Levine, & Calvanio, 1988), perceptual stimuli will interfere with concurrent mental imagery generation (Sherwood & Pearson, 2010), and mental imagery can influence subsequent perceptual experiences (Pearson, Clifford, & Tong, 2008).

These studies, and many others using functional imaging (Cabeza & Nyberg, 1997, 2000; Fletcher et al., 1995; Ganis, Thompson, & Kosslyn, 2004; Knauff, Kassubek, Mulack, & Greenlee, 2000; Kosslyn et al., 1999; Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998; O'Craven & Kanwisher, 2000), single cell recordings (Kreiman, Koch, & Fried, 2000), and transcranial magnetic stimulation (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Kosslyn et al., 1999; Sack, Camprodon, Pascual-Leone, & Goebel, 2005; Sparing et al., 2002), have provided a wealth of neural and behavioral evidence that similar brain areas are used for both imagery and perception. Chapter 3 provides further evidence for this similarity

by showing that mental imagery can undergo associative learning in the same way as perceptual stimuli.

Despite the processing similarities of imagery and perception, there are also clear differences. Perception will occur automatically upon stimulus sensation, whereas mental imagery can either be voluntarily generated or involuntarily evoked by associated perceptual stimuli (Albright, 2012). Also, it is possible to create mental imagery that differs greatly from the corresponding perceptual stimuli through the combination and transformation of the sensory and motor information stored within memory (Mast, Tartaglia, & Herzog). Yet, perhaps the largest difference between imagery and perception is that imagery is typically comprised of only the most important or diagnostic information about the imagined concept (Barsalou, 1999, 2003), which is heavily influenced by recent perceptual experiences (Barsalou, 2009). Consequently, mental imagery tends to be a more simplified, or impoverished, experience than perception. As it requires a great deal of cognitive effort to generate and maintain a mental image (Kosslyn, Brunn, Cave, & Wallach, 1984), this simplification allows for the more efficient use of limited cognitive resources that all forms of mental imagery require.

Visual imagery is perhaps the most well studied and commonly experienced form of mental imagery. The ability to generate visual imagery is well known to differ between individuals (Cui, Jeter, Yang, Montague, & Eagleman, 2007; Kosslyn et al., 1984). It has recently been demonstrated that individuals are generally aware of their imagery abilities and may possibly be able to improve them through practice (Pearson, Rademaker, & Tong, 2011; Rademaker & Pearson, 2012). For visual perception, object shape and visual scene contours are

generally considered to be the most important information (Biederman & Ju, 1988), often resulting in neglect for other kinds of visual information. However, other visual features such as color can also be very important under certain conditions (Bramão, Reis, Petersson, & Faísca, 2011), especially if shape and contours are unavailable or ambiguous (Laws & Hunter, 2006). As mental imagery and perception appear to be very similar, it seems likely that visual imagery may also be contour-based unless otherwise required. This possibility is investigated within Chapters 3 and 4. As can be seen in the conclusions drawn from these studies (Chapters 3.5.3. and 4.5.1.) mental imagery and perception do indeed appear to share some important similarities.

1.2.2. Color

Color is a very important aspect of the human visual experience and accordingly a great deal of research has focused on determining how it is processed within the brain (Gegenfurtner, 2003). It has become well established that color associations are represented within concept knowledge, but whether this knowledge uses the same neural substrates as actual color perception has not been sufficiently investigated. The importance of color information for object concepts has remained similarly unclear, despite the fact that many objects have very strong associations with color (eg. traffic-lights). Such objects are commonly referred to as being high in color diagnosticity, as they tend to have a specific coloration which, when learned, will provide additional information about their identity (J. W. Tanaka & Presnell, 1999). This improvement in identification ability appears to involve more than simply using color information to help define

contours, as the addition of color can greatly facilitate the identification of objects or events high in color-diagnostics, but little to no facilitation is generally found for objects or events that are not color diagnostic (Chapter 2.1.1). It seems likely that this facilitation is the result of color knowledge being grounded within modality specific systems. The experiments detailed in Chapters 4 and 5 investigate this possibility by exploring the role of color in object recognition.

Unfortunately, very few behavioral studies have investigated color grounding. The first behavioral study supporting this theory demonstrated that the recognition of various objects can be inhibited by previously presenting the name or picture of an object known to typically have the same color (Joseph, 1997; Joseph & Proffitt, 1996). This kind of negative-color-priming has been replicated by Connell (2007), who showed that colors implied by the context of a sentence could inhibit the recognition of subsequently presented objects matching the implied color. However, Richter and Zwaan (2009) have shown that visually presented colors and matching color words could also be used to positively prime each other. These findings have provided some evidence that color is perceptually grounded by showing that color knowledge can prime color perception. As any such priming is indicative of an interaction between perception and knowledge-based color processing, the directionality of these kinds of priming effects is irrelevant.

Case and neuroimaging studies have produced a relatively greater amount of evidence both in support and opposition to the idea that color knowledge is perceptually grounded. Patients with cerebral achromatopsia, a rare condition wherein color information is either lost or degraded due to occipital cortex damage (Jaeger, Krastel, & Braun, 1988; Meadows, 1974), have generally demonstrated

color knowledge deficits with corresponding color perception deficits (De Vreese, 1991; Miceli et al., 2001), but not all patients have shown such corresponding deficits (Bartolomeo, Bachoud-Lévi, & Denes, 1997; Goldenberg, Mullbacher, & Nowak, 1995; Luzzatti & Davidoff, 1994; Shuren, Brott, Schefft, & Houston, 1996). Accordingly, a high degree of overlap has been observed between brain activity patterns associated with the processing of color knowledge and color perception (Goldberg, Perfetti, & Schneider, 2006; Hsu, Frankland, & Thompson-Schill, 2012; Hsu, Kraemer, Oliver, Schlichting, & Thompson-Schill, 2011; Kan et al., 2003; Kellenbach, Brett, & Patterson, 2001; Rich et al., 2006; W. K. Simmons et al., 2007). However, large differences in these patterns of activity have also been observed (Bramão, Faísca, Forkstam, Reis, & Petersson, 2010; Chao & Martin, 1999; Howard et al., 1998; Lu et al., 2010; A. Martin et al., 1995). This conflicting evidence has led to a large amount of debate as to whether concepts are, or can be, grounded within perceptual color processing systems.

Further research is required in order to resolve these conflicts within the literature, and to determine if the processing of color knowledge and color perception do have a meaningful amount of overlap. Though many of the previous studies appear to support the theory that color knowledge is grounded within modality specific systems, there is currently too much dissonance within the data to make any conclusions. For this reason the studies described in Chapters 4 and 5 are conducted to further investigate the possibility of an overlap in the processing of color knowledge (memories) and color perception. The conclusions drawn from these studies (Chapters 4.5.1. and 5.5.4.) help resolve this dissonance. Discussion concerning the potential resolution to this issue is also provided in Chapter 7.1.1.

1.2.3. Object Interaction

Interaction, or how we manipulate objects in the environment, is the defining feature of many objects (e.g. lever). Accordingly, while the processing of manipulable object concepts and their associated forms of interaction is known to involve activity throughout the brain (Assmus, Giessing, Weiss, & Fink, 2007; Johnson-Frey, 2004), activity in motor areas appears to be the defining aspect of their neural representation (see Beauchamp & Martin, 2007; Willems, Hagoort, & Casasanto, 2010). For example, a classic study by Chao and Martin (2000) found significantly greater activation within motor areas when viewing and naming manipulable objects than viewing and naming non-manipulable objects. Also the perception of manipulable objects, or their names, has been shown to prime the manner in which one tries to interact with subsequently presented objects (Bub & Masson, 2012; Tucker & Ellis, 2004). These kinds of studies have helped clarify the differences between dorsal and ventral stream processing (see Section 1.1.1) and have shaped the theory of modality grounded cognition into its current form by providing evidence that concepts can be grounded within motion processing areas.

Yee, Chrysikou, Hoffman, and Thompson-Schill (2013) demonstrated the consequences of this motion grounding in a very recent study showing interaction between hand movements and visual object recognition processing. Participants in this study were found to take significantly longer to determine that the name of a manipulable object corresponds to a “concrete” object – one that has physical qualities – when concurrently performing an unrelated manual task. This kind of irrelevant motor cortex activity appears to produce a conflict, or interference, during the recognition of manipulable objects, strongly suggesting that these areas are

involved in the processing of manipulable object concepts. Additionally, the extent of the observed interference was found to be modulated by knowledge of how these objects are manipulated, which seems highly similar to the color diagnosticity effects discussed in Section 1.2.2.

While this grounding of manipulable object concepts within motor cortex is generally accepted, the specific details regarding what kinds of visual-motion information it is based upon is not. Also, whether non-motion cortex areas play an important role in the neural representation of manipulable object concepts has not yet been determined. The study within Chapter 6 investigates these possibilities by showing facilitation for visual tool recognition using animated and non-animated tool-use primes. The conclusions of this study (Chapter 6.5.6.) offer some suggestions regarding the modality grounding of manipulable object concepts. Further discussion of these issues and the contributions of the current study are provided in Chapter 7.1.2.

1.3. Aim

The aim of this thesis is to investigate unresolved aspects of the theory of modality grounded cognition as it applies to visual perception. As there currently are many contentious issues within the grounded cognition literature preventing its more widespread adoption, their timely resolution is imperative. It is important to note however that the current studies concern the visual features of color and motion, which may be grounded in a different way from more general cognitive processes. Regardless, it is not the aim of the current study to provide a broad

commentary on the theory of modality grounded cognition, as many such studies have already been published (Section 1.2.). Instead, the four studies contained within this thesis answer the following specific questions:

- Study 1: Can associative learning occur for voluntary mental imagery?
- Study 2: Can color play a role in mental imagery?
- Study 3: Can perceptual colors activate stored color knowledge?
- Study 4: Can visually implied actions facilitate the recognition of corresponding tools?

Together the answers to these questions could potentially explain the role of feature diagnosticity within object concepts as well as the mechanism through which the theory of modality grounded cognition might be able to represent abstract concepts. Resolving these issues will facilitate mainstream acceptance of this theory, which has the potential to unify current scientific and non-scientific thought on the nature and organization of concept knowledge.

1.4. Thesis Structure

This thesis is a compilation of four independently designed and conducted studies. Their unique backgrounds, methodologies and results are discussed in detail within their separate chapters. These study chapters are bookended by an introduction to current thoughts concerning the nature and organization of concept knowledge and a general discussion of the findings presented within this thesis.

- Chapter 1 explains the theoretical background of the research being presented, with a focus on the theory of modality grounded cognition.

- Chapter 2 describes the general methodologies used within this thesis and explains their significance in the field.
- Chapters 3 through 6 report the goals, methods and results of each study within this thesis. A brief introduction and discussion is also provided.
 - Chapter 3: Associative learning with mental imagery
 - Chapter 4: Mental imagery for color
 - Chapter 5: Object memories defined by color
 - Chapter 6: Functional interactions between concepts
- Chapter 7 provides a general discussion of the current findings, and how they contribute to our understanding of object concepts.

2. GENERAL METHODOLOGY

Modality grounded cognition has received support from numerous studies using various kinds of neuroscientific and behavioral methodologies (Chapter 1.2). However, alternative theories such as computationalism (Chapter 1.1) have remained dominant because the theory of grounded cognition has failed to provide an explanation for numerous important issues. To fully address these issues convergent evidence from a wide range of studies is required. For this reason, behavioral methodologies were purposefully designed for each of the four studies contained within this thesis. Each study's methodology was independently developed, and are discussed in detail within Chapters 3 through 6. However, there are a few underlying experimental techniques that span many of the studies within this thesis. These methodological paradigms are object recognition, priming, and binocular rivalry. The purpose of the current chapter is to discuss the theoretical background and current trends of each one of these methods.

2.1. Object Recognition

Visual object recognition is essential to everyday life but requires complex mental processing (for reviews see Biederman, 1995; Logothetis & Sheinberg, 1996). Before object recognition can even occur the observer must first detect the presence of the object and determine its location within a visual scene. Then visual information about the object can be transmitted to the observer's primary visual cortex (area V1) where it will undergo preliminary processing of some of the most basic visual features (Movshon, Thompson, & Tolhurst, 1978a, 1978b). This

information is then passed along to progressively higher-level processing areas such as V2-V5 and beyond, where it undergoes further processing based upon the nature of its content (Chapter 1.1.1).

Despite the complexity of visual processing humans and other sighted animals have the ability to quickly and accurately recognize a wide range of objects with little to no effort. Our visual recognition system is robust, in that it is largely unaffected by changes in an object's size, orientation, color, or setting (Farah, Rochlin, & Klein, 1994; Rolls, 1994; K. Tanaka, 1997). This is no small feat, as many objects can give off completely different visual information depending on the angle they are viewed at or the light source that they are illuminated by. Additionally, even if we do fail to recognize the specific identity of an object, often we can still determine what category of objects that it likely belongs to (Chapter 1.1.2). As visual object recognition is such an important and commonplace task in our everyday lives, each study contained within this thesis uses it as a central methodological concept and theories of object recognition are directly addressed within Chapters 5 and 6.

One of the primary driving forces of human visual object recognition research has been attempts to replicate its capabilities using machines. Findings on human object recognition processing have heavily influenced computer vision research and vice-versa (Serre, Wolf, Bileschi, Riesenhuber, & Poggio, 2007). To this day it remains one of the primary goals of artificial intelligence research to develop a computer system capable of emulating the robust object recognition capability demonstrated by humans and many other sighted animals. As much remains unknown about our object recognition system it is believed that its

emulation would also serve to inform us about the underlying processes that most likely occur within the brain (Fukushima, 1980). Despite major breakthroughs and the concerted effort of a wide range of computer scientists (Belongie, Malik, & Puzicha, 2002; Fukushima, 1980; Lowe, 1999), this goal has not yet been achieved. Though highly advanced computer recognition systems have recently been developed (Leibe, Leonardis, & Schiele, 2008; Serre et al., 2007), these systems still lack the efficiency and reliability seen in the human visual system. To this day, even the youngest of children are capable of performing visual recognition that is well beyond the most advanced computer system. Perhaps our advanced ability to recognize objects is due, at least in part, to concept knowledge (A. Martin, 2007). This possibility, and how the findings presented within Chapters 5 and 6 could be applied to the development of advanced computer vision systems are discussed within Chapter 7.2.2.

As discussed in Chapter 1, concept knowledge consists of all our previous sensory experiences and semantic information about a particular category of objects. This knowledge is known to be stored within various neural areas, specifically those within the occipito-ventral stream (Chao et al., 1999; Miyashita, 1993), which are also active during the perception and subsequent perception of objects (Chapter 1.1.1). For the purposes of this thesis, the term “recognition” is defined as the extraction of a visually presented object’s descriptive information and the subsequent comparison of that information to prior experiences stored in memory. Unfortunately how the brain performs this task has never been fully understood, which has led to centuries of debate.

Researchers from a wide range of scientific disciplines have used various methods to try to determine the inner mechanisms of object recognition (Biederman, 1987; Gross, Rocha-Miranda, & Bender, 1972; Marr & Nishihara, 1978; Pinker, 1984; Ullman, 1989). The debates spawned by these studies have lead to the development of many highly detailed and influential models of object recognition (Kersten, 2003; Lowe, 1999, 2000; Riesenhuber & Poggio, 1999, 2000; Serre et al., 2007; Ullman & Power, 1997). The most successful models have tended to focus on shape information while ignoring or downplaying the importance of other kinds of visual information (Barenholtz & Tarr, 2006; Belongie et al., 2002; Biederman & Ju, 1988; Grossberg & Mingolla, 1985; Proverbio, Burco, del Zotto, & Zani, 2004). In particular, the influence of an object's surface features on its recognition has been largely ignored despite the fact that a large amount of visual processing is dedicated to such features.

2.1.1. Surface Features

An increasingly large amount of evidence has suggested that surface features play an important role in visual object recognition (Cant, Large, McCall, & Goodale, 2008; Chainay & Humphreys, 2001; Humphrey, Goodale, Jakobson, & Servos, 1994; Price & Humphreys, 1989; Rossion & Pourtois, 2004; Sanocki, Bowyer, Heath, & Sarkar, 1998; J. W. Tanaka & Presnell, 1999; Wurm, Legge, Isenberg, & Luebker, 1993). In general these studies have concluded that though surface features are generally not as informative as shape information, their contributions can become rather significant under conditions wherein the object's shape information is blurred or degraded in some way (Laws & Hunter, 2006; J. W.

Tanaka & Presnell, 1999; Yip & Sinha, 2002). Consequently they have argued for surface features to become fully incorporated into models of object recognition.

Of all the surface features, color seems to be the most informative as it has been shown to be a defining visual feature of a wide range of objects (J. W. Tanaka & Presnell, 1999). These objects are referred to as being highly color diagnostic, as they have strong associations with one or more colors whose visibility will provide additional information about their identity (for review see Bramão, Reis, et al., 2011). Though the addition of color information has been shown to facilitate the visual recognition for all kinds of objects regardless of whether they are color diagnostic (Biederman & Ju, 1988; Bramão, Inácio, Faísca, Reis, & Petersson, 2011; Rossion & Pourtois, 2004; Uttl, Graf, & Santacruz, 2006; Wurm et al., 1993) – perhaps through using the color channels to help define the contours of an object – many studies have found significantly greater facilitation for objects that are highly color-diagnostic (Lu et al., 2010; Nagai & Yokosawa, 2003; Rossion & Pourtois, 2004; J. W. Tanaka & Presnell, 1999; Therriault, Yaxley, & Zwaan, 2009; Uttl et al., 2006). These findings seem to support an alternative object recognition model known as the shape + surface feature model, which emphasizes the importance of the object's surface features, including color (Humphrey et al., 1994; Wurm et al., 1993). A discussion of the potential superiority of this alternative model is included in Chapter 5.

2.2. Priming

Priming is a kind of implicit memory that can greatly influence perception (Schacter, 1992). In general, priming involves the presentation of an initial stimulus (the prime) in order to facilitate processing of second stimulus (the target). This facilitation is evidenced by faster reaction times or heightened accuracy during object recognition and detection tasks. As priming will only work for prime-target combinations that are similar in some way (Taylor, 1977; Tulving & Schacter, 1990), priming has proven to be a reliable way to measure the taxonomic or thematic similarity of two stimuli (for review see Schacter & Buckner, 1998). Each study contained within this thesis uses priming as a key methodological procedure (Chapters 3.3., 4.3., 5.3., and 6.3.).

2.2.1. Types of Priming

There are numerous forms of priming, which can be classified along two basic types, perceptual and conceptual (Schacter & Buckner, 1998). Though most examples of priming in the literature include both perceptual and conceptual components, there are important differences between these two basic types. Perceptual priming occurs whenever stimuli have shared perceptual features and is modality specific, fast acting, and does not require the observer to elaborate on the meaning of the stimuli. In Chapter 4 perceptual priming is used to increase the cognitive salience of a colored stimulus during binocular rivalry.

Conceptual priming occurs whenever stimuli have some form of shared meaning or significance. This type of priming does not require any perceptual similarity between the stimuli and tends to take longer than perceptual priming

because the observer needs to process the meaning of the stimuli being presented. In Chapter 3 affective priming – a form of conceptual priming – is used (Fazio, Sanbonmatsu, Powell, & Kardes, 1986; Hermans, De Houwer, & Eelen, 1994). Affective priming is based upon a similarity in the stimuli's emotional content, and in this study it is used to evaluate the emotional content of previously neutral mental imagery. In Chapter 5 a novel form of conceptual priming is used that has been given the name “color-associate priming”. This type of priming involves the visual presentation of a colored patch to facilitate subsequent recognition for achromatically presented objects known to have that color (eg. yellow / banana). In Chapter 6 a form of conceptual priming is used that is known as thematic priming. Thematic priming is based upon the thematic relationships that can form between objects (Chapter 1.1.2). In this study it is used to facilitate the recognition of hand-held tool objects through the prior presentation of corresponding tool-use pantomimes.

2.2.2. Cognitive Mechanisms

Priming appears to include at least two component mechanisms: an implicit automatic process and an explicit strategic process (Mummery, Shallice, & Price, 1999; Neely, 1977; Neely, Keefe, & Ross, 1989; Posner & Snyder, 1975). The first mechanism is believed to be the result of the automatic spreading of neural activity to related concepts (Collins & Loftus, 1975), which occurs without awareness. The amount of activation that these other concepts receive is proportional to how related they are, with the most related receiving the greatest activation. This

automatic process appears to be the dominant mechanism of priming for stimulus onset synchronies (SOAs) of 400ms or less (Neely, 1977).

The second mechanism is strategically employed and is predominantly involved at longer SOAs, after the prime has been fully identified (den Heyer, Briand, & Dannenbring, 1983). At this point the observer will “expand” upon the meaning of the prime and begin to generate expectancies for related stimuli that are likely to follow (Rossell, Price, & Nobre, 2003; Tweedy & Lapinski, 1981). These expectancies are generated more slowly, and will further increase the conceptual activation produced by the first mechanism. Unlike the first mechanism which only increases activation for similar stimuli, this strategic process can actually have an inhibitory effect for unexpected stimuli. Though these two mechanisms of priming have different periods of dominance, they both play an important role across all SOAs.

2.2.3. Neurological Correlates

While the current studies do not include any neuroimaging or electrophysiological procedures, studies using these methods have helped explain the neural mechanisms underlying priming. Event-related potentials (ERPs), specifically the N400, have repeatedly been used to measure the strength of priming effects (Franklin, Dien, Neely, Huber, & Waterson, 2007). The amplitude of N400 is reduced when an observer is presented with a conceptually related prime and target, with the greatest reduction for perfectly identical stimuli. N400 amplitude appears to reflect a process occurring after the implicit spreading of activation, wherein high-level conceptual information is retrieved about the identity

of the stimulus (Brown & Hagoort, 1993). In line with the theory that the N400 reflects high-level conceptual processing, active attention to the stimuli has been shown to be necessary to reduce N400 amplitude (Chwilla, Brown, & Hagoort, 1995; Holcomb, 1988). Finally, the N400 appears to be an amodal index of conceptual similarity, as its modulation has been observed for both words and pictures (Nigam, Hoffman, & Simons, 1992).

The N300 appears to play a special role for pictures, as its amplitude is reduced when presented with conceptually related pictures, but not words (Barrett & Rugg, 1990). Also, the N300 appears to be unaffected by changes in the specific target exemplar, indicating that it is involved in a more broad categorical access wherein the pictured object has not yet been fully identified (Hamm, Johnson, & Kirk, 2002; McPherson & Holcomb, 1999; West & Holcomb, 2002).

Functional magnetic resonance imaging (fMRI) studies have commonly shown a haemodynamic decrease for primed targets, in comparison to non-primed targets (Henson, 2003). This haemodynamic decrease indicates an increase in processing efficiency, as if the prime “warmed up” the neurons to process subsequently presented similar stimuli more efficiently. This effect is known as repetition suppression (Grill-Spector, Henson, & Martin, 2006). Its effects are normally seen in the left inferior prefrontal cortex, specifically Brodmann’s areas 47 and 45 (Poldrack et al., 1999), and are believed to play an important role in the access of conceptual information (Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; Wagner, Desmond, Demb, Glover, & Gabrieli, 1997). Repetition suppression can also be seen in more specialized brain areas corresponding to the kinds of stimuli being presented.

Researchers like Grill-Spector et al. (2006; 1999) have taken advantage of the haemodynamic decreases of repetition suppression to study the inner organization of the lateral occipital complex (LOC), which is known to be highly involved in the processing of visually presented objects. Using a technique they call fMRI adaptation, they have shown that by comparing the haemodynamic decreases observed when the prime and target are identical with that of a target that had been altered in some specific way, it is possible to identify the specific neurological sites responsible for processing the altered parts of the stimulus. Such techniques have since gone on to become more mainstream.

2.3. Binocular Rivalry

Under normal conditions our two forward facing eyes receive highly similar information. The only differences in their incoming visual information tend to be due to parallax – systematic differences in the position and orientation of objects within a visual scene due to the slight difference in position of the two eyes. The visual system will automatically take advantage of this parallax by using it to determine stereoscopic depth cues, with the end result being a single “fused” percept that has additional depth information (Wheatstone, 1838). However, if completely different stimuli are shown to the same location of the two eyes then stereopsis cannot occur and binocular rivalry will instead be experienced (Blake, 1989; Blake & Logothetis, 2002; Blake & Tong, 2008). This form of binocular stimulus presentation is used for different purposes within Studies 2 and 4.

Binocular rivalry is a type of multi-stable perception (Leopold & Logothetis, 1999; Sterzer, Kleinschmidt, & Rees, 2009) that can be produced by presenting

two dissimilar stimuli to the two eyes through the use of a mirror stereoscope or similar device (Wheatstone, 1838). During rivalry the observer will experience periodic alternations in awareness between the two stimuli, where one of them will be more visible than the other for a period of time. The stimulus that is most visible during one of these periods is known as the “dominant” stimulus as it will suppress the other stimulus from awareness. For larger stimuli this perceptual dominance tends to be piecemeal, in that different parts of the two stimuli will independently rival with each other (Blake, 1989). Shifts in perceptual dominance are gradual, travelling in a wave-like fashion across the visual scene until the previously suppressed stimulus becomes the dominant stimulus (Genç et al., 2011; Pearson & Clifford, 2005a; H. R. Wilson, Blake, & Lee, 2001). Though these shifts in perceptual dominance will automatically occur at regular intervals, the length of these dominance periods can be manipulated (Pearson & Brascamp, 2008).

Perhaps binocular rivalry is poorly named, as it does not always occur between the visual inputs of the two eyes. For example, neuroimaging studies have demonstrated that activity within high-level visual areas, such as the fusiform face area (FFA) and the parahippocampal place area (PPA), correspond to shifts in perceptual dominance (Tong, Nakayama, Vaughan, & Kanwisher, 1998). It has even been demonstrated that binocular rivalry can occur between two different images when they are mixed together – half of each image is presented to each eye (Kovács, Papathomas, Yang, & Fehér, 1996; Treisman, 1962). Such findings have lent a great deal of support to the theory that binocular rivalry is processed by a neural mechanism spanning multiple levels of visual processing (Blake & Logothetis, 2002; Pearson & Clifford, 2005b; Tong, Meng, & Blake, 2006).

Cognitive neuroscientific studies have been able to utilize binocular rivalry as a new way to investigate awareness and attention. Using rivalry it is possible to reliably and efficiently judge the relative cognitive salience, or ability to attract attention, of two stimuli (Blake, 1989). Factors known to increase this cognitive salience include image features such as high contrast (Hollins, 1980), emotional significance (Alpers & Pauli, 2006), and motion information (Blake, Yu, Lokey, & Norman, 1998). Additionally, it has been shown that images of recognizable objects, such as a human face, are more salient than random patterns (Yu & Blake, 1992) and less meaningful objects (Lo Sciuto & Hartley, 1963; Walker, 1978). The rivalry stimulus that is more salient will dominate at the stimulus onset and tends to have longer periods of dominance than the suppressed stimulus (see Blake & Tong, 2008). In Chapter 4 binocular rivalry is used to measure the relative salience of differently colored stimuli after one has undergone perceptual priming with a mental imagery stimulus.

Continuous flash suppression (CFS) is another way that binocular rivalry has been used in the literature (Tsuchiya & Koch, 2004, 2005). CFS involves the presentation of a rapidly flashing and brightly colored pattern to one eye that can dominate perception for an indefinite period of time, allowing for the prolonged presentation of stimuli to the other eye without the observer's awareness. Stimuli suppressed by CFS are perceptually invisible to the observer but can still exert an influence on concurrent or subsequent perception (Pearson & Clifford, 2005a). In particular, CFS appears to suppress visual processing within the ventral stream while sparing some of the dorsal stream processing (Almeida et al., 2010; Almeida et al., 2008). As the dorsal stream is mostly involved in the perception of motion

and spatial information (Chapter 1.1.1) this finding seems to suggest that a stimulus with strong motion information could undergo a great deal of processing despite the observer being completely unaware of its presence. In Chapter 6 continuous flash suppression is used to determine whether the implied motion information of pantomime hand photographs can be used to prime the recognition of corresponding tool objects despite being suppressed from awareness.

3. STUDY 1: ASSOCIATIVE LEARNING WITH MENTAL IMAGERY

3.1. Introduction

There has been rapid growth in research examining the learning of fear and hedonic processes (Lissek et al., 2005), perceptual learning (Sasaki, Nanez, & Watanabe, 2010), motor learning (Jeannerod, 1995) and learning driven by neural-feedback signals (Shibata, Watanabe, Sasaki, & Kawato, 2011). Additionally, the learning of associative links between objects or events has been well documented using various kinds of perceptual stimuli (De Houwer, Thomas, & Baeyens, 2001; I. Martin & Levey, 1978; Milad, Rauch, Pitman, & Quirk, 2006). However in much of this research, and most general theories of learning, it is assumed that the stimuli must be physically present in order for learning to occur.

Mental imagery is a perception-like experience that does not require stimuli to be physically present. As discussed in Chapter 1.2.1 mental imagery is based on the memories of perceptual experiences, can influence normal perceptual processing, and is in many ways the mental simulation of these experiences. This is indicative of the high degree of similarity between imagery and perception as predicted by the theory of grounded cognition (Chapter 1.2). Accordingly, a large number of studies have provided evidence indicating that mental imagery can play an important role in what are traditionally considered to be perceptual processes, such as associative learning (see Dadds, Bovbjerg, Redd, & Cutmore, 1997). The evidence suggests that imagery may be able to influence associative learning for perceptual stimuli. The current study builds upon this evidence by demonstrating the interchangeability of imagery and perception in associative learning.

3.1.1. Current Study

Using an associative learning paradigm the voluntarily generated mental imagery of oriented Gabor patterns is paired with the content of emotion-evoking photographs. Emotion-evoking photographs were used as it is well known that associative learning tends to occur quicker and forms stronger associative links when the stimuli evoke powerful emotional responses. If mental imagery can indeed undergo associative learning then this pairing will emotionally charge the imagery Gabors. Being emotionally charged will allow the Gabors to be used as affective primes (Chapter 2.2.1), which could be used to facilitate the recognition of subsequently presented photographs with similar emotional content. Measuring the magnitude of this facilitation would be a measurement of the strength of the associative links that form between the mental imagery and the emotion-evoking photographs. The finding of significantly strong links would indicate that mental imagery can undergo associative learning in the same way as perceptual stimuli, thus demonstrating that imagery and perception are similarly processed within the brain as predicted by the theory of modality grounded cognition (Chapter 1.2.1).

In four separate experiments our associative learning methodology and its ability to influence the emotional content of mental imagery stimuli is investigated. Experiment 1 determines whether our associative learning method can be used for perceptual stimuli. Experiment 2 investigates whether associative learning can occur for Gabor patterns that differ in color and orientation. Experiment 3 examines whether color plays an important role in this associative learning as it is well known that colors can have strong emotional associations (Gao et al., 2007; Kaya & Epps, 2004). Additional tests are conducted within this experiment to rule out alternative

(non-imagery based) accounts of these learning effects. Experiment 4 measures the orientation specificity of this learning – which is mostly processed within low-level visual areas (Blakemore & Campbell, 1969; Fang, Murray, Kersten, & He, 2005; Hubel & Wiesel, 1968) – by systematically altering the orientation of the Gabor patterns presented during the affective priming phase. If significant affective priming is found in these experiments it will indicate that associative learning can occur with mental imagery, showing that perceptual stimuli do not need to be physically present for associative learning to occur. This study has recently been published by *Clinical Psychological Science* and the publication version is included as Appendix A (Lewis, O'Reilly, Khuu, & Pearson, 2013).

3.2. Hypotheses

1. Our associative learning methodology can be used for perceptual stimuli.
2. Voluntary mental imagery can undergo associative learning in the same way as perceptual stimuli. Either seeing or imagining a particular pattern prior to the presentation of an emotion-evoking photograph will lead to associative learning.
3. The color of this mental imagery is not needed for this associative learning to occur. This learning cannot be explained by the formation of associative links between the perceptual cues used to evoke the mental imagery.
4. Associative learning for visual mental imagery is orientation specific, indicating that it requires processing within the same low-level visual areas as visual perception.

3.3. Method

3.3.1. Participants

A total of 143 students from the University of New South Wales were recruited for this study ($n_{\text{experiment 1}} = 79$; $n_{\text{experiment 2}} = 30$; $n_{\text{experiment 3}} = 19$; $n_{\text{experiment 4}} = 15$). All participants were students from the University of New South Wales who gave written informed consent before the start of each experimental session. New participants were recruited for each experiment via web advertisements. Fewer participants were recruited for each successive experiment in the attempt to produce a more conservative replication of the original results and to increase efficiency. Course credit or money was awarded upon completion of the study. This study received ethical approval from the UNSW Human Research Ethics Advisory Panel (HREA).

3.3.2. Stimuli: All Experiments

All stimuli were created and presented using Psychtoolbox (Brainard, 1997) for Matlab (version 7.10.0 R2010a) on a Mac Mini computer and were displayed on a 27cm x 35.5cm Philips 109P4 monitor at a resolution of 1152 x 870 at 75Hz. Stimuli were presented on a screen with a black background and a circular fixation mark (diameter = 0.62°) in the center.

3.3.3. Stimuli: Experiments 1, 2, and 4

In Experiments 1, 2 and 4, a pair of Gabor patterns ($\sigma = 4^\circ$; SF = 1 cycles/degree) were used as conditioned stimuli (CS): a red vertical pattern (CIE x

=0.6 $y = 0.37$) and a green horizontal pattern (CIE $x = 0.27$, $y = 0.62$). In Experiment 3, the achromatic imagery experiment, both Gabors were grayscale (contrast 100%; max luminance = 45.0 cd/m²). In all experiments the screen's background was black (max luminance = 0.01 cd/m²), as background luminance has been shown to attenuate imagery generation (Pearson et al., 2008; Sherwood & Pearson, 2010). Two categories of affective photographs were used as the unconditioned stimuli (US), which were sourced from the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2008). "Pleasant" IAPS photos were those rated low on arousal and high on pleasantness; "Aversive" IAPS photos were those rated high on arousal and low on pleasantness. Photos rated high on both scales were not used as they are mostly sexually explicit in nature. Photos rated low on both scales were not used as they had no emotional content. In the associative learning phase a set of 12 photos (6 pleasant; 6 aversive) were used and in the test phase a different set of 12 were used.

3.3.4. Stimuli: Experiment 4

In Experiment 4, the orientation specificity experiment, the two original Gabor patterns (red=90° green=0°) were accompanied by similar patterns that had been rotated 22° and 45°. The number of IAPS photos was also increased; twelve photographs were added to the associative learning phase (6 pleasant; 6 aversive) and 36 were added to the test phases (18 pleasant; 18 aversive). These additional photos were added to accommodate for an increase in the total number of trials.

3.3.5. Procedure

All participants were seated in a dark room with their heads stabilized on a headrest approximately 57cm from the monitor. Participants undergoing associative learning for mental imagery had previously been shown both Gabor patterns and were instructed to imagine them when a corresponding letter cue was shown. In Experiments 2 and 4 the letter cue “R” corresponded to the red vertical Gabor and “G” corresponded to the green horizontal Gabor. In Experiment 3, the achromatic imagery experiment, the letter cue “V” corresponded to the vertical Gabor and “H” corresponded to the horizontal Gabor. Participants were instructed to fixate on a circular fixation mark in the center of the screen for the duration of the experimental session. Figure 3.1 shows the trial designs for the two associative learning phases and three test phases used in this study. These designs are discussed in further detail in the following sub-sections.

It is important to note that voluntary mental imagery was only used in the associative learning phase and not in the test phase. Hence, any effect of learning in this design is inherently a generalization, or cross-over, from a voluntary imagined representation to a perceptual one.

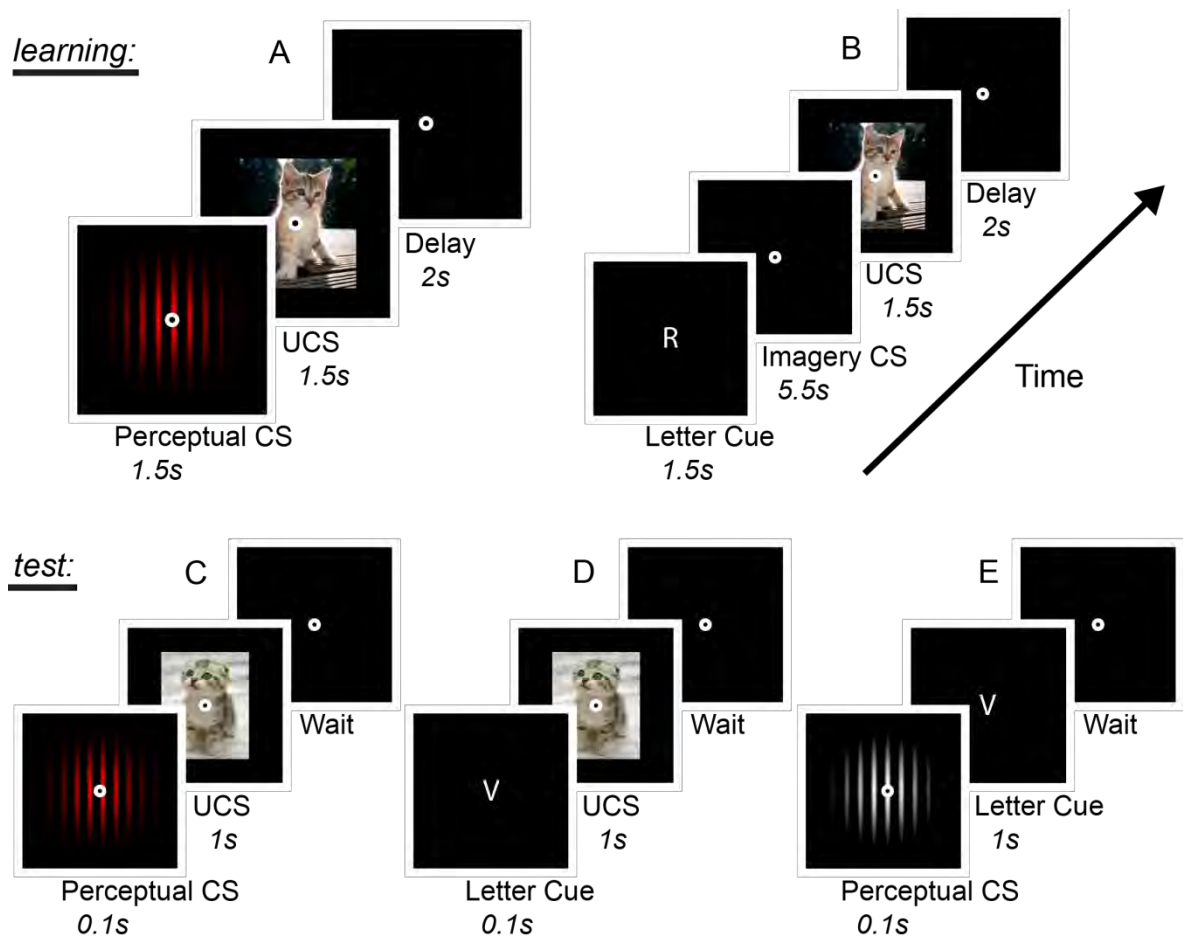


Figure 3.1. Experimental timelines. (A) Experiment 1. Associative learning with perceptual stimuli. Immediately following the perceptual presentation of a colored Gabor pattern an emotion-evoking stimulus would be displayed. (B) Experiments 2, 3 & 4. Associative learning with mental imagery. Upon letter cue presentation the participants were instructed to generate mental imagery of the cued Gabor pattern for 5.5s, which was then followed by the display of an emotion-evoking stimulus. (C) All Experiments. Test of association between perceptual Gabor and emotional photograph. A perceptual Gabor was briefly displayed prior to an emotion-evoking stimulus. The participants were required to judge the emotional content of the stimulus as quickly as possible. (D) Experiment 3. Test of association between letter cue and emotional photograph. A letter cue was briefly displayed prior to an emotion-evoking stimulus. The participants were required to judge the emotional content of the stimulus as quickly as possible. (E) Experiment 3. Test of association between perceptual Gabor and letter cue. A perceptual Gabor was briefly displayed prior to one of the previously used letter cues. The participants were required to indicate which cue was being shown as quickly as possible. All photographs shown above are not actual IAPS photographs, as they are not to be used outside experimental settings.

Associative learning phase

At the start of each experiment participants completed multiple trials of the associative learning task. As shown in Figure 3.1A, the perceptual stimuli trials started with the presentation of one of the two randomly chosen perceptual Gabors for 1.5s, followed immediately by the emotional photograph for 1.5s. The screen would then remain blank for a 2s inter-trial interval. As shown in Figure 3.1B, the mental imagery trials started with the presentation of one of the two randomly chosen letter cues for 1.5s. This was followed by a blank screen for 5.5s, during which the participants were to imagine the pattern indicated by the letter cue. Then either a pleasant or aversive photograph was displayed for 1.5s, followed by a 2s inter-trial interval wherein the screen would remain black. In both learning tasks the participants were required to press the space bar as soon as the photo image was presented in order to help them maintain vigilance. This kind of associative learning technique is commonly used to associate emotional content with neutral sensory stimuli (De Houwer et al., 2001).

Throughout the associative learning phase the relationship between the Gabors and their associated emotion-evoking photographs remained constant. The stimulus associations were counterbalanced across participants: for half of the participants the vertical Gabors were paired with aversive photos and the horizontal Gabors with pleasant photos, and vice-versa for the other half. Each Gabor was paired with all corresponding emotion-evoking photographs an equal number of times. The Gabor-photograph pairs were presented in random order.

In Experiment 1 a total of 40 associative learning trials were conducted. In Experiments 2 and 3 a total of 84 learning trials with mental imagery were

conducted. In Experiment 4 the number of learning trials was increased to 144, with 102 trials at the beginning of the study and another 42 halfway through the test phase. This “top-up” was done to accommodate for any potential extinction due to the increased number of test trials.

Gabor: Test phase

Following the learning trials the participants in all experiments completed 120 trials of a choice reaction time task on a new set of emotion-evoking photographs to test the strength of the previously learned associations. Figure 3.1C shows the design of an individual Gabor pattern test trial. One of the two previously imagined Gabor patterns was presented for 100ms followed immediately by the presentation of an IAPS photograph for 1s. Participants were required to judge the emotional content of the photographs upon their presentation as quickly and accurately as possible. They could judge the photos as either “Pleasant” or “Aversive” by pushing either the 1 or 3 button on the keyboard. Participants were instructed to respond as fast as possible without sacrificing accuracy. If conditioning did occur then reaction times should be faster when the pattern’s associated emotion accurately predicts the emotional content of the subsequent photograph due to priming (see Chapter 2.2).

In Experiment 4 the number of Gabor test trials was increased to 288, which were split evenly between the six Gabor patterns of different orientations (red 90°, red 68°, red 45°, green 0°, green 22°, and green 45°) and presented in random order. These specific orientations were selected based upon previous evidence of orientation specificity for mental imagery (Pearson et al., 2008).

Letter Cue: Test phase

Participants in Experiment 3 completed an additional priming task to test the strength of any learned association between the emotional content and the letter cues used in the associative learning task. As Figure 3.1D shows, this letter cue test phase was identical to the Gabor test phase except that the Gabor patterns were replaced with their corresponding letter cues. The order of test phase presentation was counterbalanced between participants with half of the participants completing the Gabor test first and the other half completing the letter cue test first.

Gabor Cue: Test phase

Participants in Experiment 3 also completed a third test to directly measure the strength of any learned association between the Gabors and their corresponding letter cues. Figure 3.1E shows the trial design for testing the priming from the Gabor patterns for the letter cues. Participants completed a total of 40 trials, consisting of 10 presentations for each combination of Gabor and letter cue. In each trial one of the two previously imagined Gabor patterns was *physically* presented for 100ms followed immediately by one of the two letter cues for 1s. Upon presentation of a letter cue, participants were required to press the corresponding key on the keyboard as quickly and accurately as possible. This Gabor-cue test was always completed last.

3.3.6. Data Preparation

Filters were applied to the data to remove outliers. Incorrect emotionality judgments were removed from the dataset, as were individual participant reaction times that were shorter than 250ms, longer than 2500ms or beyond 2.5 standard deviations from the participants' means. Additionally, 2 outlying participants were excluded from analysis in Experiment 3 due to having mean mismatch-match scores beyond 2.5 standard deviations of the overall group mean. How these matched and mismatched scores were determined is detailed below.

3.4. Results

To measure the strength of the associative learning for the voluntary mental imagery each participant's reaction-time data was split into matched and mismatched trials. Matched trials included the stimulus pairs that were presented during the associative learning, while mismatched trials consisted of stimulus pairs that were not. If matched trials showed significantly faster reaction times this would be indicative of affective priming, which would suggest that the previously neutral Gabor patterns had gained emotional content due to associative learning. Figure 3.2 shows the average reaction times for matched and mismatched trials for Experiment 1, 2 and 3.

3.4.1. Experiment 1: Perceptual Stimuli

As the goal of this study was to investigate associative learning for mentally generated stimuli, we first needed to validate the effectiveness of our associative learning task. Figure 3.2A shows the data from the preliminary experiment wherein

both the CS and UCS were perceptual stimuli. A paired-samples comparison showed that reaction times were significantly faster when the preceding pattern's associated emotion matched the emotional photograph ($M = 563.9\text{ms}$, $SEM = 7.84\text{ms}$) than when it was mismatched ($M = 572.5\text{ms}$, $SEM = 8.05\text{ms}$), $t(78) = 3.29$, $p < .005$, $\eta^2 = .12$. This shows that our associative learning task performs as expected for perceptual stimuli.

3.4.2. Experiment 2: Colored Imagery

To test our main hypothesis we determined whether our task can also produce associative learning for mentally generated stimuli. Figure 3.2B shows the data from the Gabor pattern test phase following associative learning with mental imagery. A paired-samples comparison showed that reaction times were significantly faster when the preceding pattern's associated emotion matched the emotional content of the photograph ($M = 587.44\text{ms}$, $SEM = 13.95\text{ms}$) than when it was mismatched ($M = 606\text{ms}$, $SEM = 15.82\text{ms}$), $t(29) = 4.14$, $p < .001$, $\eta^2 = .37$. This finding suggests that associative learning can occur between mentally generated stimuli and the emotional content of photographs.

3.4.3. Experiment 3: Achromatic Imagery

We attempted to replicate the previous results using achromatic Gabor patterns, as it was believed that the color of the Gabors might have influenced our previous results. Figure 3.2C shows the data from the Gabor test phase following associative learning with achromatic mental imagery. A paired-samples comparison showed significantly faster reaction times when the pattern's previously associated emotion matched the emotional photograph ($M = 586.7\text{ms}$,

$SEM = 18.05ms$) than when it was mismatched ($M = 599.7$, $SEM = 18.6ms$), $t(16) = 2.50$, $p < .05$, $\eta^2 = .281$. These data once again show a significant effect of associative learning with mental imagery. This replication provides further evidence that mental imagery can undergo associative learning, and also suggests that color information is not crucial for such associative learning.

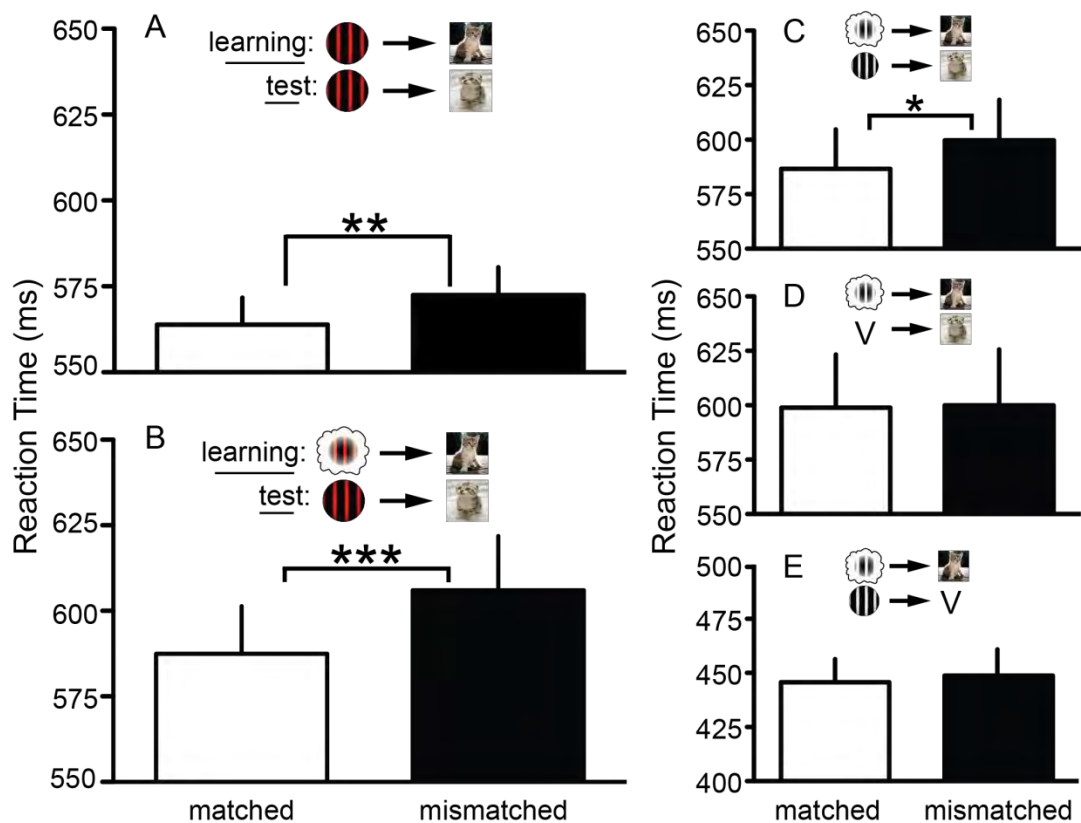


Figure 3.2. Mean reaction times for matched and mismatched stimuli during the test phases. Data indicate associative learning effects from sensory stimuli and imagined stimuli. (A) Experiment 1. Gabor-photo test preceded by perceptual conditioning ($n = 79$). (B) Experiment 2. Gabor-photo test preceded by imagery conditioning ($n = 30$). (C) Experiment 3. Achromatic Gabor-photo test preceded by achromatic imagery conditioning ($n = 17$). (D) Experiment 3. Cue-photo test preceded by achromatic imagery conditioning ($n = 17$). (E) Experiment 3. Achromatic Gabor-cue test preceded by achromatic imagery conditioning ($n = 17$). Photographs shown above are not actual IAPS photographs, as they are not to be used outside experimental settings. Error bars show +1 SEM. * = $p < .05$ ** = $p < .005$ *** $p < .001$.

However, it may have been that during the test phase the perceptual Gabor patterns induced a representation of the corresponding letter cues, and these letter cues were actually the driving force of the affective priming shown in Figure 3.2C. To test this alternative account we conducted two additional tests to measure the strength of the associations between the letter cues and the photographs, and between the perceptual Gabor patterns and the letter cues. Significant priming effects need to be found in *both* of these tests to suggest that mental imagery did not necessarily undergo associative learning, as only their combined effects will provide evidence supporting this alternative account of the data.

Figure 3.2D shows the data from the letter cue test phase following associative learning with achromatic mental imagery. This test was conducted to determine if there was any direct link between the imagery cues and the emotion-evoking photographs. Associative learning found in this task would be attributable to either conditioning between the cue and the emotional photographs, or indirect association via the mental imagery Gabors. However, a paired-samples comparison showed no significant difference in the reaction times between matched ($M = 598.9$, $SEM = 24.44\text{ms}$) and mismatched pairs ($M = 599.9$, $SEM = 25.69\text{ms}$), $t(16) = 0.21$, $p = .838$. These data indicate that the letter cues did not undergo significant associative learning. Approximately half of the participants completed this letter cue test before completing the Gabor test.

Figure 3.2E shows the data from this Gabor-cue test phase following associative learning with achromatic mental imagery. This test was conducted to determine if the Gabor patterns were associatively linked to the letter cues. A paired-samples comparison showed no significant difference in reaction times

between the matched ($M = 445.7$, $SEM = 10.73\text{ms}$) and mismatched conditions ($M = 449.1$, $SEM = 11.78\text{ms}$), $t(16) = 0.43$, $p = .675$. This indicates that participants did not reliably associate the Gabor patterns with their letter cues, despite being shown physical versions of the Gabors at the start of the experiment and being instructed to imagine them when the appropriate letter cue was shown. It seems that even though participants were told of the relationship between the letter cue and the Gabor pattern, no strong associative link formed between them. This test phase was conducted after the other two test phases had been completed.

3.4.4. Experiment 4: Oriented Imagery

In this final experiment we sought to determine whether associative learning with mental imagery is orientation specific. Figure 3.3 shows the average reaction-time differences between the matched and mismatched trials for Gabor patterns rotated 0° , 22° , and 45° . A repeated-measures ANOVA indicated significant changes across the three levels of orientation, $F(2, 28) = 4.11$, $p < .05$, $\eta^2 = .23$, $n = 15$. Post-hoc analyses showed that the difference scores for Gabors rotated 0° ($M = -18.05\text{ms}$, $SEM = 7.89\text{ms}$) and 22° ($M = -16.76\text{ms}$, $SEM = 7.43\text{ms}$) were significantly different than Gabor patterns rotated 45° ($M = 12.06\text{ms}$, $SEM = 11.75\text{ms}$), $p < .05$. These results show that altering the orientation of the Gabor patterns modulated the associative learning effects.

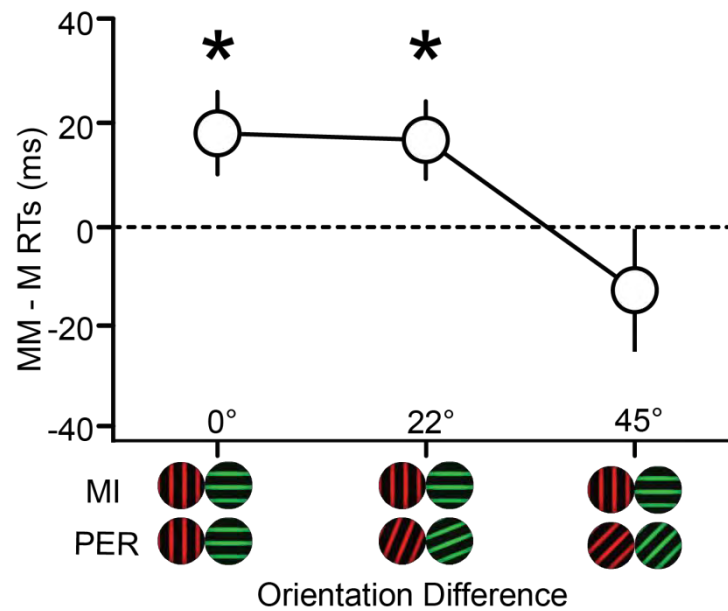


Figure 3.3. Reaction time difference between mismatched and matched pairs using Gabors rotated 0°, 22° and 45° from those used in the associative learning phase. MI = Mental imagery Gabors used in the associative learning phase. PER = Perceptual Gabors used the test phase. Error bars show between subjects ± 1 SEM. Significant differences shown indicate paired-samples analyses between matched and mismatched conditions for individual orientations ($n = 15$). * = $p < .05$

We then sought to determine if a significant amount of associative learning had occurred in any of the three orientation conditions. For each test pattern orientation the matched and mismatched reaction times were compared in the same manner as the previous experiments. Reaction times for 0° rotated Gabors were significantly faster for matched pairs ($M = 640.98\text{ms}$, $SEM = 13.52\text{ms}$) than mismatched pairs ($M = 659.03\text{ms}$, $SEM = 16.51\text{ms}$), $t(14) = 2.29$, $p < .05$, $\eta^2 = .27$, providing yet another replication of our findings from Experiments 2 and 3.

Reaction times for 22° rotated Gabors were also significantly faster for matched pairs ($M = 646.86\text{ms}$, $SEM = 12.13\text{ms}$) than mismatched pairs ($M = 663.62\text{ms}$, $SEM = 16.45\text{ms}$), $t(14) = 2.26$, $p < .05$, $\eta^2 = .27$, indicating a degree of

generalization between similarly oriented Gabors. However, when the patterns were rotated 45° the reaction times for matched pairs ($M = 656.66\text{ms}$, $SEM = 17.26\text{ms}$) were not significantly different from mismatched pairs ($M = 644.60\text{ms}$, $SEM = 13.13\text{ms}$), $t(14) = 1.03$, $p = .322$. Additionally, these data also show that the Gabor pattern colors were unable to independently elicit the learned emotion, which dovetails nicely with the results of Experiment 3 (achromatic stimuli).

3.5. Discussion

We have shown strong evidence that associative learning can occur for mental imagery. Perceptual Gabor patterns were found to elicit a measurable emotional response after voluntary mental imagery of these Gabors was paired with emotion-evoking stimuli. Hence, by definition, our dependent measures include generalization from an internally generated mental image to a sensory representation. The observed effects were substantial across all studies, similar to previous findings of associative learning with perceptual stimuli (De Houwer et al., 2001; I. Martin & Levey, 1978; Milad et al., 2006). This finding has implications for the treatment of various anxiety disorders (Chapter 7.2.1) and potentially explains how abstract concepts – those which have no inherent sensory or motor information – may gain their meaning (see Chapter 7.1.3).

The current results cannot be accounted for by associative learning for the imagery cues themselves during the test phase. If associative learning had occurred for the letter cues instead of the imagery Gabors, and the Gabors within the test phase produced a recall of the letter cues, this could account for the

previously observed priming effects. If this non-mental imagery account were valid then the imagery cues should be able to prime the emotion-evoking IAPS images, *and* the perceptual Gabors should be able to prime the imagery cues. However, we found that the imagery cues did not prime the emotion-evoking photographs (Figure 3.2D), and the perceptual Gabor patterns did not prime the imagery cues (Figure 3.2E), thus ruling out this alternative account (Section 3.4.3.). Additionally, the failure of this alternative account may be explained by the temporal relationships between the stimuli. It has been shown that the strength of a learned association between two stimuli is negatively correlated with the temporal distance and number of stimuli presented between them (Balsam, Drew, & Gallistel, 2010). Hence, the lack of associative learning for the letter cues may simply be due to the large amount of time between the cues and the emotion-evoking photographs.

3.5.1. Orientation Specificity

These findings correspond with previous research showing orientation specificity for mental imagery (Pearson et al., 2008), though the present findings show a broader degree of orientation tuning than previously reported (Section 3.4.4.). Orientation specificity is a well-known hallmark of early levels of processing in the visual cortex (Blakemore & Campbell, 1969; Hubel & Wiesel, 1968; Ling, Pearson, & Blake, 2009). Our findings suggest that associative learning with voluntary mental imagery selectively involves these early-level visual areas, sensitive to spatial orientation. This finding is surprising seeing that previous work suggested high-level, object-selective inferior temporal cortex as the neural substrate for associative learning (Jones, 1974; Meyer & Yates, 1955; Miyashita,

1993; Sakai & Miyashita, 1991; Yakovlev, Fusi, Berman, & Zohary, 1998). If associative learning with voluntary imagery was primarily occurring in this neural area then we would not expect to see such a strong effect of only changing the orientation of the stimuli without changing the color.

3.5.2. Similarities between Imagery and Perception

These results provide further evidence that mental imagery and sensory perception involve overlapping processes through demonstrating their interchangeability within associative learning (Section 3.4.). However imagery is an inherently private affair making it difficult to study using traditional research methods. The private nature of mental imagery has resulted in many compelling criticisms of imagery research. The founder of the behaviorism movement, Watson (1913), argued that mental imagery plays no role in thought or behavior; the generation of mental images simply does not occur. This idea was revisited by Skinner (1977), who claimed that everything required to explain human behavior can be found within the environment. Mental imagery is redundant and studying it is unnecessary. Pylyshn (1973, 1981) argued that people do in fact generate mental images, but the term “image” is misleading as it actually involves a form of “mentalese” - the combination of multiple abstract symbols. These kinds of theories have driven psychological science for decades (Chapter 1.1). However, in recent years a great deal of neuroimaging and behavioral research has provided compelling new evidence that many kinds of mental imagery are indeed pictorial, in that they use the same neural areas and are processed similarly to perceptual stimuli (Chapter 1.2.1). Additional research is required to determine if there are any

important differences between these two processes (Chapter 7.3.1).

3.5.3. Conclusions

This study demonstrates that associative learning can occur between a voluntarily generated mental image and the emotional content of a photograph. This interchangeability of imagery and perceptual stimuli provides further support for the pictorial theory of mental imagery, which is predicted by the theory of modality grounded cognition. For the first time it is demonstrated that a stimulus not physically present can become emotionally charged after being paired with an emotion-evoking photograph. This suggests that the way we evaluate mental images and even the physiological and emotional states they induce can be selectively altered by directly pairing them with specific perceptual stimuli. This suggestion has strong implications for the treatment of anxiety disorders. These findings also potentially provide a framework through which abstract concepts – those with no inherent sensory or motor information – may gain their meaning. It still remains to be seen what the relative strength of associative learning for mental imagery is, and if there are limits to the kinds of imagery that can be used.

4. STUDY 2: MENTAL IMAGERY FOR COLOR

4.1. Introduction

Concept knowledge is known to contain color information (Chapter 1.2.2). Color knowledge is gained through exposure to objects or events that have strong color associations which are stored in the brain as memories (see Bramão, Reis, et al., 2011). Recalling the perceptual memories of these objects or events can influence the concurrent and subsequent perception of color, as clearly demonstrated by the color memory effect wherein an object's actual colors are automatically and instantaneously adjusted to what they "should" be based upon previous experience (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Hering, 1920; Pérez-Carpinell, de Fez, Baldoví, & Soriano, 1998). This effect appears to suggest that color perception and color knowledge involve similar neural processing. Though the underlying mechanisms remain unknown, it seems possible that these knowledge based effects occur through the generation of mental imagery for color.

In Chapter 3 it is demonstrated that mental imagery can be used in place of perceptual stimuli in an associative learning task. This demonstration provides new evidence that the sensory content of imagery is similar to that of normal perceptual stimuli, which lends additional support to the theory of modality grounded cognition (Chapter 1.2). However, though the stimuli used in this study had color information, no color-based effects were found. This finding may indicate that the participants were unable to produce mental imagery with vivid color information. Yet in none of the experiments of Chapter 3 were the participants specifically instructed to

generate colored mental imagery. Therefore it may simply be the case that the participants focused their limited cognitive resources on creating mental representations of the stimuli's other features (e.g. orientation).

Color imagery is still a relatively new field of research. Consequently, consensus has not yet been reached regarding many of its aspects. In particular some neuroimaging studies have found similar patterns of activity for color perception and color imagery (Hsu et al., 2012; Hsu et al., 2011; Rich et al., 2006; W. K. Simmons et al., 2007), while others have not (Bramão, Faísca, Forkstam, et al., 2010; Chao & Martin, 1999; Lu et al., 2010). Case studies of brain damaged patients has produced similarly inconclusive evidence (De Vreese, 1991; Farah et al., 1988; Goldenberg et al., 1995; Luzzatti & Davidoff, 1994; Shuren et al., 1996). It seems likely that this conflicting evidence may be due to differences in the way some of these studies assessed color imagery.

Various methods have been used to determine whether an individual is able to generate and maintain color imagery. These tasks can be divided into their two most common types, color naming and color comparison. Color naming tasks require the visualization of an object followed by the naming of its colors (Shuren et al., 1996). Color comparison tasks require the visualization of two different objects and the subsequent comparison of their colors along some dimension (e.g. "Is a raspberry darker red than a strawberry?"; Howard et al., 1998). These tasks tend to require imagery of real objects, such as raspberries, which inherently have many different kinds of visual information (Chapter 2.1.1). Therefore, despite being instructed to focus on the color of a particular object, the attempt to form the mental image of such a multi-featured object could potentially squander cognitive

resources that could have otherwise been used for color imagery. It also seems likely that both of these kinds of tasks could be performed using only semantic memory; no perceptual processing may actually be required. To conclusively show that color imagery is perceptual in nature would require a different kind of task. It would require a task that shows color imagery can influence color perception.

4.1.1. Current Study

The goal of the current study is to more directly address whether the generation of color imagery can influence the subsequent perception of color. A unique task was developed to achieve this goal, which involves both perceptual priming and binocular rivalry (see Chapters 2.2 and 2.3). In this task participants are instructed to generate mental imagery of a particular color in order to bias the perception of subsequently presented colors undergoing binocular rivalry. Measuring this kind of perceptual bias has previously been shown to be indicative of the vividness of the mental imagery (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010). As the current study uses stimuli that only differ in their color, this will allow the participants to focus squarely upon the generation of color imagery. This focus should allow the participants to form the most vivid color imagery possible.

Three experimental conditions are tested to measure perceptual bias due to color imagery. The first condition involves the generation of color imagery in the absence of any visual stimuli, as prior studies have shown that concurrent visual perception can interfere with the generation of other kinds of mental imagery (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). The

second condition includes a brightly illuminated background to test whether this kind of interference can affect color imagery. The third condition does not involve the generation of any mental imagery stimuli whatsoever. In this condition the participants passively viewed weak (low luminance) perceptual stimuli, which have previously been shown to have similar priming effects as mental imagery (Pearson et al., 2008). If color imagery can be shown to produce a perceptual bias on the subsequent perception of color, and these findings are replicated for the weak perceptual stimuli, this will demonstrate that vivid mental imagery for color is possible and is processed similarly to the perception of color as predicted by the theory of grounded cognition. This study is the first experiment of a larger study currently being prepared for publication by the Journal of Vision and the final editorial version is included as Appendix B (Chang, Lewis, & Pearson, in press).

4.2. Hypothesis

The color information of a mental imagery stimulus can influence the subsequent visual perception of color.

4.3. Method

4.3.1. Participants

Nine individuals (2 females), were recruited for this study. All participants had normal or corrected to normal vision and gave written informed consent. This

experiment was approved by the UNSW Human Research Ethics Advisory Panel (HREA) for Psychology.

4.3.2. Stimuli

Stimuli were displayed on a Sony Trinitron G520 CRT monitor with 1280 × 960 resolution and 75-Hz refresh rate. Stimuli were generated using Matlab 7.9.0 (R2009b) and the Psychophysics toolbox (Brainard, 1997) running on an iMac computer with an Nvidia GeForce GT120 graphics chip. A circular fixation mark (diameter = 0.3° visual angle) was used to help participants maintain fixation.

The stimuli consisted of six differently colored Gaussian blobs (mean diameter $\approx 5.67^\circ$ visual angle) presented at fixation. The CIE color values of the Gaussians were as follows: red: $x = 0.633$, $y = 0.340$; cyan: $x = 0.208$, $y = 0.326$; green: $x = 0.274$, $y = 0.406$; violet: $x = 0.293$, $y = 0.157$; blue: $x = 0.142$, $y = 0.075$; yellow: $x = 0.387$, $y = 0.521$. These Gaussians were split into three separate pairs of stimuli: red/cyan, green/purple, blue/yellow. The luminance values of the two colors in each pair were adjusted to perceptual isoluminance for each participant using an eye-dominance test adapted from previous studies (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010)

4.3.3. Procedure

At the start of each experimental session the participant was seated in a darkened room with their head stabilized using a mirror stereoscope with a headrest. An eye-dominance test was conducted for each color pair in order to adjust the relative luminance of the two Gaussians in each pair to achieve perceptual isoluminance for each participant. This test involved making

incremental changes to the luminance of the two colored Gaussians until they appeared to be of equal brightness.

Each participant completed 4 experimental sessions, each being separated into three color-pair sections: red/cyan, green/purple, blue/yellow. Each session consisted of 54 trials; 18 trials for each color pair divided evenly among the three conditions: imagery, background-luminance, and perception. Though participants were told which colors would be presented at the start of each color-pair section, the condition being tested on each individual trial was randomly determined.

As can be seen in Figure 4.1, at the start of each imagery and background luminance trial a word cue was presented at fixation for 1s. This cue indicated which color the participant should imagine during the following 9s mental imagery interval. In the imagery condition the background remained black to facilitate mental imagery. In the background luminance condition the brightness of the background ramped on over a period of 1s, remained at full brightness for 6s, and was then ramped off for 2s. After the mental imagery interval a colored binocular rivalry stimulus was presented for 1s followed by a 5s inter-trial interval. Upon seeing this binocular rivalry stimulus the participants were required to report the initially dominant color by pressing one of two different buttons. The participants could also indicate that the stimuli appeared equal by pressing a third button.

In the perception condition the word cue was always “FOCUS”. This word cue indicated to the participants that they should not attempt to generate any mental imagery during the mental imagery interval. During this interval a perceptual Gaussian was presented at fixation. The Gaussian was ramped on for

approximately 0.5s, remained at full brightness for 6.5s, and was then ramped off for about 1.5s. All other procedures were the same as the two imagery conditions.

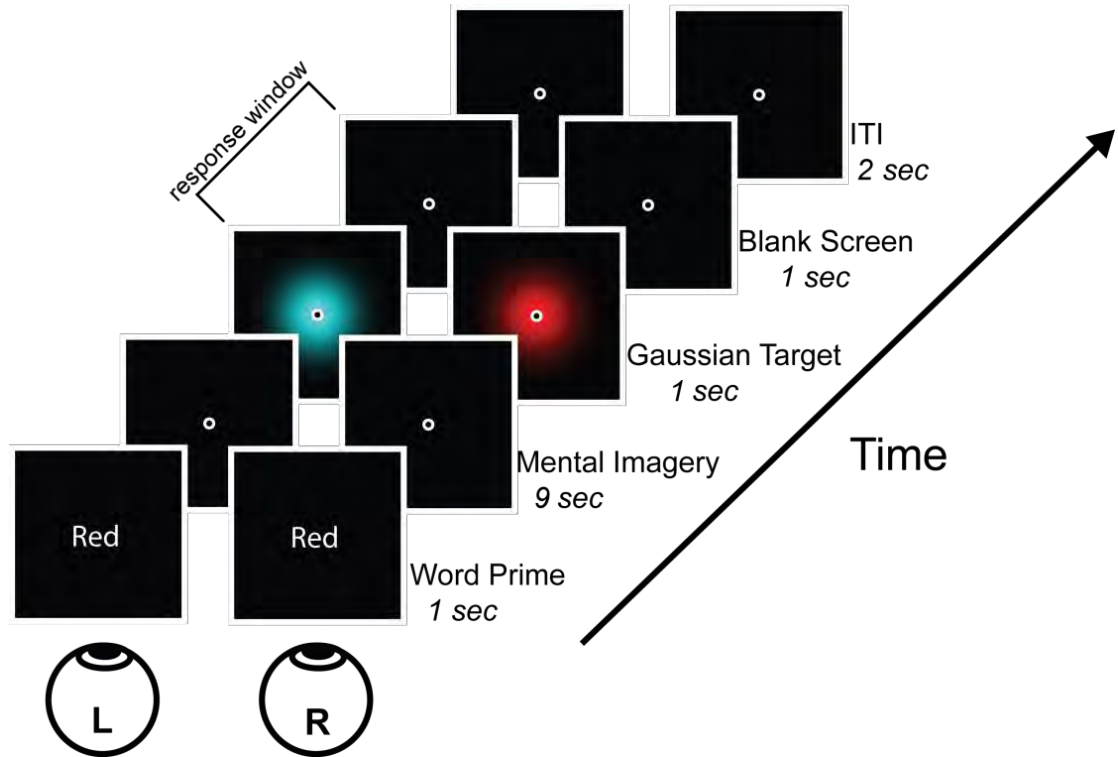


Figure 4.1. Experimental timeline for the imagery condition. In each trial the participants were instructed to generate a vivid mental image of the color indicated by the word prime during the 9s mental imagery interval. This was immediately followed by binocular rivalry for 1s wherein the participants were instructed to indicate which stimulus appeared to be initially dominant. Failure to respond within 2s of stimulus onset resulted in the repetition of that trial. In the background luminance condition the screen was gradually ramped on to full brightness during the first 2s of the mental imagery interval, and then ramped off during the last 2s. In the weak perception condition the word “FOCUS” was displayed as the word prime, and a colored Gaussian of low luminance was ramped on during the first 2s of the mental imagery interval, and then ramped off during the last 2s.

A total of 9 mock trials were also included within each experimental session (3 per color-pair), which were randomly assigned to one of the imagery conditions. These mock trials were included to determine if the participants’ responses were being influenced by the word cue presented at the start of each trial. This non-

perceptual bias would be apparent if the participants indicated that one of two stimuli was dominant during the binocular rivalry task despite the stimuli being perfectly balanced. These mock rivalry stimuli were created by combining the two colors of each pair together into a split-half Gaussian. The mock stimuli were presented simultaneously to both eyes to ensure that the two colors were perfectly balanced. The mock rivalry stimuli can be seen in Figure 4.2.

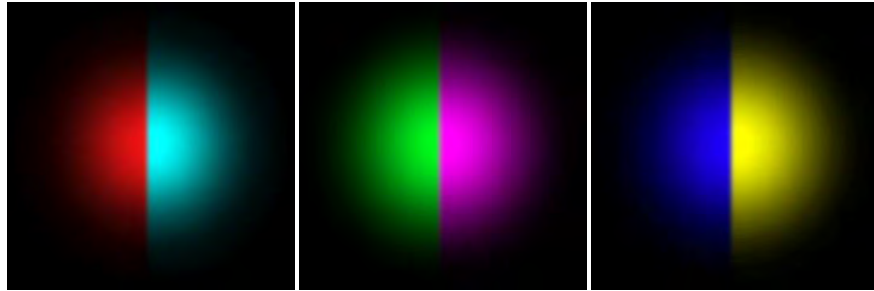


Figure 4.2. Mock rivalry stimuli. Depending on the color pair being tested (red/cyan; green/violet; blue/yellow) one of these stimuli would be presented to both eyes during mock trials to ensure that neither color could dominate perception. The luminance of each mock stimulus's two component colors were adjusted based upon the participants' subjective isoluminance values determined at the start of each experimental session.

4.4. Results

To determine if the color imagery primes could bias the perception of the colored Gaussians undergoing binocular rivalry the mean proportion of positively primed trials for the three color pairs was computed. Figure 4.3 shows the mean proportion primed for the three conditions, which were $M_{imagery} = 0.67$, $M_{background\ luminance} = 0.56$, $M_{weak\ perception} = 0.64$.

Three one sample *t*-tests were conducted to compare the priming effects observed within each experimental condition to chance (chance = 0.5). As can be seen in Figure 4.3, significant color priming effects were found in the imagery condition ($M = 0.67$, $SEM = 0.048$) $t(8) = 3.46$, $p < .01$, and in the weak perception condition ($M = 0.64$, $SEM = 0.04$) $t(8) = 3.48$, $p < .01$, but not in the imagery with background luminance condition ($M = 0.56$, $SEM = 0.025$) $t(8) = 2.23$, $p = .056$. These results support our hypothesis by showing that color imagery can bias the subsequent perception of color to a similar extent as weak perceptual stimuli. As also predicted, when the luminance of the background was increased statistically significant color priming effects were not found.

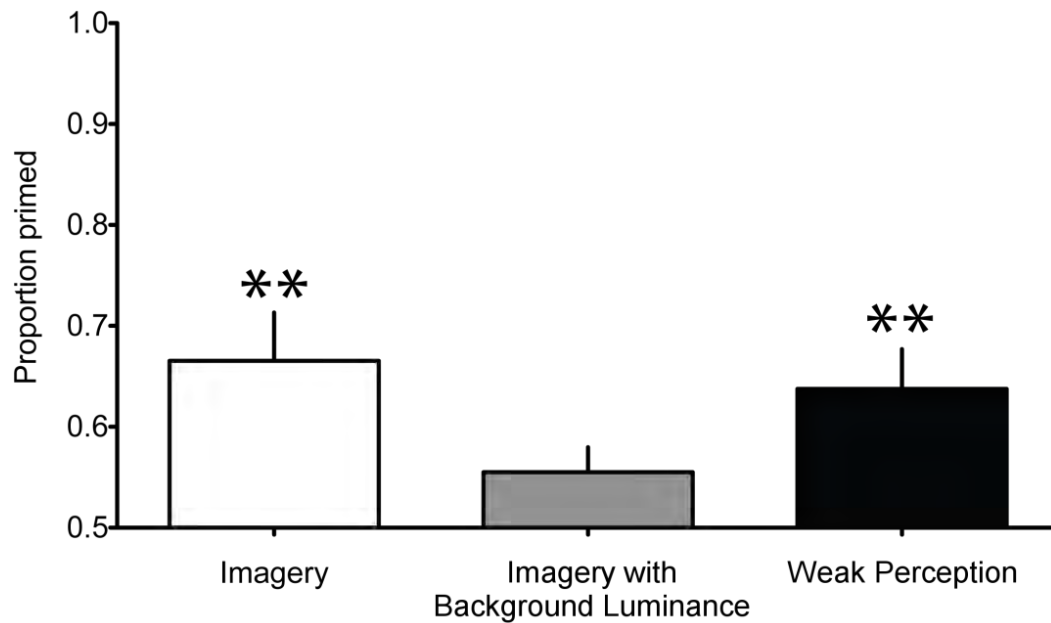


Figure 4.3. Mean proportion primed during the binocular rivalry task for the three experimental conditions. Proportion primed values closer to 1.0 indicate that the dominant color during rivalry often matched the color of the prime, while values closer to 0.5 indicate no relationship between the prime color and the dominant rivalry color. Error bars show +1 SEM. ** = $p < .01$.

A one-way ANOVA was also conducted to compare the priming effects of the three conditions to each other. A significant difference between the three conditions was found $F(2, 16) = 4.85, p < .05$. A post-hoc Bonferroni's multiple comparisons test found a significant difference in the priming effects of the imagery condition ($M = 0.67, SEM = 0.048$) and the imagery with background luminance condition ($M = 0.56, SEM = 0.025$) $t = 3.00, p < .05$. This seems to indicate that the addition of an illuminated background resulted in significantly weaker mental imagery for color.

The participants' responses during the 9 mock trials were also independently analyzed to determine if the participants' rivalry judgments were being biased by the word cue that was shown at the start of each trial. This mock trial analysis was conducted because the presence of this kind of semantic, non-perceptual bias could potentially account for the reported results. Though some evidence of this bias was found for certain individuals, the mean non-perceptual bias was not statistically significant ($M = 0.51, SEM = 0.007$) $t(8) = 1.41, p = .20$.

4.5. Discussion

This study has provided evidence that visual mental imagery can contain perception-like color information. Visual imagery of pure color Gaussians was found to selectively predispose the subsequent perception of differently colored Gaussians within a binocular rivalry display. This ability of color imagery to produce a perceptual bias is in line with the findings presented in Chapter 3 and previous

studies (Behrmann, 2000; Kosslyn et al., 2001; Pearson et al., 2008) by providing further evidence that visual mental imagery can be pictorial in nature.

These results also indicate the presence of an overlap in the processing of color knowledge and color perception. Though previous studies have attempted to address this particular issue (Chao & Martin, 1999; De Vreese, 1991; Farah et al., 1988; Goldenberg et al., 1995; Howard et al., 1998; Luzzatti & Davidoff, 1994; Shuren et al., 1996), they have produced a great deal of conflicting evidence. This disagreement is likely due to the fact that many of these studies did not directly compare knowledge based processing to perceptual based processing (e.g. Howard et al., 1998; Shuren et al., 1996). The current study does involve the direct comparison of these two processes by demonstrating that the generation of color imagery – which is based upon stored color knowledge (Chapter 1.2.1) – can influence the subsequent perception of color. These findings support the theory of modality grounded cognition as applied to color (see Chapter 7.1.1).

An alternative, non-mental imagery, explanation could potentially account for the observed priming effects. As previous studies have shown that words can be used to prime their corresponding visually presented objects (Bajo, 1988; Carr, McCauley, Sperber, & Parmelee, 1982; Damian & Rahman, 2003) or colors (Burt, 1994; McClain, 1983), the word cues used in the current study may in fact be directly responsible for the observed effects; color mental imagery may not actually be involved. Though possible, this alternative account of the present results seems unlikely for two different reasons. Firstly, increasing the brightness of the background during the mental imagery interval did not in any way interfere with visibility of the word cues presented at the start of each trial, but the priming effects

were still attenuated. If the word cues were responsible for the observed priming effects, and not color imagery, then this experimental modification should have produced no effect. However, as the priming effects were clearly reduced in this condition this seems to strongly suggest that color imagery was the driving force of these priming effects. Secondly, the mock trial analysis did not indicate any significant amount of non-perceptual bias. If the word cues were able to produce a response bias during the binocular rivalry task, then this bias should have also been observable during the mock trials. These results rule out word cue based accounts of the current findings.

4.5.1. Conclusions

This study experimentally demonstrates that mental imagery of color is possible. Visual imagery of pure color Gaussians was found capable of predisposing the observer's perceptual system for the imagined color in a binocular rivalry task. This perceptual bias produced by mental imagery appears to show that color imagery can influence the subsequent perception of color. This finding is in line with those presented in Chapter 3, and previous studies that have produced evidence that various kinds of mental imagery are pictorial in nature. Taken together, these findings seem to indicate that all forms of visual mental imagery involve processing within perceptual areas, which provides strong support for the theory of modality grounded cognition.

5. STUDY 3: OBJECT MEMORIES DEFINED BY COLOR

5.1. Introduction

Color can be highly informative of an object's identity. Accordingly, most animals have some ability to perceive color, including mammals which typically have dichromatic color vision (Jacobs, 1993; Surridge, Osorio, & Mundy, 2003). The trichromatic color vision of humans and other primates is a relatively new genetic development, allowing for improved discrimination between various shades of red and green (Bowmaker, 1998). This evolution is theorized to have been driven by the color of tropical fruits (Allen, 1879; Regan et al., 2001; Sumner & Mollon, 2000a), resulting in the development of a visual system especially well tuned to long wavelength colors (red, orange and yellow), which often signal the most nutritious fruit (Sumner & Mollon, 2000b). These evolutionary theories of color vision have gained popularity and support in recent years, but have typically made no attempt to explain contributions of higher-level cognitive processes such as how an object's color information is represented within concept knowledge systems (Chapter 1.2.2).

Many objects, such as ripened fruit, tend to have specific colors. For example, ripe bananas and lemons are always colored yellow. Such objects are commonly referred to as being highly color diagnostic, as their colors will provide additional information about their identity (Bramão, Reis, et al., 2011). As a result, when the shape of an object is made ambiguous through image blur, its colors can have a strong facilitatory effect on its recognition (Chapter 2.1.1). This effect appears stronger for highly color diagnostic objects than non-diagnostic objects,

and makes object recognition faster through the activation of a more extensive neural network in comparison to colorless images (Bramão, Faísca, Forkstam, et al., 2010). These studies have illustrated how object recognition can be facilitated by the color specific information stored within memory.

Memory of these object-color associations can also greatly influence the apparent coloration of a visually presented object. A seminal study on such memory color effects (Hering, 1920) demonstrated that an object's perceived color is skewed towards what the observer expects it to be, based on knowledge gained from previous experience. These memory color effects are independent of the influence of color constancy in that they are observable even when all objects in a scene are uniformly colored or when an object is presented in isolation. Therefore, while color constancy attempts to determine the "true" color of an object by estimating and then discounting the color of the illumination (D'Zmura & Lennie, 1986), this memory color effect adjusts the perceived colors of an object to match the association held within memory. This effect occurs involuntarily and has been demonstrated for both natural objects (Hansen et al., 2006; Hurlbert & Ling, 2005; Olkkonen, Hansen, & Gegenfurtner, 2008; Pérez-Carpinell et al., 1998) and man-made objects (Witzel, Valkova, Hansen, & Gegenfurtner, 2011). Along with the previously discussed literature, this memory color effect shows that an object's identity and its coloration can be highly interactive. However, the mechanisms underlying these interactions remain largely unknown.

Chapter 4 provides evidence that the neural processing involved in the perception of color and stored color knowledge have some degree of overlap. Though previous behavioral and neurological studies support this claim, some

evidence has suggested that these two processes are independent (Chapter 1.2.2). If these two processes are truly independent it would be indicative of a double dissociation of color perception and color knowledge. However, if perceptual color processing was clearly shown to have a strong effect on the retrieval of object color knowledge this would support the theory of modality grounded cognition as applied to color perception, which would in turn facilitate a resolution to this ongoing debate.

Many behavioral studies have already made important contributions to this resolution. It has been shown that object recognition can be interfered with through the prior presentation of the name or picture of an object known to be the same color (Joseph, 1997; Joseph & Proffitt, 1996). This appears to be a kind of color-knowledge-based negative priming (Chapter 2.2) that will only occur if the observer knows that the two objects are typically the same color. However, this interference has been shown to only occur when the object to be recognized is shown in its appropriate color (Bramão, Faísca, Petersson, & Reis, 2010); no recognition interference was observed for colorless or inappropriately colored objects. This shows that color knowledge can play a role in object recognition processing, but it appears as though this knowledge may require activation by the visual coloration of the object to be recognized (Bramão et al., 2012).

Contrasting these results, a type of knowledge-based positive color priming has recently been demonstrated. In a study by Yee et al. (2012) the names of objects known to share similar colors were found to prime each other in a word recognition task. As these object names were merely colorless words, this priming did not involve the presentation of any visual colors. This form of color priming is

based on the object's known color associates, indicating that the stored knowledge of similarly colored objects appear to have overlapping neural representations. However, this priming was entirely semantic and did not involve the processing of any perceptual colors, therefore the results do not demonstrate that object knowledge is stored within color perception areas. It may simply be that there is an overlap between the neural representations of these objects that does not involve any perceptual color processing areas.

The previously mentioned studies have shown that color knowledge can play an important role in visual object recognition. However, whether perceptual colors can have an influence on stored color knowledge has not yet been clearly demonstrated. The demonstration of this kind of influence would suggest that processing for color perception and color knowledge involve the same neural mechanisms, as predicted by the theory of modality grounded knowledge (Chapter 1.2.2). The aim of the present study is to build upon these previous findings by determining if such an interaction is possible.

5.1.1. Current Study

The aim of the current study is to determine if color can play an important role in the grounding of object concepts by showing that perceptual colors can interact with the stored knowledge of achromatically presented highly color diagnostic objects. Specifically, we test whether the recognition of achromatically presented fruit objects can be facilitated using visual color primes (Chapter 2.2). Achromatic presentation of fruit objects ensures that the only possible links between them and the perceptual color primes are those stored within memory. If

significant facilitation is found using such a priming task it will suggest that memory for highly color diagnostic objects is at least partially stored within the same neural areas involved in the processing of their perceptual colors. Such a result will provide compelling support for the theory that object color knowledge is grounded in perceptual color processing areas.

We assess the effectiveness of our color primes using two separate experimental tasks, object naming (Experiment 1) and object categorization (Experiment 2). As the presence of an object's surface details are known to have different effects on its categorization and naming (Price & Humphreys, 1989), it seems possible that our color primes will also have different effects in these two tasks. In the categorization task observers were merely required to categorize the objects as either a "Fruit" or "Car", they were not required to determine the objects' specific identities. As a result, our color primes may be ineffective for this task, as it is the specific identities of the fruit that are known to be associated with different colors. This result seems rather likely as visual objects are known to be categorized before their specific identities can be determined (Hamm et al., 2002; Large, Kiss, & McMullen, 2004; Rogers & Patterson, 2007).

In both experiments we test this priming under different visibility conditions. Previous object recognition studies have shown that visual colors can produce greater facilitation for blurred or degraded object images (Mapelli & Behrmann, 1997; Price & Humphreys, 1989; Therriault et al., 2009), suggesting that our color priming may also be maximally effective under these conditions. Therefore, in addition to normal achromatic photographs, we also test highly blurred images that preserved the low spatial-frequency luminance information while removing most of

the objects' shape and texture. In Experiment 1 we also test an edges-only version of the photographs that preserved the objects' high spatial-frequency shape and texture while removing most of the luminance information. To reiterate, there are no shared visual features between the color primes and the achromatic object targets used in any of these experiments. Therefore, any observed priming must be based upon on object specific color knowledge stored in memory (see Chapter 1.2.2). This study has recently been published by PLoS ONE and the publication version is included as Appendix C (Lewis, Pearson, & Khuu, 2013).

5.2. Hypothesis

The presentation of a perceptual color stimulus (not attached to any object) will prime subsequently presented achromatic objects known to have that color.

5.3. Method

5.3.1. Participants

A total of 21 students (9 males) were recruited from the University of New South Wales for this study ($n_{naming} = 11$; $n_{categorization} = 15$). Five individuals participated in both the naming and the categorization experiments. All participants had normal, or corrected-to-normal visual acuity and color perception.

This study received ethical approval from the University of New South Wales Human Research Ethics Advisory (HREA) panel. All participants gave written, informed consent before the start of the experiment. Upon completion the participants were debriefed in a follow-up interview.

5.3.2. Stimuli: Both Experiments

All stimuli were presented using MATLAB (version 7.10.0 R2010a).

Experiment 1 used a 32cm x 51cm iMac monitor with a Nvidia GeForce GT 120 chipset at a resolution of 1920 x 1200. Experiment 2 used a 27cm x 35.5cm Philips 109P4 monitor at a resolution of 1152 x 870 @ 75Hz. Both experiments involved the presentation of colored Gaussian blobs and achromatic photographs on a black background (luminance $< 0.01 \text{ cd/m}^2$). Stimuli were presented in the center of the screen with a circular fixation mark overlaid (diameter = 0.3°).

The Gaussian blobs were created using Psychtoolbox (Brainard, 1997) for MATLAB. Six differently colored Gaussians ($\sigma_{\text{width}} = 2.7^\circ$; $\sigma_{\text{height}} = 1.8^\circ$) were used in this study: red (CIE $x = 0.628$ $y = 0.338$ $\text{lum} = 61.7 \text{ cd/m}^2$), orange (CIE $x = 0.506$ $y = 0.431$ $\text{lum} = 110 \text{ cd/m}^2$), yellow (CIE $x = 0.392$ $y = 0.515$ $\text{lum} = 234 \text{ cd/m}^2$), yellow-green (CIE $x = 0.344$ $y = 0.553$ $\text{lum} = 134 \text{ cd/m}^2$), green (CIE $x = 0.279$ $y = 0.600$ $\text{lum} = 200 \text{ cd/m}^2$) and blue (CIE $x = 0.142$ $y = 0.071$ $\text{lum} = 24 \text{ cd/m}^2$). These colors were chosen due to their relevance to fruit perception, with the exception of blue which acted as a control. These colors were not isoluminant.

The photographs chosen for this study consisted of various kinds of fruit and cars. Fruit photographs were taken in the lab using a Nikon D50 camera and store-bought fruits. All fruits were photographed from a canonical angle; as though the viewer is looking down at them upon a table. Any photographs containing extraneous or distracting visual features such as blemishes, discolorations, and lighting effects were discarded. The chosen fruit types were apples, bananas, grapes, lemons, oranges, pears, persimmons and strawberries. Fruit types were

selected based upon their familiarity and color diagnosticity as determined in previous color diagnosticity studies using fruit stimuli (Naor-Raz, Tarr, & Kersten, 2003; J. W. Tanaka & Presnell, 1999; Therriault et al., 2009), not upon the particular colors that they are diagnostic for. The fruit rated high in color diagnosticity were bananas (yellow), lemons (yellow), oranges (orange), and strawberries (red), while those rated moderate to low in color diagnosticity were apples, grapes, and pears. Though it would have been preferred that each fruit object be diagnostic for a different color, the fact that this is not the case (i.e. banana and lemon) was not considered problematic. Persimmons were included as an experiential control, as it is our understanding that they have not been used in any prior color diagnosticity experiments, likely because most people are unfamiliar with them. Consequently, though persimmons always appear in a particular shade of reddish-orange, it is highly unlikely that any of the participants had this knowledge, making it a non-color diagnostic object. Car photographs were obtained using various internet sources. The car photographs were included as a non-fruit control condition, as cars have been consistently rated very low in color diagnosticity in previous research. The chosen car types are classic cars, convertibles, luxury cars, sedans, smart cars, sport-utility vehicles, pickup-trucks and vans. All objects were displayed in achromatic grayscale with their backgrounds removed. These objects were then centered and resized to fit on top of a grayscale background (width = 16.2°; height = 10.9°). See the left side of Figure 5.1 for example stimuli.

5.3.3. Stimuli: Experiment 1

In Experiment 1, the naming experiment, a total of 54 photographs were used: six photographs of each kind of fruit, except persimmons, and only one photograph of each kind of car, except sports-cars, pickup-trucks and vans. This resulted in a total of 8 different kinds of objects used in this experiment. Depending on the experimental condition, the photographs were filtered to remove either the low or high spatial-frequency information. The low spatial-frequency versions were created by convolving each photograph with a 2-D Gaussian filter of the same size as the photographs and a standard deviation of 5 pixels ($\sigma \approx 0.3^\circ$). The high spatial-frequency versions were created by subtracting the low spatial-frequency versions from the original photographs.

5.3.4. Stimuli: Experiment 2

In Experiment 2, the categorization experiment, a total of 96 photographs were used: six photographs of each kind of fruit and car. An equal number of car and fruit photographs were used in this experiment to ensure that photographs of objects in the two categories had an equal probability of being shown on any given trial. Additionally, only the normal and low spatial-frequency versions of the photographs were used in this experiment as no significant effects were found with the high-spatial frequency versions used in Experiment 1.

5.3.5. Procedure

All participants were seated in a dark room approximately 57cm from the monitor. A chinrest was not used in Experiment 1 as it would interfere with the participants' ability to vocalize their responses. Vocalized responses were used in

Experiment 1 as there were a total of 8 possible responses on each trial, which was thought to be far too many to keep track of using buttons. The basic experimental timeline shown on the right side of Figure 5.1 was used in both experiments. At the start of each trial the Gaussian color prime was shown for 150ms, followed by a 250ms blank screen. Then the target photograph was shown for 1s, followed by a 1s blank screen. Participants were only allowed to vocalize their responses during this 2s response window. Then a randomized white noise pattern was displayed for 500ms to remove any luminance after-effects produced by the photographs, which was followed by a 500ms inter-trial interval during which the screen would remain blank.

In Experiment 2 the blank screen immediately following the target photograph was removed, thus shortening the response window to only 1s. This shortening of the response window was due to the observation that the button-press reaction times were generally much quicker than the vocalized response reaction times. Failure to react within the response window for either experiment resulted in the trial being repeated at a randomly determined point later in the session.

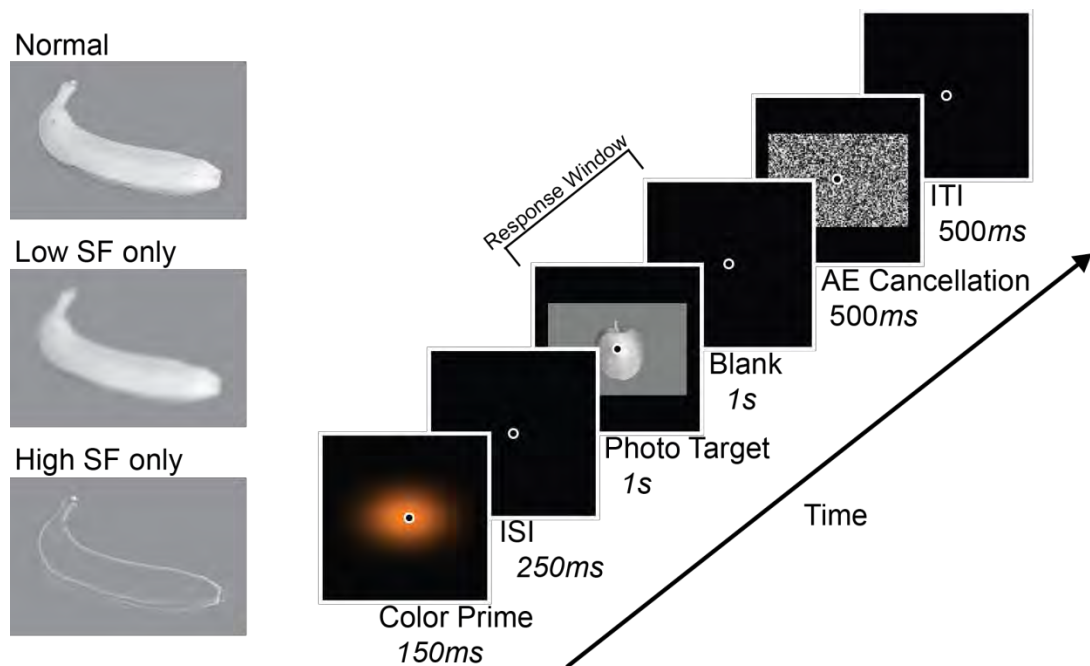


Figure 5.1. Example photographic stimuli and experimental timeline. (Left) Example photograph targets as shown in each of the three conditions. All photographs were presented on a black screen, in grayscale, with their backgrounds removed. (Right) Experimental timeline. A colored Gaussian was shown for 150ms, followed by a 250ms inter-stimulus interval, and then an object photograph for 1s. The participants were required to identify the object being shown as quickly as possible. Failure to respond within 2s of photograph onset resulted in the repetition of that trial at a randomly determined point later in the session. Each trial ended with the presentation of a dynamic colored noise stimulus for 500ms to facilitate the cancellation of any afterimages that may have been experienced. In Experiment 2 the blank screen immediately following the photograph target was removed, thus shortening the response window to only 1s.

In Experiment 1 the participants were instructed to speak aloud the name of the object being displayed in the target photograph as quickly and accurately as possible. Participants were urged to vocalize whichever term they best associated with the object's specific identity (e.g., "apple"). The only exception to this was the car photographs, which the participants were asked to respond to simply as "car".

In Experiment 2 the participants were instructed to categorize the objects in the target photographs as a fruit or car by pressing the "F" or "C" keys on the

keyboard as quickly and accurately as possible. Incorrect responses resulted in the trial being repeated at a randomly determined point later on in the experimental session and a buzzer noise was played to notify the participants of their error.

5.3.6. Data Preparation

In Experiment 1 the naming accuracy and vocalization reaction time for each trial were manually determined after the experimental session was completed. The visual waveform and auditory playback were reviewed for each trial using a MATLAB program written specifically to analyze the sound-waves of this study. Reaction times were determined by marking the point of vocalization onset, as indicated by systematic changes in the waveforms' amplitudes while ignoring ambient noises and non-verbal utterances. Variations in the waveform shapes due to individual differences were also taken into consideration when marking this onset of vocalization. Accuracy was determined by comparing the auditory playback to the correct answer being textually displayed in the program window. The raters were blind as to the color prime of each trial; only the participant's vocalization and the correct answer were shown.

In Experiment 2 the program automatically determined the accuracy and reaction time of each participant's button-press responses. All incorrect responses were recorded and the trial was repeated at a randomly determined point later in the block. Incorrect responses were excluded from analysis in both experiments due to the participants having made too few errors to allow proper statistical procedures to be conducted. In the normal-image condition of Experiment 2 a

single participant's data was excluded from analysis due to consistently producing outlying reaction times.

5.4. Results

Mean reaction times were computed to measure the priming effects of the colored Gaussians on the recognition of the achromatic target objects. These means were computed by first averaging the reaction times for each target photograph, as primed by each of the 6 different colored Gaussians, across the participants' experimental sessions. Next the reaction times of all 6 photographs of each type of object (e.g. apples), as primed by each of the 6 different colored Gaussians, were averaged together. This resulted in a single mean reaction time for each object type / prime color combination for each participant. The two experiments in this study utilized a 6 x 8 within subjects design. The two independent variables were prime color and object type. In each experiment the potential interactions between the levels of prime color and object type were tested independently for each spatial-frequency condition.

As these analyses include multiple independent variables various ways to simplify the data were considered, such as comparing the average reaction times for related colors and non-related colors across the multiple objects used in each experiment. However, there are two reasons why this kind of analysis cannot be done with the current data. Firstly, for the highly color-diagnostic fruits only 1 color is diagnostic while the other 5 are non-diagnostic. Therefore, in order to perform such a comparison an average of these 5 "non-related" colors would have to be

compared to the single “related” color. This kind of comparison is highly unbalanced and far too great of an oversimplification of the current data. Secondly, half of the objects included were low, or non-diagnostic, for color (eg. cars), meaning that they have no clearly defined “related color” making this form of simplification impossible. Therefore, while a more simplistic statistical analysis (i.e. a *t*-test) has the potential to produce more straightforward results, the design of the current study simply does not allow it.

5.4.1. Experiment 1: Naming

In this experiment we sought to determine if naming speeds for the achromatic photographs of fruit objects could be facilitated through the presentation of color primes. Object types used in this experiment were apples, bananas, grapes, lemons, oranges, pears, strawberries and cars. Priming for these objects was tested using photographs that contained three different kinds of spatial-frequency information (normal photographs, low spatial-frequencies only, high spatial-frequencies only). Our hypothesis predicted an interaction between the color primes and the object types, with diagnostic colors resulting in the fastest reaction times. It was also predicted that the priming effects would be strongest in the low spatial-frequency condition, as it has been shown that an object’s color will maximally facilitate its recognition when the shape is hard to determine (Mapelli & Behrmann, 1997; Price & Humphreys, 1989; Theriault et al., 2009).

A preliminary 3-way ANOVA across the 3 spatial-frequency conditions, 6 prime colors, and 8 object types was conducted. A significant interaction was found between these 3 factors $F(70, 700)=1.51$, $p = 0.006$, observed $1-\beta = 1.00$. This

indicates that the removal of certain kinds of spatial-frequency information had a significant effect on the color primes' ability to facilitate the recognition for the target objects. However, this result does not indicate whether a statistically significant amount of color-associate priming was found in any or all of the spatial-frequency conditions. Additional tests were conducted to more directly address the main hypothesis.

For the normal, unfiltered photographs a 2-way ANOVA across the 6 prime colors and the 8 object types was conducted. A significant interaction was found between object type and prime color $F(35, 350) = 1.50$, $p = 0.039$, observed $1 - \beta = 0.99$. As can be seen in Figure 5.2, the color orange was the most effective color prime for oranges, but the diagnostic colors of the other fruits do not seem to be any more effective than the non-diagnostic colors. A total of 20 Bonferroni corrected analyses were conducted for the highly color-diagnostic objects to determine if their diagnostic colors resulted in significantly faster naming speeds than their non-diagnostic colors. For the bananas, yellow was found to produce significantly faster naming speeds than yellow-green ($t = 3.61$, $p < 0.001$). For the oranges, the color orange was found to produce significantly faster naming speeds than red ($t = 3.82$, $p < 0.001$), yellow-green ($t = 4.61$, $p < 0.001$), and blue ($t = 3.49$, $p < 0.001$). For the lemons and strawberries no significant differences in naming speed were found. Though only two of the four highly color-diagnostic fruits showed significant differences between their diagnostic and non-diagnostic colors, these findings support our hypothesis by showing priming effects driven by the known color associates of the achromatically presented fruits.

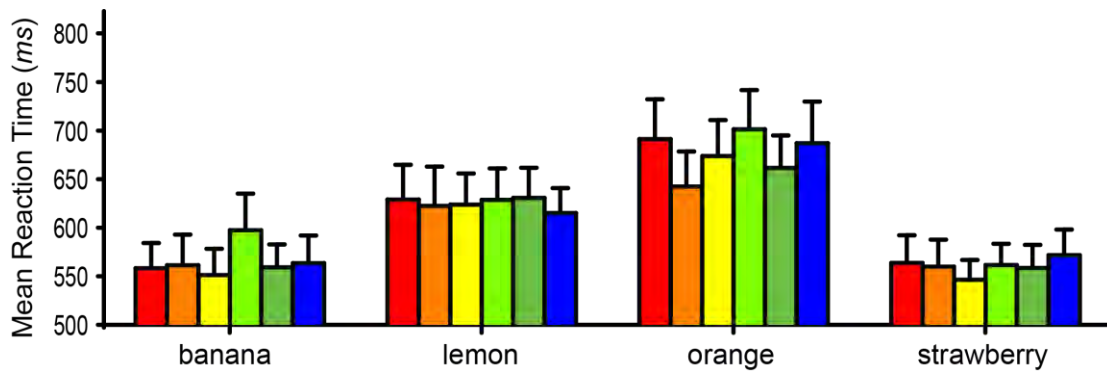


Figure 5.2. Naming reaction times for highly color-diagnostic objects. Bar color indicates prime color. Error bars show +1 SEM. $n = 11$

A significant main effect of color prime was found $F(5, 50) = 3.54$, $p = 0.008$, indicating that one or more of the color primes produced significantly faster reaction times than the others across all object types. Additionally, a highly significant main effect of object type was found $F(7, 70) = 27.14$, $p < 0.0001$, indicating that some of the objects could be named faster than the others regardless of prime color. This effect can be clearly seen in Figure 5.2, wherein average reaction times for the bananas and strawberries were much faster than the lemons and oranges. This illustrates that the distinctiveness of the objects' shapes had a large influence on their recognition speeds.

For the high spatial-frequency photographs a 2-way ANOVA across the 6 prime colors and the 8 object types was conducted. No significant interaction was found between object type and prime color $F(35, 350) = 0.88$, $p = 0.664$, observed $1 - \beta = 0.85$. This indicates that the priming was ineffective when the low spatial-frequencies were removed from the object photographs. Only a marginally significant main effect of prime color was found $F(5, 50) = 2.32$, $p = 0.057$. However, a highly significant main effect of object type was found $F(7, 70) = 24.41$,

$p < 0.001$, once again indicating that some of the objects could be named faster than others regardless of the color of the prime.

For the low spatial-frequency photographs a 2-way ANOVA across the 6 prime colors and the 8 object types was conducted. A significant interaction was found between object type and prime color $F(35, 350)=1.55$, $p = 0.027$, observed $1-\beta = 0.99$. As can be seen in Figure 5.3, the most effective color prime was *yellow* for the bananas and lemons, but *orange* was not the most effective for oranges, and *red* was not the most effective for strawberries. A total of 20 Bonferroni corrected analyses were conducted to determine if there were any differences in the naming speeds for each highly color-diagnostic object's associated color and its non-associated colors. For the lemons, *yellow* was found to produce significantly faster naming speeds than *red* ($t = 3.62$, $p < 0.01$). For the bananas, oranges, and strawberries no significant differences in naming speed were found. Though only one of the four highly color-diagnostic fruits showed significant differences between their diagnostic and non-diagnostic colors, this finding supports our hypothesis by showing significant priming effects driven by the known color associates of the achromatically presented fruits.

Additionally, for the low spatial-frequency photographs a significant main effect of prime color was found $F(5, 50)=4.26$, $p = 0.003$, indicating that the color primes produced significantly different reaction times across all object types. A highly significant main effect of object type was also found $F(7,70)=42.54$, $p < 0.0001$, indicating that the participants were able to name some of the objects quicker than others regardless of prime color.

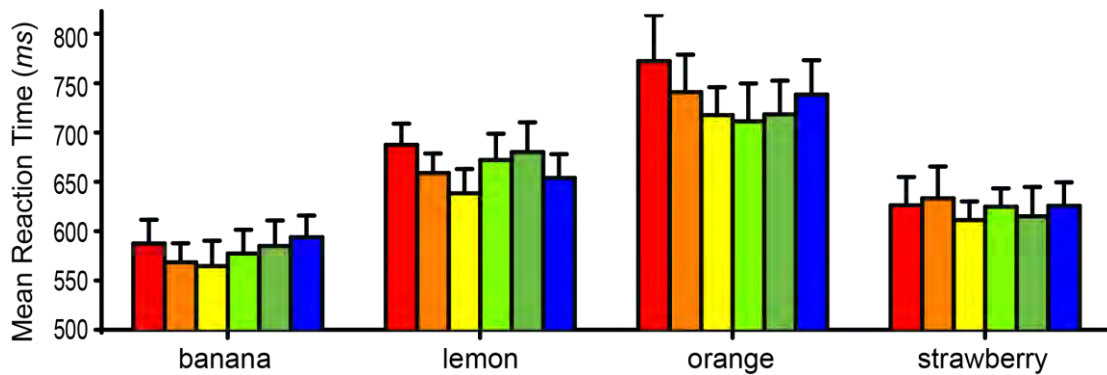


Figure 5.3. Naming reaction times for the highly color-diagnostic low spatial-frequency objects. Bar color indicates prime color. Error bars show +1 SEM. $n = 11$

Additionally, for the low spatial-frequency photographs a significant main effect of prime color was found $F(5, 50) = 4.26$, $p = 0.003$, indicating that the color primes produced significantly different reaction times across all object types. A highly significant main effect of object type was also found $F(7, 70) = 42.54$, $p < 0.0001$, once again indicating that the participants were able to name some of the objects quicker than others regardless of prime color.

5.4.2. Experiment 2: Categorization

In Experiment 2 we sought to determine if similar results could be produced using a categorization task. Object types tested in this experiment were objects within the categories “Fruit” and “Car”. The fruit objects were apples, bananas, grapes, lemons, oranges, pears, strawberries and persimmons. The car objects were classic cars, convertibles, luxury cars, sedans, smart cars, sport-utility vehicles, pickup-trucks and vans. Unlike Experiment 1, priming of these objects was only tested using photographs that contained two different kinds of spatial-frequency information (normal photographs, low spatial-frequencies only).

It was once again predicted that the objects' diagnostic colors would result in the fastest reaction times, with the strongest effects being observed within the low spatial-frequency condition. However, it seemed likely that our color primes would have different effects in this categorization task, as an object's color is known to have different effects on its categorization and naming (Price & Humphreys, 1989). No interaction was predicted between the color primes and car types, as cars are generally not color diagnostic.

Potential interactions between prime color and object type were independently analyzed for each of the two object categories. This independent analysis was conducted to more directly compare the effects of the 6 differently colored primes across the 8 object types within each category ("Fruit" and "Car"). Though these two categorical labels are not on the same hierarchical level (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976), the car stimuli were merely used as a control condition and have no bearing on the hypothesis. Additionally, no statistical comparisons were made across the two categories of objects. Unfortunately, for various reasons 10 of the 15 individuals who participated in this experiment only completed one of the two spatial-frequency conditions ($n_{\text{both}} = 5$, $n_{\text{normal_only}} = 7$, $n_{\text{LSF_only}} = 3$). Though it would have been preferable to have all participants complete both conditions, as this would allow for comparisons across spatial-frequency, it is not required to test our hypothesis. Consequently, 3-way ANOVAs similar to that of Experiment 1 were not conducted for this data.

For the normal fruit photographs a 2-way ANOVA across the 6 prime colors and the 8 fruit types was conducted. No significant interaction between object type and prime color was found $F(35, 385) = 1.32$, $p = 0.108$, observed $1 - \beta = 0.98$. Like

Experiment 1, a significant difference in the mean reaction times was found between the 8 fruit types $F(7, 77) = 3.74, p = 0.002$, indicating that some of the fruit objects were more easy to recognize as belonging to the “fruit” category than others. Also, a highly significant difference was found between the 6 prime colors $F(5, 55) = 4.21, p = 0.003$, suggesting that some colors were better than others at priming the recognition of objects belonging to the “fruit” category. As can be seen on the top-left side of Figure 5.4 the color orange appeared to produce the fastest reaction times regardless of fruit type. A total of 5 Bonferroni corrected analyses were conducted to determine if the reaction times for orange were significantly faster than the other 5 colors across the 8 different fruit types. The color orange produced significantly faster reaction times than red ($t = 3.62, p = 0.003$), and yellow ($t = 3.50, p = 0.0045$).

For the normal car photographs a 2-way ANOVA across the 6 prime colors and the 8 car types was conducted. No significant interaction between object type and prime color was found $F(35, 385) = 1.17, p = 0.108$, observed $1 - \beta = 0.96$. No significant difference in the mean reaction times was found between the 8 car types $F(7, 77) = 0.87, p = 0.534$. This seems to indicate that all of the car objects were equally easy to recognize as belonging to the “car” category. No significant difference was found between the 6 prime colors $F(5, 55) = 1.66, p = 0.160$. However, as can be seen on the top-right side of Figure 5.4 the color yellow-green appeared to produce the fastest reaction times regardless of car type.

For the low spatial-frequency fruit photographs a 2-way ANOVA across the 6 prime colors and the 8 fruit types was conducted. Unlike the normal spatial-frequency condition a significant interaction between fruit type and prime color was

found $F(35, 245)=1.56$, $p = 0.028$, observed $1-\beta = 0.99$. A total of 20 Bonferroni corrected analyses were conducted to determine if there were any differences in the naming speeds for each highly color-diagnostic object's associated color and its non-associated colors, but no significant differences were found.

Unlike the normal spatial-frequency condition, no significant difference in the mean reaction times was found between the 8 fruit types $F(7,49)=1.24$, $p = 0.302$. This indicates that when high spatial-frequency information is removed from the images, the fruit objects are equally easy to recognize as belonging to the "fruit" category. No significant difference in the mean reaction times was found between the 6 prime colors $F(5, 35)=1.79$, $p = 0.14$.

For the low spatial-frequency car photographs a 2-way ANOVA across the 6 prime colors and the 8 car types was conducted. No significant interaction between car type and prime color was found $F(35, 245)=0.68$, $p = 0.912$, observed $1-\beta = 0.69$. However, a highly significant difference in the mean reaction times was found between the 8 car types $F(7, 49)=5.31$, $p < 0.001$. No significant difference was found in the mean reaction times between the 6 prime colors $F(5, 35)=0.59$, $p = 0.710$.

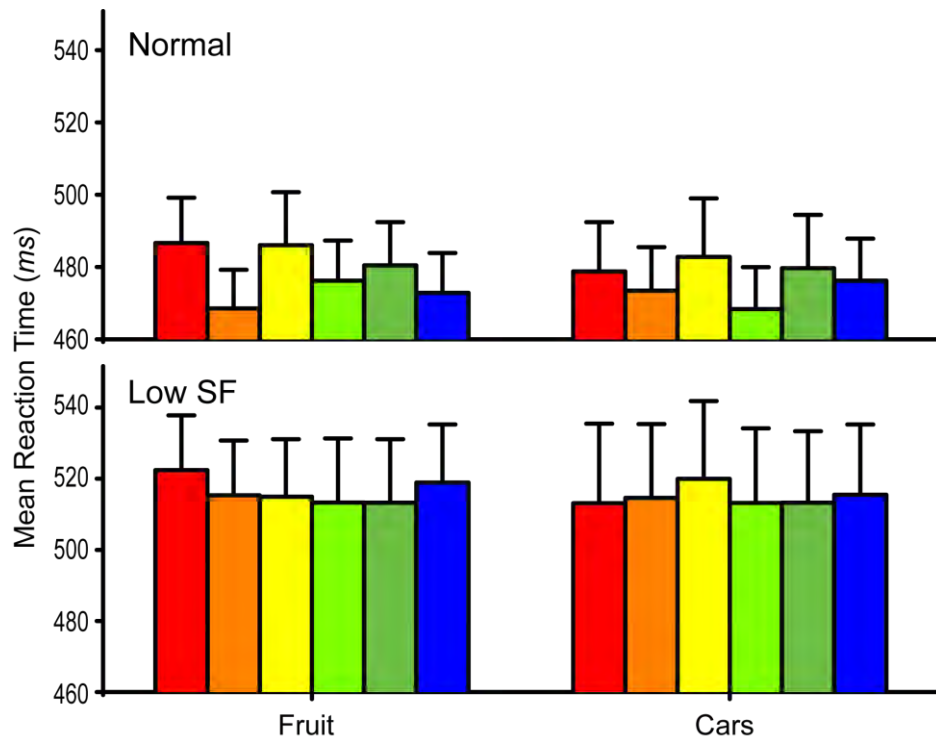


Figure 5.4. Mean categorization reaction times across all objects separated by category and spatial-frequency condition. (Top) Normal: Unfiltered target photographs $n = 12$. (Bottom) Low SF: Low spatial-frequency target photographs $n = 8$. Bar color indicates prime color. Error bars show $+1$ SEM.

5.5. Discussion

This study appears to show the priming of object recognition by known color associates. Facilitating the recognition of achromatic object photographs through prior exposure to their known color associates provides evidence of a functional relationship between the processing of color perception and color knowledge (memory). While the current results only show a small amount of evidence supporting this conclusion, the fact that any such evidence has been found supports the theory that color knowledge is grounded within modality specific systems (Chapter 7.1.1). This color associate priming appears to be driven by the color diagnosticity of the fruit objects, the low spatial-frequency information of the

images, and the level of identity specificity required for the recognition task.

Though there are likely other factors that can also influence this form of color priming, these three have been positively identified and are discussed in detail below.

5.5.1. Identity Specificity

The color priming appeared to have different effects for the object naming and categorization tasks. Though significant interactions between prime color and fruit type were found in the low spatial-frequency conditions of both tasks these two results are very different. The follow-up tests in the naming task yielded significant results (Section 5.4.1.), but those of the categorization task did not (Section 5.4.2.). None of the highly color-diagnostic objects were primed by their diagnostic colors when the participants were required to categorize the fruit objects, which does not provide evidence of color associate priming. This difference between the two tasks may be due to the differences in how the participants were evaluating the stimuli.

In Experiment 2 the participants categorized the objects as being either “fruit” or “car”, but were not required to identify what kind of fruit or car it was. In other research, the ability of an object’s color to facilitate its recognition has been shown to be modulated by the level of identity the observer is attempting to determine (Price & Humphreys, 1989). Additionally, in the normal time course of object recognition, processing the general categories to which an object belongs is determined before its specific identity is achieved (Hamm et al., 2002; Large et al., 2004; Rogers & Patterson, 2007). Therefore, though object recognition normally requires only a fraction of a second, it is highly likely that the participants were

responding well before they were able to determine the object's specific identity. In fact, many participants claimed to have used this kind of strategy in the follow-up interviews. Simply put, it seems that the fruit objects were not primed by their color associates in the categorization task simply because the participants were not required to recognize them at such a specific level.

However, the time course of object recognition suggests an alternative interpretation of these results. It may be the case that priming did indeed occur, but it facilitated recognition for objects within the "fruit" category instead of specific fruit types. This would explain the lack of a significant interaction between prime color and fruit type and the highly significant main effects of prime color for the normal, unfiltered object photographs. As Figure 5.4 shows, the orange prime produced the fastest reactions across all types of fruit, and the follow-up statistical analyses confirmed that these reaction times were highly significantly different from most of the other prime colors, which seems to suggest that orange is the color most closely associated with the category "fruit".

This interpretation is particularly intriguing as it could have been predicted based on the evolutionary theories of color vision in primates. In tropical rainforests primates are known to predominantly seek out and consume yellow/orange fruits (Bowmaker, 1998; Regan et al., 2001), as these colors are typically indicative of ripeness (Sumner & Mollon, 2000b). Therefore it may be that evolutionary processes have strengthened the link between yellow/orange colors and the recognition of fruits. Alternatively, it may actually be the case that viewing the orange Gaussian color activated the word "orange" which then worked as a semantic prime for the other fruit objects, or it may simply be that the participants

had formed strong prior associations between this particular range of fruit types and the color orange. Regardless, the orange prime produced the greatest facilitation for categorizing the fruit objects used in this study, even for types of fruit that do not normally appear orange.

5.5.2. Spatial-frequency Information

Object recognition is greatly facilitated by the presence of an object's many visual features, including shape, texture and luminance. The facilitatory effects of these features can be so great that the contributions of color information may be diminished to the point of being inconsequential for object recognition purposes (Mapelli & Behrmann, 1997; Price & Humphreys, 1989; Theriault et al., 2009). Therefore, in both experiments we attempted to amplify the color priming effects by removing one or more of these visual features from the target photographs.

In Experiment 1 the naming reaction times were measured for the original photographs, photographs that contained only the low spatial-frequency luminance information, and photographs that contained only the high spatial-frequency shape and texture information (Section 5.3.3.). All three conditions produced the same general trends, suggesting that the presence or absence of the other visual features did not greatly influence the effectiveness of the color primes. The only obvious difference between the three conditions was in their overall reaction time speeds. The low and high spatial-frequency conditions had much slower reaction times than the normal condition, likely reflecting an increase of task difficulty. Despite this overall similarity, significant color priming effects were only found for the normal and low spatial-frequency conditions; no color priming was found for the

high spatial-frequency condition (Section 5.4.1.). Interestingly this suggests that the color associate priming was driven by the low spatial-frequency luminance information of the target objects. Despite our predictions, and those of the previous research, it does not appear that color became more informative of the objects' identities when their shape information had been degraded. A discussion of this intriguing result and its potential cause is provided within Chapter 7.3.2.

5.5.3. Color Diagnosticity

Color information is a feature of almost all visual objects. The inclusion of color within an image has been shown to facilitate the recognition of a wide range of objects (Biederman & Ju, 1988; Uttl et al., 2006; Wurm et al., 1993). However, studies have shown that the recognition of color-diagnostic objects, those objects well known to have a specific coloration (Bramão, Inácio, et al., 2011), generally show the greatest benefit from the inclusion of color information (Chapter 2.1.1). Therefore, the current study compared the effectiveness of various color primes across a range of objects varying in their color diagnosticity. It was predicted that the most color diagnostic objects (bananas, lemons, oranges and strawberries) would show the strongest priming effects. It is important to note that the color primes used in this study were not isoluminant, but their luminance differences did not appear to have a measurable influence on the priming effects.

Across the normal and low spatial-frequency conditions of Experiment 1 the bananas, lemons and oranges were found to be differentially influenced by the color primes at a statistically significant level (Section 5.4.1.). These objects were most primed by their diagnostic colors (*yellow-banana, yellow-lemon, orange-*

orange), which supports our hypothesis. Though these data may appear somewhat understated due to the finding of only some of the predicted priming effects, evidence of any such priming is necessarily indicative of an interaction between color perception and color knowledge processing. This interaction is likely due to an overlap between the processing of visually presented colors and the color knowledge associated with these highly color-diagnostic fruit objects. This novel finding provides support for the theory of modality grounded cognition, as highly color-diagnostic object concepts appears to involve processing within perceptual color areas (Chapter 7.1.1).

5.5.4. Number of Participants

Though significant color-based facilitation was found in the current study, it seems likely that more significant priming effects could be found if the number of participants was increased. This would increase statistical power, making it easier to detect significant interactions between prime color and object type for the highly color-diagnostic objects. In particular, this could allow for the observation of significant priming effects in Experiment 2 (Section 5.4.2.), indicating that color-associate priming can also occur at the categorical level. However, the power of the current analyses are already very high (Section 5.4.). Therefore, while collecting data from additional participants has the potential to produce more robust findings, it is also very likely that the current findings accurately reflect the limitations of this color-based priming. Regardless, significant color-associate priming effects were observed in this study, which supports the main hypothesis.

5.5.5. Conclusions

The recognition of achromatic objects can be facilitated through the prior presentation of their known color associates. This color associate priming seems to be based entirely on the color information stored within object knowledge. Three factors that have an influence on this priming have been identified: the color-diagnostics of the objects, their low spatial-frequency information, and the level of identification specificity. These findings are in line with previous behavioral and neurological research, and provide additional support for the theory that object color knowledge is grounded within perceptual color processing systems.

6. STUDY 4: FUNCTIONAL INTERACTIONS BETWEEN CONCEPTS

6.1. Introduction

In Chapter 5 it is shown that the recognition of highly color-diagnostic fruits can be facilitated through the prior presentation of their associated colors. This suggests that concept knowledge of such fruits is at least partially stored within the same neural areas responsible for the perceptual processing of their colors. This finding provides some behavioral support for the theory of modality grounded cognition, but as explained in Chapter 1.2 this theory encompasses all knowledge associated with a particular concept; not just color information. Consequently, it is likely that other kinds of objects are more closely associated with other forms of visual information. In particular it seems probable that action-based functional information is highly associated with hand-held tools. The existence of this kind of functionally-interactive relationship (see thematic categories in Chapter 1.1.2) would indicate that neural activity for tool concepts involves activity within the same motor areas that are active during their use. The current chapter discusses our investigation into this possibility.

Tools and other frequently manipulated objects generally afford specific forms of functional interaction. Knowledge about these forms of interaction is known to be represented within object concepts (Bub & Masson, 2006; Creem-Regehr & Lee, 2005; Klatzky, Pellegrino, McCloskey, & Lederman, 1993; Mizelle & Wheaton, 2010), and appears to involve activity within neural areas separate from those that process other forms of object knowledge (Arévalo et al., 2007; Borghi & Riggio, 2009; Spunt, Falk, & Lieberman, 2010). The perception of manipulable

objects has been shown to involve activity spanning parietal, frontal, and temporal lobe areas (for review see Johnson-Frey, 2004). Accordingly the processing of information about actions involves a similar network of activity (Assmus et al., 2007) wherein specific tool-use actions are processed mostly within parietal areas, while the goals of those actions (irrespective of the tools used or actions being performed) are processed in higher-level frontal cortex areas (Gallivan, McLean, Valyear, & Culham, 2013; Umiltà et al., 2008). Unlike non-manipulable objects (eg. houses), this neural processing of tools and their actions predominantly occurs within dorsal stream areas (Chapter 1.1.1).

Key dorsal stream areas for the processing of tools include the left parietal cortex which appears to be involved in the storage and recall of how they are used (Chao & Martin, 2000; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Mahon, Schwarzbach, & Caramazza, 2010; Moll et al., 2000), the supramarginal gyrus which appears to store knowledge of the arm and hand positions required for tool use (Buxbaum, Kyle, Tang, & Detre, 2006; Ohgami, Matsuo, Uchida, & Nakai, 2004), and the precuneus which appears to store visuo-spatial information about how tools are manipulated (Vingerhoets, 2008). The left ventral premotor cortex and the lateral temporal cortex have also been identified as important areas for tool processing (Chao & Martin, 2000; Gerlach, Law, Gade, & Paulson, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Kellenbach, Brett, & Patterson, 2003), but these areas may be more involved in the general processing of motion information about objects (Chao et al., 1999; Gerlach, Law, Gade, & Paulson, 2002; Gerlach, Law, & Paulson, 2002; Jeannerod et al., 1995). These findings, particularly those of the precuneus, suggest there may be an overlap between the neural areas involved in

the visual perception of tools and the performance of hand movements required for their functional use.

These studies have shown broad patterns of activity within the motor cortex for tools, but the specificity of these neural areas has remained largely unknown. As different kinds of tools require unique forms of interaction, it follows that their conceptual representations should be separable and based within the precise motor areas responsible for performing those actions. Some evidence of this kind of specificity has been produced for the names of various tool objects. The names of objects that have a specific form of manipulation (e.g. tools) tend to involve more activity in the vPMC, the inferior parietal cortex, and the pre-supplementary motor area when compared to objects that do not have a specific form of manipulation (Rueschemeyer, van Rooij, Lindemann, Willems, & Bekkering, 2009). The names of objects that normally move towards the user during their functional use (eg. cup) tend to involve more activity in the extrastriate body area, middle occipital gyrus, and inferior temporal lobe when compared to objects that move away (Rueschemeyer, Pfeiffer, & Bekkering, 2010). Though these studies used only textual representations of tools it seems likely that similar results could be produced using visually presented tools. The development of higher-resolution imaging methods will likely lead to the discovery of even more highly specific functional information processing areas as behavioral methods have already provided indirect evidence that they exist.

Numerous behavioral studies have demonstrated that certain kinds of action information are central to the identity of various kinds of manipulable objects. In particular, studies using priming methodologies (Chapter 2.2) have shown that the

perception of manipulable objects can prime the manner in which they are grasped (Bub, Masson, & Cree, 2008; Ellis & Tucker, 2000; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003), the mimicry of visually presented hand gestures corresponding to the object (Bub & Masson, 2006; Gianelli, Dalla Volta, Barbieri, & Gentilucci, 2008), the manner in which one attempts to grasp a different object (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Craighero et al., 1996; Gianelli et al., 2008; Tucker & Ellis, 2004), and the recognition of subsequently presented objects that are manipulated in the same way (Helbig, Graf, & Kiefer, 2006). Similarly, the visual presentation of a hand in a specific posture can prime the performance of that posture (Vogt et al., 2003), the determination of whether that posture is sensible for grasping a particular object (Bruzzo, Borghi, & Ghirlanda, 2008), the identification of physical properties of an object (Liuzza, Setti, & Borghi, 2012), and the recognition of objects that could be grasped using that posture (Borghi et al., 2007; Kalénine, Bonthoux, & Borghi, 2009; Vainio, Symes, Ellis, Tucker, & Ottoboni, 2008). These studies have shown that tools can become strongly associated with certain kinds of action information. However knowledge of the hand-movements required for the grasping of tools and their functional use are known to involve different neural areas (Boronat et al., 2005; Buxbaum et al., 2006; Randerath, Goldenberg, Spijkers, Li, & Hermsdörfer, 2010). Therefore the previous studies have only demonstrated that strong associations can form between the identities of graspable objects and how they are grasped; they provide no evidence regarding associations with tool-use.

Pantomimes can be used to study the functional information associated with a particular object. This form of mimicry involves the demonstration of how an

object is normally manipulated for its functional use without actually showing the object. Though the left intraparietal and dorsolateral frontal cortices are known to play major roles in the processing of pantomime actions (Moll et al., 2000), tool-use pantomiming and actual tool-use tends to produce highly similar patterns of neural activity (Hermsdörfer, Terlinden, Mühlau, Goldenberg, & Wohlschläger, 2007). As the performance of this form of mimicry requires the use of functional knowledge it is widely used in tests for ideomotor apraxia (Buxbaum, Johnson-Frey, & Bartlett-Williams, 2005; Buxbaum, Veramontil, & Schwartz, 2000; Goldenberg, Hartmann, & Schlott, 2003; Wheaton & Hallett, 2007), a disorder wherein individuals cannot identify what an object is used for but have no problem visually recognizing or properly grasping it. Pantomiming is ideal for the study of functional object knowledge, yet only two studies have used it in this regard.

Bub and Masson (2006) showed in a series of seven experiments that the mimicry of a visually presented hand-pantomime can be facilitated by the prior visual presentation of a corresponding tool prime. In this study the pantomimes were achromatic photographs of hands shown from an allocentric perspective that depicted the canonical postures for the functional use of the tools previously shown. Facilitation for the performance of this hand-mimicry was only observed when the participants were required to also identify the tool primes. This seems to suggest that tool identification, not mere perception, can prime the motor movements required for the functional use of that tool.

Mounoud, Duscherer, Moy, and Perraudin (2007) showed in two experiments that videos of an actor pantomiming the canonical functional use of a tool can facilitate the subsequent visual recognition of that tool. These videos

depicted the full body of the actor who mimicked the use of various tool. Tool recognition facilitation was observed to be the strongest for the youngest participants (ages 5 - 9) with significant but weaker facilitation for the oldest participants (mean age = 27.75). Age is clearly an important factor for this kind of priming, but it does seem likely that some amount of facilitation could be observed for participants of all ages.

Together these studies have produced some evidence of an overlap in the neural processing of an object's identity and the actions required for its functional use. If this overlap does truly exist then it would strongly support the theory of modality grounded cognition by showing that the perception of specific hand movements can activate stored knowledge of manipulable objects that are typically interacted with using those movements. The small amount of evidence produced thus far, however significant it may be, is not enough to support this theory.

6.1.1. Current Study

In the current study we seek to further investigate the potential overlap between the conceptual representations of tools and the specific hand movements associated with their functional use. A series of three experiments were conducted in order to provide evidence of this overlap through the demonstration of a form of thematic priming (Chapter 2.2.1) wherein the recognition of a tool would be facilitated by the prior presentation of a photograph of its associated hand pantomime. It is predicted that the hand pantomime photographs that best matched the posture required for the functional use of a particular tool will provide the greatest amount of facilitation for the subsequent visual recognition of that tool.

Experiment 1 was conducted to validate the priming methodology using taxonomically related stimuli (eg. face/face; hammer/hammer) and produce some evidence of functionally-interactive thematic relationships (eg. hand/hammer). The effectiveness of animated and non-animated pantomime primes for the recognition of the tool targets is measured. To verify that any observed priming effects were due to the high-level identity of the actions and objects being displayed, not their low-level color and luminance information, text and phase-scrambled versions of the primes are also included. As the detection of an object's shape is heavily based upon its phase information (Oppenheim & Lim, 1981), scrambling the primes' phase information will make recognition of the hand shapes impossible while not affecting their color and luminance information (Dakin, Hess, Ledgeway, & Achtman, 2002; Olman, Ugurbil, & Kersten, 2004). If priming is abolished under these conditions then it cannot be based upon this kind of low-level information. Action verbs and their corresponding hand movements have been shown to involve similar patterns of neural activity (Péran et al., 2010), therefore the text primes should also be effective assuming they accurately convey the same kind of information as the photographic and animated primes.

Experiment 2 was conducted to show more general evidence of functionally-interactive thematic relationships. Photographs of a wide variety of tools are included as target stimuli, along with non-animated photographs of the hand postures corresponding to their functional use as prime stimuli. As it has been shown that the visual presentation of a hand in a specific grasping posture can prime the recognition of objects that it could grasp (Borghi et al., 2007; Kalénine et

al., 2009; Vainio et al., 2008), it seems likely that a hand in a specific functional-interaction posture can prime the recognition of objects that it could interact with.

Experiment 3 was conducted to determine if awareness of the pantomime primes is required. The non-animated primes and target stimuli used in Experiment 1 are presented using a binocular rivalry methodology, which allows for the presentation of different stimuli to each eye. To selectively modulate awareness of the pantomime primes continuous flash suppression is used (CFS; Tsuchiya & Koch, 2005). CFS involves the presentation of a dynamic and highly perceptually salient stimulus to one eye in order to “suppress” any stimuli being presented at the same retinal location in the other eye. This stimulus presentation method effectively makes the non-CFS stimulus appear invisible to the observer. Despite this lack of awareness the visual system seems to still be able to process certain kinds of information about CFS suppressed stimuli (Fang & He, 2005; Pearson & Clifford, 2005a; Tong et al., 1998). This information appears to be largely motion-based and is processed in dorsal stream areas (Chapter 1.1.1). However, exactly what kinds of visual-motion information can be perceived without awareness is still being determined.

In the attempt to resolve this issue Almeida et al. (2008) produced evidence that the visual recognition of tools can be primed using tool images that were suppressed using CFS. This finding appears to indicate that the action information associated with tools can undergo dorsal stream processing outside of awareness. However, in a more recent study these authors suggested that the only information that can be perceived when the image of a tool is suppressed using CFS is that it is a manipulable object; the specific functional use of that tool cannot be perceived

(Almeida et al., 2010). The validity of these suggestions and whether information about tools can truly be processed outside of awareness by dorsal stream areas has been recently called into question. Evidence produced by Sakuraba et al. (2012) shows that the dorsal stream is responsive to images of all kinds of elongated shapes that are suppressed from awareness, not just images of tools and other manipulable objects. Consequently, awareness may in fact be required to process any visual information regarding the manipulable nature of an object. Determining whether functional-interaction priming can occur during CFS will help clarify exactly what kinds of manipulable object information can be perceived outside of awareness.

6.2. Hypotheses

1. The visual presentation of a hand pantomime depicting the posture required for the canonical functional use of a particular tool can prime the visual recognition of that tool.
2. This functional-interaction tool-use priming can occur outside of awareness.

6.3. Method

6.3.1. Participants

A total of 42 University of New South Wales students participated in this study ($n_{\text{experiment 1}} = 6$; $n_{\text{experiment 2}} = 13$; $n_{\text{experiment 3}} = 29$). The author participated in Experiments 1 and 2. Participants in Experiment 3 received course credit upon

completion. All participants gave written, informed consent before the start of the experiment. This study received ethical approval from Human Research Ethics Advisory Panel (HREA).

6.3.2. Stimuli: All Experiments

All stimuli were presented using MATLAB (version 7.10.0 R2010a). Experiments 1 and 2 used a 27cm x 35.5cm Philips 109P4 monitor at a resolution of 1152 x 870 @ 75Hz while Experiment 3 used a 32cm x 51cm iMac monitor with a Nvidia GeForce GT 120 chipset at a resolution of 1920 x 1200. All experiments involved the presentation of photographic stimuli of faces, hands, and tools. Stimuli were presented in the center of the screen with a black background (luminance = 0.01 cd/m^2) and overlaid by a circular fixation mark (diameter = 0.3° visual angle).

Face stimuli were taken from CALTECH's online archive (<http://www.vision.caltech.edu/archive.html>). Face photographs were selected from this archive that expressed neutral emotionality, had even lighting, were forward facing and had no highly distinctive features. Tool stimuli consisted of multiple photographs of hammers, cups, wrenches, eating utensils, axes, house keys, computer mice, pencils, and scissors, which were taken from various internet sources, along with Experiment 1's non-pantomime hand and house primes. All other hand stimuli were created in the lab using a Nikon D50 camera. The hand photographs consisted of functional tool use pantomimes for the selected tools from an allocentric viewpoint. To create the stimuli, the objects within all of the photographs were extracted and placed on top of an achromatic gray rectangle

(width = 11° visual angle; height = 11° visual angle; luminance = 62 cd/m²). See the top row of Figure 6.1 for examples of these stimuli.

The phase-scrambled primes were created by randomizing their phase spectrum within a Fourier transformation. Without changing the amplitude spectrum, the phases of each color channel (*r*, *g*, *b*) were identically randomized to preserve the color and luminance values present within the original photographs. See the bottom row of Figure 6.1 for examples of phase-scrambled versions of the top-row stimuli.

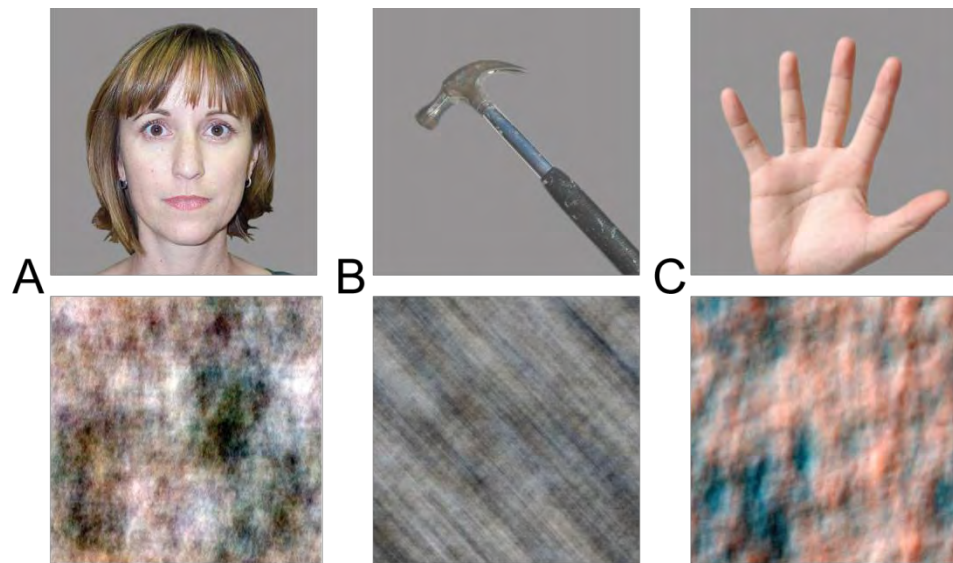


Figure 6.1. Example photographs. Top Row: color photographs with backgrounds removed. Bottom Row: phase-scrambled versions of the top row photographs. (A) Face photograph used as a prime and target. (B) Hammer photograph used as a prime and target. (C) Hand photograph used as a prime only.

6.3.3. Stimuli: Experiment 1

Experiment 1 included the use of animated, non-animated, and text primes. Phase-scrambled versions of the photographic and animated primes were also included. In Experiment 1A only a face, a hammer, a hand, and a house were used

as prime stimuli. Figure 6.1 displays three of these primes and their phase-scrambled versions. As can be seen in Figure 6.1C, this hand photograph does not pantomime the functional use of any kind of tool. The text primes used in this experiment were the nouns “face”, “hammer”, “hand”, and “house”. The target stimuli consisted of 4 face photographs and 4 hammer photographs, including the same hammer and face photographs used as prime stimuli.

Experiments 1B and 1C only used pantomime hands and their text versions as prime stimuli. The same target stimuli were used, along with an additional 4 face and 4 cup photographs. The prime photographs displayed the manner in which the hand and forearm appears during the canonical functional use of a hammer and a cup. Experiment 1B’s animated primes consisted of 4 frames displayed at a rate of 17.78 frames per second. Experiment 1C non-animated primes consisted of only the third frame of the previously used animations. Experiment 1C also included text primes that consisted of the verbs “swing” and “pour”. These stimuli are shown in the legend of Figure 6.5.

6.3.4. Stimuli: Experiment 2

Experiment 2 included the use of 7 new non-animated pantomime hand photographs and the face, hammer, and non-pantomime hand primes used in Experiment 1. The pantomime hands depicted the canonical manner in which the following objects are held during their functional use: cup, hammer/axe/wrench, computer-mouse, pencil, house-key, eating-utensil, and scissors. Target stimuli consisted of 18 face photographs (including all those used in the previous

experiment) and 18 tool photographs (2 different photographs of each of the previously mentioned tool types).

6.3.5. Stimuli: Experiment 3

Experiment 3 included the use of achromatic versions of the non-animated prime and target stimuli used in Experiment 1C, except for the cup photographs. Four new photographs of cups that do not have handles were taken from various internet sources, due to the concern that the handles may present alternative ways of functionally interacting with the cups. The blue color-channel was removed from all photographs used in this experiment and red/green anaglyph lenses were used to split the two remaining color channels between the eyes. This dichoptic presentation allows for two different images to be presented simultaneously to a single location by displaying one image in the red channel and the other image in the green channel, resulting in binocular rivalry. This binocular rivalry methodology was used to modulate awareness of the prime stimuli.

Figure 6.2 displays a schematic of how the prime stimuli were constructed in Experiment 3. The prime photographs were presented in one of the two color channels while a continuous flash-suppression (CFS) pattern was presented in the other. The CFS consisted of a high-contrast pattern of squares that was randomized at a rate of approximately 75 Hz. On each trial this highly dynamic CFS was randomly assigned to one of the two color channels, with the prime being assigned to the other. In the “prime aware” condition the contrast of the CFS pattern was reduced by 40% to facilitate perceptual dominance of the prime photograph. In the “prime unaware” condition the contrast of the prime photograph

was reduced by 40% to facilitate perceptual dominance of the CFS pattern. Additionally, to produce perceptual isoluminance of the two color channels the brightness of the green channel was reduced by 50%, resulting in an overall orange coloration when viewed without the anaglyph lenses.

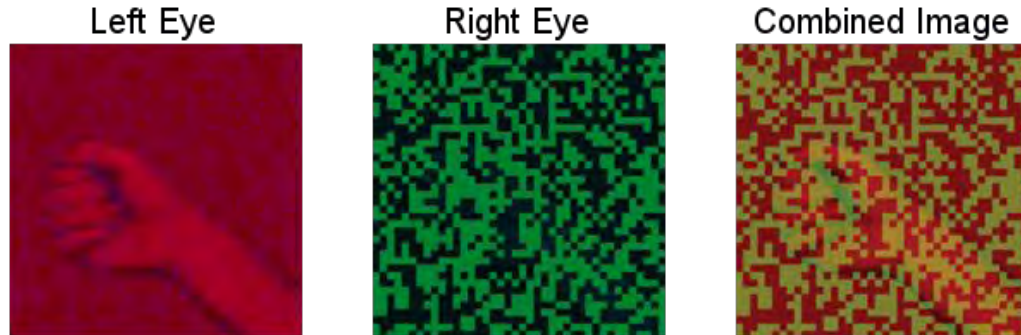


Figure 6.2. Red/green binocular rivalry primes used in Experiment 3. Prime photographs and continuous flash-suppression (CFS) presented in separate color channels. The color channel containing the prime photograph was randomly determined on each trial.

6.3.6. Procedure

All participants were seated in a dark room approximately 57cm from the monitor. A chinrest was used to stabilize the participants' head position. Figure 6.3 shows the experimental timelines used in this study. Each experimental session consisted of numerous trials wherein every possible combination of prime and target photograph was presented for each condition. In all experiments the participants were required to categorize the target photo as either a "Face" by pressing the F key or a "Tool" by pressing the T key as quickly as possible. Each experiment was conducted separately and in the order presented within this manuscript, including the three parts of Experiment 1.

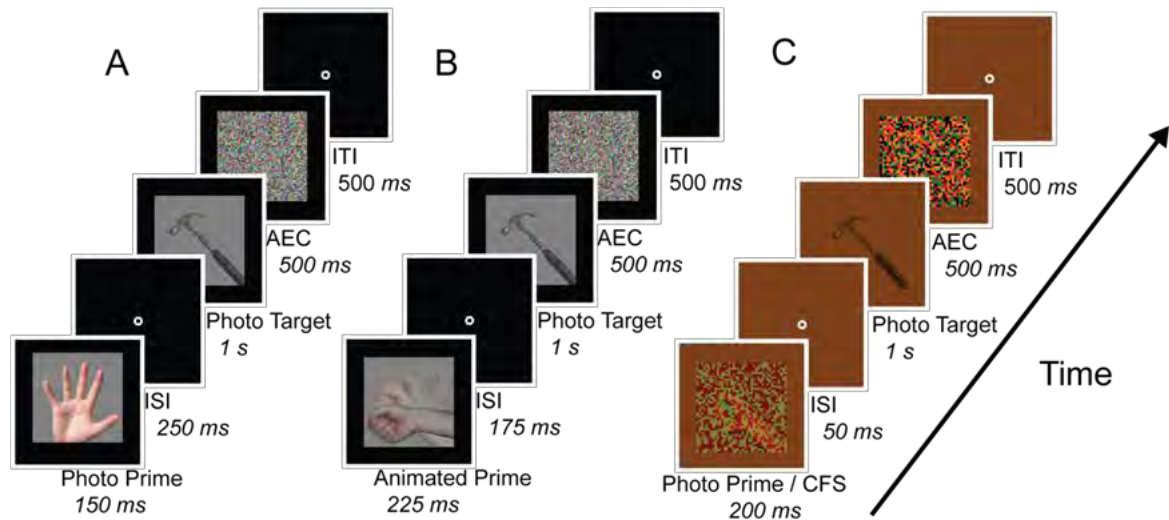


Figure 6.3. Experimental timelines. All timelines are similar with exception to how the primes were displayed. ISI: inter-stimulus interval. AEC: after-effect cancellation. ITI: inter-trial interval. (A) Experiments 1A, 1C, and 2 displayed a non-animated prime for 150ms. (B) Experiment 1B displayed an animated prime for 225ms. These animations consisted of 4 frames, each shown for 56.25ms. (C) Experiment 3 used red/green anaglyph lenses to present the non-animated prime to one eye and a continuous flash-suppression (CFS) pattern to the other eye for 200ms. Target stimuli and after-effect cancellation were presented to both eyes.

Figure 6.3A displays the experimental timelines used in Experiments 1A, 1C, and 2. During each trial the participants were shown a prime for 150ms, followed by a 250ms inter-stimulus interval. This was then followed by the target photograph for 1s, which participants categorized as a “Face” or “Tool” by pressing corresponding buttons on the keyboard. They were instructed to respond as quickly as possible, but avoid making mistakes. If participants took longer than 1s from stimulus onset to respond, or if they responded incorrectly, a buzzer sound would be played and the trial would be repeated at a randomly determined point later in the session. Immediately following the target photograph an after-effect cancellation image was shown for 500ms to eliminate any perceptual after-images

from viewing the photographs. After an additional 500ms inter-trial interval the next trial would begin.

Figure 6.3B displays the experimental timeline used in Experiment 1B. Though largely similar to the previous timeline, some adjustments had to be made to better suit the variations in stimuli and task. The 4-frame animated primes were displayed for 225ms (56.25ms per frame), which was followed by a 175ms inter-stimulus interval. All other presentation timings were identical to the non-animated experimental timeline, and the stimulus onset asynchrony between the prime and target stimuli remained unchanged (400ms).

Figure 6.3C displays the experimental timeline used in Experiment 3. Participants in this study were required to wear red/green anaglyph lenses to split the two color channels between the eyes. This allowed for the simultaneous and dichoptic presentation of the continuous flash-suppression (CFS) and the photograph prime, resulting in binocular rivalry. The rivaling stimuli were displayed for 200ms, followed by a 50ms inter-stimulus interval. All other presentation timings were identical to the previous experimental timelines. Additionally, at the end of each trial the participants were required to indicate whether or not they could identify the prime presented during the rivalry by pressing one of two buttons at the end of each trial. This procedure was included to verify that the primes were being suppressed from awareness in the “Unaware” condition and were not being suppressed in the “Aware” condition.

6.3.7. Data Preparation

Incorrect responses were recorded but excluded from analysis in all experiments. When an incorrect response was made a buzzing sound would be played through the computer's speakers and that particular trial would be repeated at a randomly determined point later in the session. Two filters were applied to the data in order to remove outliers. Firstly, all reaction times faster than 200ms or slower than 700ms were excluded. Secondly, any reaction times beyond 2.5 standard deviations from the participant's mean for that prime-target combination were excluded. This filtered data was then normalized to facilitate comparison across participants.

6.4. Results

Mean reaction times were computed to measure the effects of each of the different prime photographs on the recognition of the target objects. The means for each participant were computed by first averaging together their reaction times for all photographs in a single category (eg. faces) for each experimental session, separated by prime condition. These category averages were then averaged across all of the participant's experimental sessions, resulting in mean reaction times for each combination of prime and target object category. Then "matched" and "mismatched" means were computed for each participant by averaging together their mean reaction times for the prime-target combinations that shared a thematic relationship, and for those that did not. These overall matched and mismatched reaction times were used in the analyses described below.

6.4.1. Experiment 1A: Non-pantomime Priming

In this experiment we sought to determine whether our non-pantomime hand photograph could prime recognition for the hammer targets due to being thematically related. The effects of the hand prime were compared to that of the face and house primes in order to determine their ability to facilitate the categorization of the hammer photographs used in this experiment. The hammer prime was excluded from this analysis as it is clearly within the same taxonomic category as the hammer targets. The data was split by prime condition (normal photographs, scrambled photographs, text). For each condition, a separate paired-samples *t*-test was conducted comparing the prime-target combinations that were thematically matched (hand-hammer) to the combinations that were mismatched (face-hammer; house-hammer). It was predicted that recognition of the hammer targets would be faster when the hand prime was shown, as tools and hands share a functional-interaction relationship.

Figure 6.4 shows the mean normalized reaction times and standard errors for matched and mismatched prime-target pairs using the normal, scrambled, and text primes. For the normal photographic primes (Figure 6.4A) no significant difference was found between the matched and mismatched pairs $t(5)=0.91$, $p = 0.41$, observed $1-\beta = 0.115$, which fails to indicate the presence of any functional interaction thematic priming (hand – hammer). This appears to indicate that non-pantomime hand prime was not sufficiently related to the hammer targets. For the phase-scrambled photographic primes (Figure 6.4B) no significant difference was found between the matched and mismatched pairs $t(5)=0.17$, $p = 0.87$, observed $1-\beta = 0.05$. This result was expected as visual recognition of the prime

photographs was made impossible. For the text primes (Figure 6.4C) no significant difference was found between the matched and mismatched pairs $t(5)=1.75$, $p = 0.14$, observed $1-\beta = 0.296$. This result could either indicate that the chosen word primes were not sufficiently related to the target photographs, or that object names are ineffective for this form of priming.

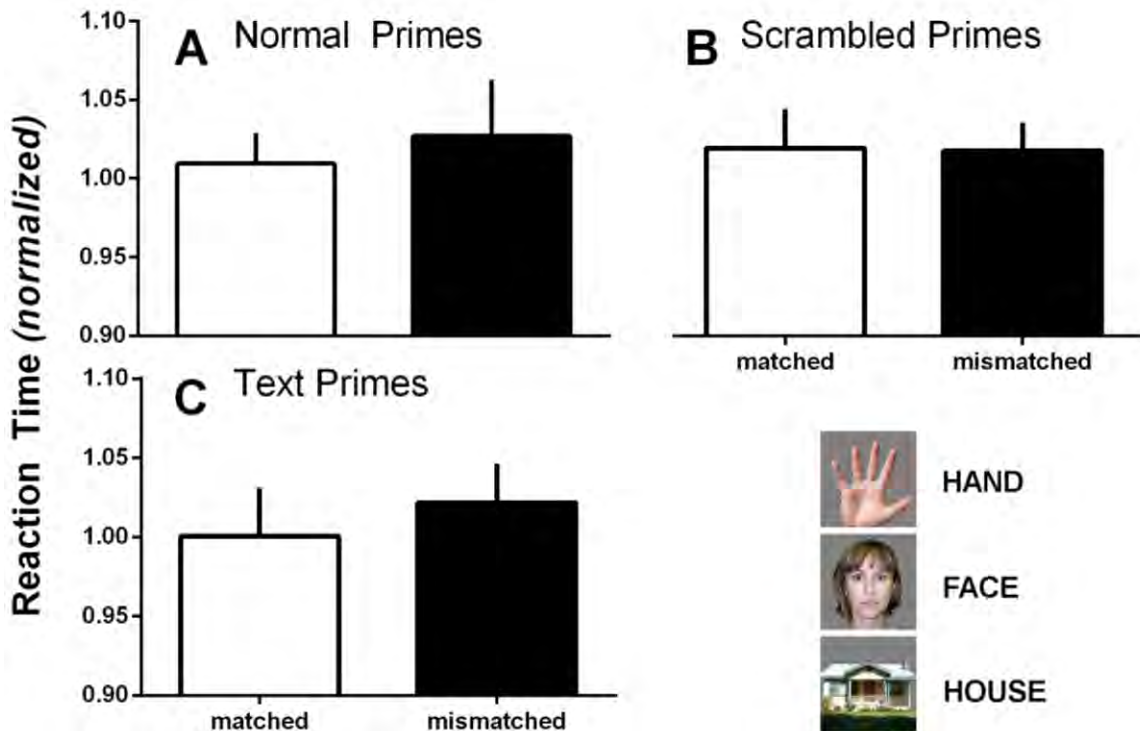


Figure 6.4. Mean normalized object categorization reaction times for matched and mismatched pairs of hand prime and target object used in Experiment 1A. (A) Normal primes. (B) Phase-scrambled primes. (C) Text primes. Normal and text prime stimuli are shown in the bottom-right. Error bars show +1 SEM.

6.4.2. Experiment 1B: Animated Pantomimes

In this experiment we sought to replicate the functional-interaction thematic priming of Mounoud et al. (2007) using similar tool-use pantomime animations. The effects of the two different pantomime prime animations were analyzed to

determine their comparative ability to facilitate recognition for the hammer and cup objects used in this experiment. The data was split by prime condition (normal animations, scrambled animations, text). For each condition, a separate paired-samples *t*-test was conducted comparing the prime-target combinations that were thematically matched (swing-animation/hammer; pour-animation/cup) to the combinations that were mismatched (pour-animation/hammer; swing-animation/cup). It was predicted that the animations depicting the proper usage of cups would facilitate recognition for cups and the animations depicting the proper usage of hammers would facilitate recognition for hammers. It was also predicted that this kind of facilitation could be produced using verbs describing these actions (swing; pour). Figure 6.5 shows the mean normalized reaction times and standard errors for the matched and mismatched prime-target pairs separated by condition used in this experiment.

For the normal animated pantomime primes (Figure 6.5A) a marginally significant difference was found between the matched and mismatched prime-target pairs $t(5)=2.34, p = 0.067$, observed $1-\beta = 0.471$. While this result indicates no significant difference in thematic priming between the matched and mismatched animated pantomime primes, it does appear to suggest that such a difference could be found using these kinds of stimuli. Post hoc analyses directly comparing the two primes appear to show that the “swing” animation works best for the hammers, and the “pour” animation works best for the cups, but it cannot be determined if these differences are due to the relative effectiveness (or ineffectiveness) of one or both of the prime animations. For the phase-scrambled animated pantomime primes (Figure 6.5B) no significant difference was found

between the matched and mismatched prime-target pairs $t(5)=0.71$, $p = 0.51$, observed $1-\beta = 0.09$. This result indicates that no significant amount of priming occurred using the phase-scrambled animated pantomime primes. For the text primes (Figure 6.5C) no significant difference was found between the matched and mismatched prime-target pairs $t(5)=1.41$, $p = 0.22$, observed $1-\beta = 0.211$. This result shows no functional-interaction priming using the verbs “SWING” and “POUR”.

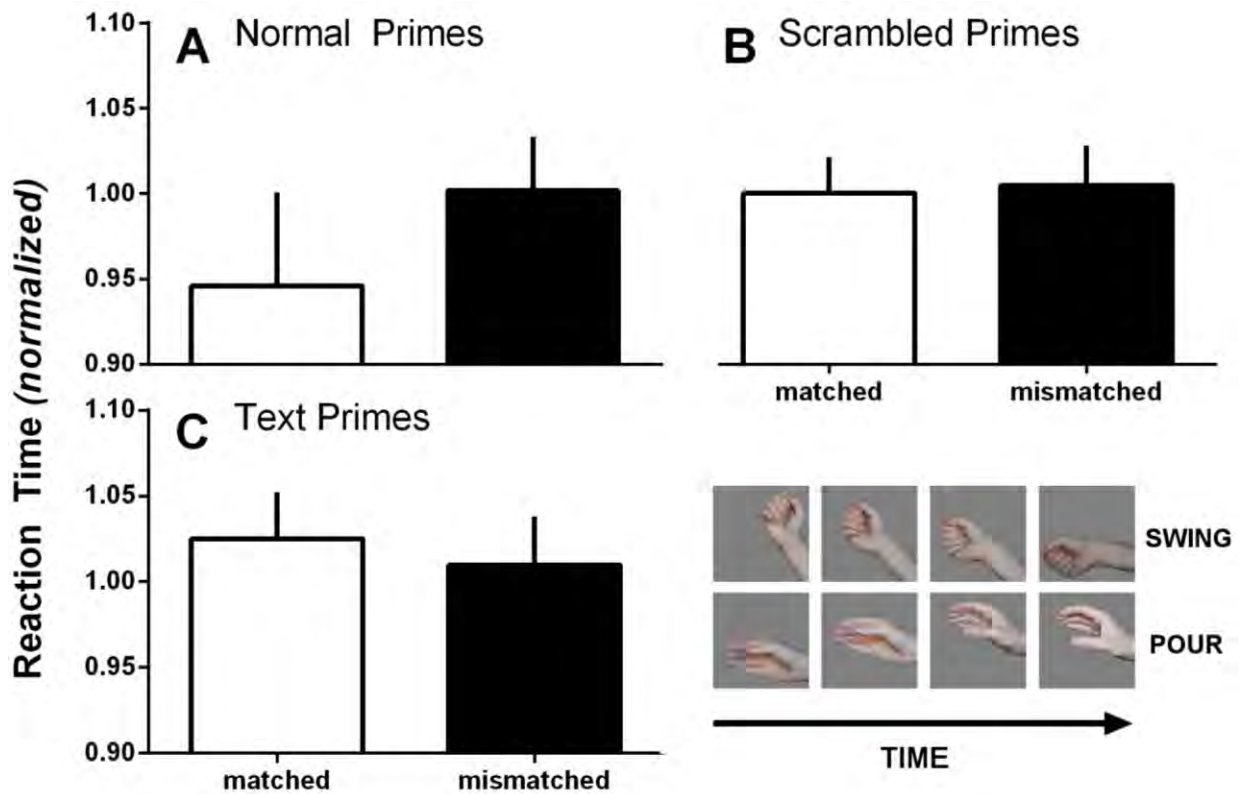


Figure 6.5. Mean normalized object categorization reaction times for matched and mismatched pairs of hand prime and target object used in Experiment 1B. (A) Normal animated primes. (B) Phase-scrambled animated primes. (C) Text primes. Each individual frame of the animations used in this experiment are shown in the bottom-right. Error bars show +1 SEM.

6.4.3. Experiment 1C: Non-animated Pantomimes

In this experiment we attempted to more directly address the main hypothesis which focuses on the hand's posture, not its motion. The resulting prime stimuli only contained this posture information, and consisted of the third frames of the previously used animations. These non-animated pantomime primes depicted the canonical posture required for the functional uses of hammers and cups. It was thought that these pantomime hand primes could facilitate the recognition of corresponding tools as it has been previously shown that the presentation of tools can facilitate the mimicry of corresponding hand-postures (Bub & Masson, 2006).

The effects of the two pantomime prime photographs were analyzed to determine their comparative ability to facilitate the categorization of the faces, hammers, and cups used in this experiment. The data were split by prime condition (normal photographs, scrambled photographs). For each condition, a separate paired-samples *t*-test was conducted comparing the prime-target combinations that were thematically matched (swing-photograph/hammer; pour- photograph/cup) to the combinations that were mismatched (pour- photograph/hammer; swing- photograph/cup). It was predicted that the pantomimes mimicking the posture required for the functional use of a tool would result in faster reaction times for that tool. Figure 6.6 shows the mean normalized reaction times and standard errors for the matched and mismatched prime-target pairs separated by condition used in this experiment.

For the normal photographic pantomime primes (Figure 6.6A) no significant difference was found between the matched and mismatched prime-target pairs

$t(5)=1.47$, $p = 0.20$, observed $1-\beta = 0.224$. This result seems quite different from that of Experiment 1B, which appears to suggest that the functional-interaction priming might require real visual motion, not implied motion, to be present within the prime stimuli. For the phase-scrambled photographic pantomime primes (Figure 6.6B) no significant difference was found between the matched and mismatched prime-target pairs $t(5)=1.23$, $p = 0.27$, observed $1-\beta = 0.172$. This result indicates no significant amount of priming occurred using the phase-scrambled pantomime primes. No priming effects were predicted for this condition.

However, it should be noted that while no significant differences were found in this experiment it cannot be concluded that none exist, especially since this pattern of results is highly similar to that of Experiment 1B. Visual comparison of Figures 6.5. and 6.6. shows that the average difference between the matched and mismatched reaction times for the normal prime condition of this experiment is highly similar to that of Experiment 1B. The only major difference between these two sets of data is that a higher degree of variability was found in Experiment 1C. Therefore, it may be the case that there is a true difference in the conditions, but that difference has been masked by relatively large SEM values.

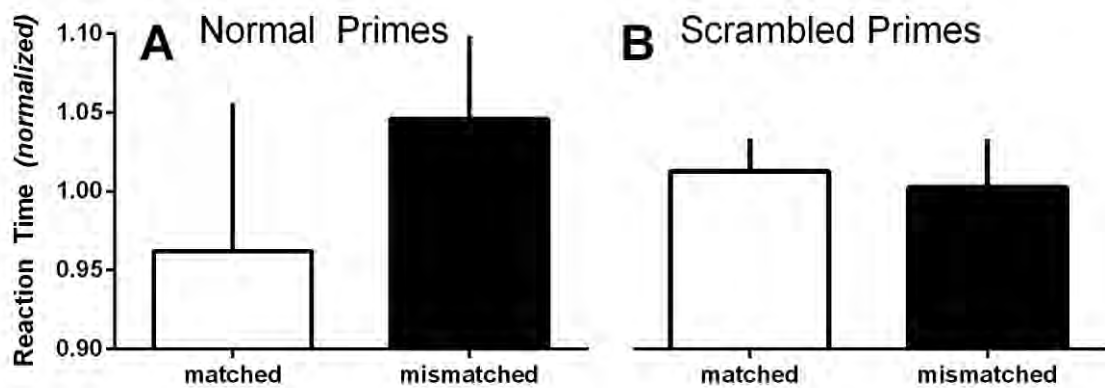


Figure 6.6. Mean normalized object categorization reaction times for matched and mismatched pairs of hand prime and target object used in Experiment 1C. (A) Normal photographic primes. (B) Phase-scrambled photographic primes. Prime photographs consisted of the third frames of the animated primes shown in Figure 6.5. Error bars show +1 SEM.

6.4.4. Experiment 2: Non-animated Pantomimes for Various Tools

In this second experiment we sought to once again test our main hypothesis using a wider range of tool objects and hand-pantomime primes. Photographs of scissors, keys, pencils, eating-utensils, computer mice, axes, and wrenches were included as target stimuli. New hand-pantomime primes were also included which depicted the canonical posture required for the functional use of each of these kinds of tools.

The effects of all 8 pantomime hand primes were analyzed to determine their comparative ability to facilitate the categorization of the various tool photographs used in this experiment. It was predicted that the presentation of hands mimicking the traditional manner in which a tool is used will prime the subsequent recognition of that tool, while mismatched hand mimicry will not. Therefore, to test this prediction the mean reaction times for the tools' matched hand primes were compared to the mean reaction times for the tools' mismatched hand primes. For this analysis the face targets were excluded.

A paired-samples *t*-test was conducted to compare the mean reaction times for all the matched prime-target pairs and the mismatched prime-target pairs. No significant difference was found between these two conditions $t(12)=0.44$, $p = 0.67$, observed $1-\beta = 0.069$. These results, which are shown in Figure 6.7, do

not show a significant amount of functional-interaction priming for the non-animated pantomime primes, which appears similar to Experiment 1C.

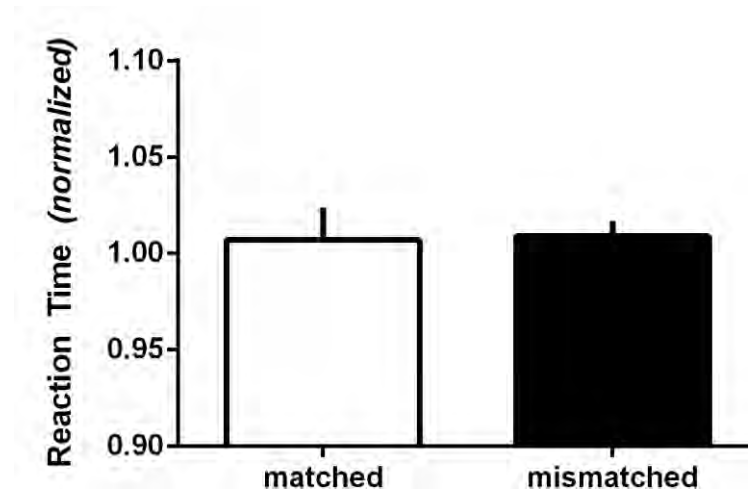


Figure 6.7. Mean normalized object categorization reaction times for the matched and mismatched hand-tool pairs used in Experiment 2. Error bars show +1 SEM.

6.4.5. Experiment 3: Prime Awareness Modulation

In this third and final experiment we sought to once again test our main hypothesis, as well as our secondary hypothesis concerning whether awareness is required for this form of priming to occur. Using a continuous flash suppression (CFS) methodology, if significant functional-interaction priming is found when the pantomime prime photographs are suppressed from awareness this would indicate that visually presented hand postures associated with tool-use can be processed outside of awareness (Almeida et al., 2010; Fang & He, 2005; Tong et al., 1998).

The face, hammer, non-tool hand, hammer-hand, and cup-hand primes that were used in Experiment 1C were also used in this study. The effects of the two tool-use pantomime hand primes were compared in order to determine their ability to facilitate the visual recognition of their matching tools (hammers; cup). For each

condition, a separate paired-samples *t*-test was conducted comparing the prime-target combinations that were thematically matched (swing-photograph/hammer; pour-photograph/cup) to the combinations that were mismatched (pour-photograph/hammer; swing-photograph/cup). It was predicted that the pantomime photographs mimicking the posture required for the functional use of a tool would result in faster reaction times for that tool. Figure 6.8 shows the mean normalized reaction times and standard errors for the matched and mismatched prime-target pairs separated by awareness condition.

Figure 6.8A shows the normalized mean reaction times for the prime aware condition. No significant difference was found between the matched and mismatched prime-target pairs $t(29)=0.65$, $p = 0.52$, observed $1-\beta = 0.096$. Like the results of Experiment 1C and Experiment 2 this result does not support the main hypothesis by showing no functional-interaction priming for the non-animated primes. Figure 6.7B shows the normalized mean reaction times for the prime unaware condition. No significant difference was found between the matched and mismatched prime-target pairs $t(29)=1.05$, $p = 0.30$, observed $1-\beta = 0.173$. This finding shows no significant functional-interaction priming for the unaware primes. However, as can be seen in Figure 6.8, there does seem to be a difference between these two conditions. Regardless of whether the prime and target stimuli were matched or mismatched, when the participants were unaware of the prime's presence they appeared to correctly categorize the target objects more quickly.

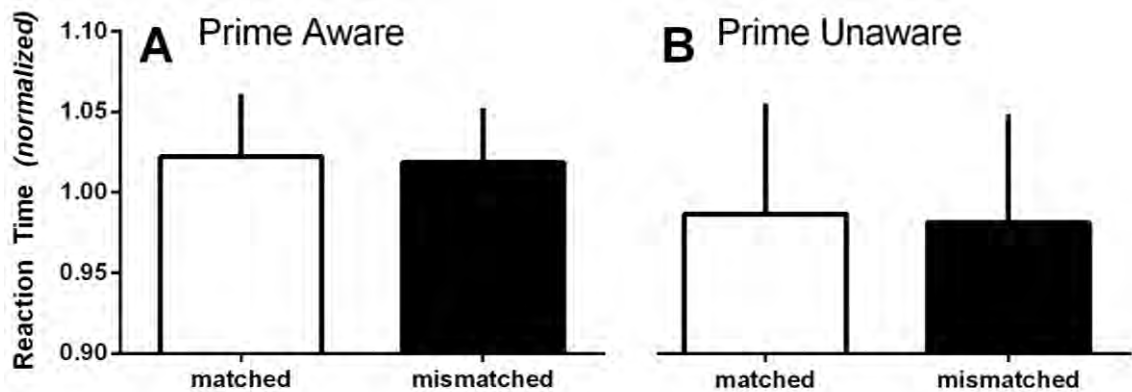


Figure 6.8. Mean normalized object categorization reaction times for the matched and mismatched hand-tool pairs used in Experiment 3. (A) Prime aware. (B) Prime unaware. Error bars show +1 SEM.

6.5. Discussion

This study does not show any significant functional-interaction priming effects using animated, non-animated, or verbal tool-use pantomimes. However, the data of the animated primes does seem to suggest that this form of thematic priming (Section 6.4.2.), which is predicted by the theory of modality grounded cognition, may in fact be possible (Chapter 7.1.2). However, no evidence was found suggesting that this form of priming can occur using non-animated primes; hand-photographs in the canonical postures required for the functional use of tools did not produce a significant amount of functional-interaction priming in this study (Sections 6.4.3., 6.4.4., and 6.4.5.). Consequently we cannot conclude that there is an overlap in the processing of a tool's identity and the hand postures required for its functional use. While there are many potential explanations for this result, it does seem to suggest that manipulable object concepts are grounded more so within motion areas (Chapter 7.3.3). Multiple factors or combinations of factors may have produced this result, but the current study's design is unlikely to be one of them for the reasons described below.

The current study sought to replicate the findings of Mounoud et al. (2007) , which used stimuli that consisted of 800ms and 1400ms videos depicting the full-body of an actor mimicking the canonical functional use of a wide range of tools. Though this study predominantly looked at age-related differences in children, significant functional-interaction priming was found for all age groups. The current study's methodology differed in a few important ways, which may account for the lack of significant results. Firstly, our tool-use pantomime animations were only 225ms long. We intentionally used shorter animations to ensure that the participants were not able to create strong mental imagery representations of the "missing" tool objects (see Pearson et al., 2008). This was a concern as it could potentially confound the contributions of the visual hand-motion information on the recognition of the tools objects being shown. Secondly, the animations were displayed at a rate of 17.78 frames per second. This frame-rate is well below modern standards for video, but was still capable of producing a compelling sense of motion despite a noticeable "choppiness". Thirdly, our pantomimes consisted of only the hand and forearm of the actor, instead of the actor's entire body. This allowed us to specifically study the visual information provided by postures and movements of the actor's hand without the potentially distracting information provided by the rest of the body. Finally, we used only adult participants, the age group that showed the weakest priming effects in Mounoud et al. (2007). All other aspects of these animated stimuli were designed to be similar to that of the previous study. However, though they were based upon stimuli previously shown to be effective, the current stimuli were not validated in their ability to accurately depict the pantomimes most closely associated with the tools used in these

experiments. Consequently, it may very-well be the case that the current stimuli are suboptimal. This potential limitation may have contributed to our finding of only marginally significant functional-interaction priming effects being produced using our animated pantomime primes.

It was predicted that non-animated tool-use pantomimes could prove to be effective as functional-interaction primes, as it has been previously shown that the visual presentation of tools can facilitate the mimicry of subsequently presented hand-postures (Bub & Masson, 2006). However, the current evidence does not support this prediction. Four factors that likely contributed to this outcome have been identified based upon the previous literature. These factors include: the small number of participants included in these studies, the perspective from which the stimuli were displayed, the accuracy of the prime stimuli in depicting the canonical postures required for the functional use of the tools targets, the orientations of the prime and target stimuli, and the participants' intentions toward the tool objects. Prime awareness was not considered to be a contributing factor as no difference was found between the aware and unaware conditions of Experiment 3. The potential influences of these four contributing factors are discussed in further detail below.

6.5.1. Number of Participants

The number of participants in Experiments 1 and 2 were relatively low. Increasing the number of participants included in these experiments could help to increase statistical power, which would make it easier to detect significant differences in the reaction times between the matched and mismatched stimulus

pairs (i.e. normal conditions). However, the low power values observed in these experiments (Section 6.4.) may also be indicating that no such differences actually exist (i.e. scrambled conditions). While the current data seems to indicate that a difference might exist between the matched and mismatched stimulus pairs of Experiment 1b's normal animations condition, it cannot be easily assumed that any other significant differences exist (e.g. Experiments 1a, 1c, 2 and 3). Therefore, collecting data from additional participants would most likely fail to change the results of these analyses.

It is important to note that the observed power values of these statistical comparisons are entirely dependent upon the observed difference between the two groups of each analysis. Therefore low power values are to be expected if no differences actually exist between the conditions. Consequently, as stated in the previous paragraph, these power values merely reflect the fact that significant differences were not found within the current data (if significant differences were found these power values would approach 0.80).

6.5.2. Perspective

Pantomime hand-primers used in the current study depicted the stimuli as though the participants were standing directly to the left of the pantomime actor. This is known as an allocentric perspective, in comparison to an egocentric perspective wherein the participant would be viewing the stimuli from the actor's point of view. An allocentric perspective was chosen for our prime and target stimuli as it has previously been shown to be effective (Mounoud et al., 2007). However functional neuroimaging studies have found marked differences in how

these two perspectives influence the neural processing of stimuli (Farrer & Frith, 2002; Jackson, Meltzoff, & Decety, 2006; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Ruby & Decety, 2001; Vogeley et al., 2004). These differences most likely correspond with behavioral differences that have been observed when viewing stimuli in these two perspectives.

Vogt et al. (2003) found that the use of an idiocentric perspective in a hand-action priming task will generally produce stronger priming effects than an allocentric perspective. They argued that this superior facilitation occurs because this perspective conveys the visual-motion information most similar to what is seen upon the self-performance of those actions. They described this as the “Own perspective advantage” as it appeared to produce a sense of ownership over the hands being shown, which is likely due to the fact that this is the perspective through which one perceives their own body.

Expanding upon these findings, Bruzzo et al. (2008) have produced evidence that this superior form of action-priming is not simply a matter of perspective. In their study the prime stimuli consisted of a gloved hand in various neutral and grip postures, while the target stimuli depicted the same gloved hand interacting with various tools in either a sensible or non-sensible manner. These prime and target stimuli were displayed using both an idiocentric and allocentric perspective. All four combinations of the two stimuli shown in the two perspectives were compared. They found that participants made much faster judgments on the sensibility of the hand-tool interaction for idiocentric than allocentric targets, but only while wearing a pair of gloves matching those shown in the stimuli. When the participants did not wear the gloves the idiocentric primes actually produced slower

reaction times than the allocentric primes. This finding indicates that the visual similarity between actor and observer plays a very important role in this sense of ownership; perspective may not be as important as previously thought. Research on mirror neurons appears to support these conclusions.

Mirror neurons are special cells found in the brains of macaque monkeys that become active during the performance or observation of another individual performing a particular behavior (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Keysers, 2009; Rizzolatti & Craighero, 2004). These neurons process both perceptual and motor information which seems to allow macaques to easily mimic and understand the behavior and emotional states of others (Gallese, 2001; Iacoboni, 2009; Williams, Whiten, Suddendorf, & Perrett, 2001). Recent evidence has indicated that humans also appear to have mirror neurons (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Fabbri-Destro & Rizzolatti, 2008; Fagioli, Ferlazzo, & Hommel, 2007; Keysers & Gazzola, 2010; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). As mirror neurons are the perfect example of a single neural area involved in the processing of both perception and knowledge, their discovery has produced strong and unambiguous evidence supporting the theory of grounded cognition (Garbarini & Adenzato, 2004; Wiedermann, 2012).

Actor-observer similarity has been identified as an important mediating factor for mirror neuron effects (Anelli, Nicoletti, Kalkan, Sahin, & Borghi, 2012; Buccino et al., 2004; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). The influence of similarity appears to mostly be based upon the fact that how an individual performs an action is highly dependent on their body-type and capabilities. Consequently, if there is a high degree of similarity between two

individuals, then it is likely that they will perform the same action in the same way. As all hand-primers used in this study depicted a male Caucasian's right hand, this potentially attenuated the effectiveness of the primes for the female, left-handed, and non-Caucasian participants.

Based upon these findings, the current study's prime and target stimuli could potentially be improved through increasing the participants' general sense of ownership for the pantomime-hand primes that were shown. To do this, it seems important to ensure a high degree of similarity between actor and observer, but the use of an idiocentric perspective does not seem as important. The optimal study design in this regard would have the participants play the role of both actor and observer. Each participant would first create a unique set of pantomime-hand primes using their own hands, and then be tested using those stimuli. An idiocentric perspective could also be used, but how important it is remains unclear.

6.5.3. Prime Accuracy

Accurate depiction of the canonical hand postures required for functional tool-use is obviously an important issue in this study. Accordingly, many methods have been developed to determine the accuracy of stimuli included in such a study. Perhaps the most commonly used behavioral method has been the completion of a preliminary stimulus-rating experiment using a separate group of participants. In such an experiment a wide array of potential stimuli would be rated on how well they exemplify the stimuli desired by the researcher. Only the stimuli receiving the highest ratings would later be used in the main experiment. No such stimulus ratings were made in the current study.

This raises the question of whether or not our prime photographs depict hand-postures that most accurately correspond to the chosen tools. This issue is central to the current study's main hypothesis, as it states that the hand stimulus that depicts the canonical posture required for the functional use of a tool can prime its recognition. However, it should be noted that many of the hand-action studies that were previously discussed did not rate the accuracy of their selected hand-stimuli (Borghi et al., 2007; Bruzzo et al., 2008; Liuzza et al., 2012; Mounoud et al., 2007; Vainio et al., 2008; Vogt et al., 2003). While it is possible that the verification and use of more accurate hand-postures may have produced greater priming effects, it seems unlikely that the postures used in the current study were completely inaccurate and therefore incapable of producing any amount of priming for the tools used in this study.

6.5.4. Stimulus Orientation

Not all of the tool targets used in Experiment 2 were correctly aligned with their corresponding pantomime-hand primes (Section 6.3.4.). For these misaligned pairs of stimuli if the two images were overlaid the tools would not fit within the hands in a manner consistent with their canonical functional use. This is potentially problematic as perception of the hand and tool stimuli used in the current study most likely involved a degree of processing within the dorsal stream (Chapter 1.1.1), which is known to be sensitive to the orientations of graspable objects (Rice, Valyear, Goodale, Milner, & Culham, 2007; Valyear, Culham, Sharif, Westwood, & Goodale, 2006). This sensitivity is logically a consequence of the fact that grasping differently oriented objects requires different sequences of hand-

movements. In accordance with this conclusion, faster reaction times have been shown when hand and tool stimuli are properly aligned (Masson, Bub, & Breuer, 2011).

To determine if prime-target misalignment had an influence on Experiment 2's data a split-half analysis was conducted. This analysis directly compared the participants' reaction-times for aligned and misaligned prime-target pairs. No significant difference was found in the primes' effectiveness between aligned and misaligned prime-target pairs, yet this of course does not prove one does not exist. This finding simply means that any influence of stimulus misalignment is undetectable within the current data. However, there are other aspects concerning the orientation of these stimuli that are potentially problematic.

The orientation of a graspable object is also known to exert a powerful influence on an observer's hand movements. It has repeatedly been shown that viewing an object that could more easily be grasped with one of the two hands will selectively facilitate movements of the corresponding hand (Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri, 2010; Phillips & Ward, 2002; Tucker & Ellis, 1998; Vainio, Ellis, & Tucker, 2007). This shows that the motor knowledge that is activated by viewing manipulable stimuli does not generalize across the two hands. When applied to the current study, this finding would suggest that tools aligned with the right hand should result in faster reaction times than tools aligned with the left hand, as all the pantomime primes depicted a right hand and all the participants used their right hand to make their responses. Yet the data show no such hand-alignment based differences. It is likely that this kind of hand-alignment

bias was avoided simply due to how the participants made their responses; they were instructed to only move their right-index or right-middle fingers.

Handedness is another potentially important factor related to stimulus orientation. Though participant handedness was not recorded, approximately 1 in 10 individuals are left-handed, making it quite probable that some of them were left hand dominant. As the prime stimuli depicted only a right hand this may have attenuated the effectiveness of the primes for these participants. However, the manner in which the brain processes this kind of information may suggest an explanation as to why this is not likely to be the case. It is well known that tool-use knowledge is processed predominantly within the brain's left hemisphere, even for left-handed individuals (Choi et al., 2001; Frey, Funnell, Gerry, & Gazzaniga, 2005; Moll et al., 2000). As the left hemisphere also coordinates movements of the right hand, using right-handed stimuli may in fact be optimal for studies concerning functional tool-use. However, recent evidence has called this assumption of handedness invariance into question (Willems, Toni, Hagoort, & Casasanto, 2009). Consequently, it is possible that left-handers experienced some level of difficulty relating to our right-handed stimuli.

6.5.5. Participant Intentions

Gibson (1979) proposed that simply looking at an object that affords interaction will activate stored knowledge about that interaction. This proposal has gained a large amount of support over the years from behavioral and neurological research (Borghi et al., 2007; Chao & Martin, 2000; Craighero et al., 2002; Craighero et al., 1998; Craighero et al., 1996; Creem-Regehr & Lee, 2005; Gianelli

et al., 2008; Grèzes et al., 2003; Helbig et al., 2006; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990; Tucker & Ellis, 1998, 2004; Vainio, Ellis, Tucker, & Symes, 2006), but has recently been challenged. Bub and colleagues (2010; 2008) have argued that the observer must actually have the intention of interacting with the objects being shown for their associated motor knowledge to become activated. Though controversial, this argument has some support. It has been shown that the recognition of a manipulable object involves different neural processes depending on whether and how an observer plans to interact with it (Chao & Martin, 2000; Fagioli, Hommel, & Schubotz, 2007; Grèzes & Decety, 2001; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003).

In the attempt to reconcile their findings with the literature Bub and colleagues (2010; 2008) have pointed out that these studies did not always involve the passive viewing of manipulable objects. Many of these studies required the participants to perform some kind of motor task related to the objects' identities, such as making a point, reach, or grasp movement. They argue that it was this motor task, not the passive viewing of stimuli, which triggered the object's interaction knowledge.

Though this is clearly still a rather contentious issue, these findings potentially indicate that the motor knowledge associated with the current study's prime and target stimuli may not have become activated due to the study's design. Our participants were not required to plan or execute any hand movements regarding the identity of the objects being shown. In fact, the participants were instructed to remain still and only move their right-index and right-middle fingers to

make the categorization responses. If intent truly does play such an important role in the activation of motor knowledge, then this may have contributed to the lack of significant functional-interaction priming effects observed in this study. Further research is required to determine the importance of the observer's intentions on the activation of action knowledge.

6.5.6. Previously Identified Factors

In the previous study identity specificity (Chapter 5.5.1.), spatial-frequency (Chapter 5.5.2.), and color diagnosticity (Chapter 5.5.3.) were identified as being important for color-associate priming. This makes it seem possible that similar factors would be important for functional-interaction priming. However, within the relatively much larger body of research on this subject no study has identified these factors as being particularly important. Secondly, functional-interaction priming effects found for the animated pantomime-hands of Experiment 1B approached statistical significance without taking these factors into consideration. Though it may be possible that one or more of these factors had a greater influence on the non-animated primes than the animated primes, such an interaction seems unlikely.

6.5.7. Conclusions

No evidence was found suggesting that the visual recognition of tool objects was facilitated by the prior visual presentation of information regarding their functional-interaction. Using a more conservative design than Mounoud et al. (2007), the current study only produced marginally significant thematic priming effects using animated pantomime-hands depicting the functional usage of tools. It

was predicted that this form of priming could occur using non-animated stimuli of hands in the canonical postures required for functional interaction with various tools, but no evidence of this was found.

Numerous factors may have potentially contributed to this outcome including the small number of participants, the participants' lack of a sense of ownership for the hand stimuli that were used, the fact that the hand postures selected may not accurately depict the canonical functional-interaction postures required for using the tools included in this study, the fact that the hand and tool stimuli were not always appropriately aligned, and the fact that the participants were not required to perform any hand movements associated with the stimuli being shown. Within the larger framework of the theory of modality grounded cognition, these results seem to suggest that concept knowledge for manipulable objects may involve areas that process associated forms of visual-motion, but perhaps not areas that process information about hand posture.

7. GENERAL DISCUSSION

Object concepts are highly perceptual in nature. Each individual concept includes all the information that is associated with a particular category of objects. As detailed in Chapter 1.1. this knowledge is represented by a complex pattern of activity distributed throughout the various sensory and motor systems of the brain (Allport, 1985; Barsalou, 1999; Gallese & Lakoff, 2005; A. Martin, 1998; McClelland & Rumelhart, 1987; Rumelhart & McClelland, 1986). The theory of modality grounded cognition (Chapter 1.2) appears to provide the simplest and most accurate description of this inner organization of concept knowledge (Barsalou, 2008, 2010; Gibbs Jr, 2005; Jirak et al., 2010; M. Wilson, 2002). This theory states that object knowledge is encoded within the same neural areas that were involved during the perception of, or interaction with, that particular object. The current thesis provides novel behavioral support for this theory.

The aim of this thesis was to address some of the more contentious issues within the theory of modality grounded cognition (Chapter 1.3.). Specifically, the goals of the current thesis were to investigate the role of color in the grounding of object concepts, to determine if the manner in which an object is manipulated influences its grounding, and to ascertain if grounded cognition can account for abstract concepts. To meet these goals a cognitive-experimental psychology approach was used consisting of various behavioral techniques including object recognition (Chapter 2.1), priming (Chapter 2.2), and binocular rivalry (Chapter 2.3). Though the theory of modality grounded cognition states that object concepts can include information gained from any sensory modality, this thesis focuses entirely on the role of visual information.

The current thesis consists of four independently designed and conducted studies that address various aspects of the theory of modality grounded cognition. Each one of these studies has produced evidence of some degree of interactivity between knowledge and perceptual-based processing. Knowledge of previously experienced stimuli was shown to influence the perception of visual stimuli in Chapters 3 and 4, and visual stimuli were also shown to influence knowledge processing in Chapters 5 and 6. These findings complement those of prior grounded cognition research within the fields of psychology, cognitive-neuroscience, and vision science (see Barsalou, 1999).

Despite this supporting evidence, the theory of modality grounded cognition has remained controversial due to its wide spread implications for fundamental theories of knowledge and perceptual-based processing. As evidence in support of grounded cognition has recently begun to mount, so have efforts to modify it to accommodate seemingly conflicting evidence (Connell, 2007; Kemmerer & Gonzalez-Castillo, 2010; Mahon & Caramazza, 2008; Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012; Pecher, Boot, & Van Dantzig, 2011; Pezzulo et al., 2011). Often critics of grounded cognition theory have pointed to previously supported conclusions or issues that are not easily explained by the theory of modality grounded cognition. For example, an empirical study by Bedny, Caramazza, Grossman, Pascual-Leone, and Saxe (2008) found that viewing action verbs elicited greater neural responses within the posterior-lateral-temporal cortex than nouns, and this pattern of activity did not involve any visual-motion processing areas. Also, large differences in patterns of neural activity for imagery and perceptual-based processing have been found (Lotze et al., 1999; Schupp et al.,

1994; Wadsworth & Kana, 2011). In a review by Chatterjee (2010) of the evidence supporting grounded cognition for language and spatial processing it was argued that much of this data is likely misinterpreted, and the theory's inability to account for abstract concepts is an important, if not critical, theoretical flaw. Another review by Hickok (2009) argued that within the current data it remains ambiguous as to whether mirror neurons underlie action understanding in primates, therefore the widespread acceptance of mirror neurons as being strong supporting evidence for grounded cognition is fallacious.

This final chapter consists of a discussion of some of these contentious issues in light of the combined findings of Chapters 3, 4, 5, and 6. The issues addressed in this chapter include how these combined findings inform the theory of modality grounded cognition, their potential real-world applications, and the possible directions they suggest for future studies on the nature and organization of object concepts.

7.1. Evidence Supporting Grounded Cognition

The findings presented within this thesis appear to support the theory of modality grounded cognition, which states that object knowledge is encoded within the same neural areas that were involved during the perception of that object. Though previous research has already provided evidence supporting various aspects of this theory (Chapter 1.2), significant issues remain. In particular, how grounded cognition can account for abstract concepts remains unclear. This uncertainty, along with the fact that grounded cognition greatly departs from

contemporary theories of the nature and organization of concept knowledge, has lead to its criticism and subsequent rejection by many researchers (Adams, 2010; Fodor & Pylyshyn, 1988; Longo, 2009; Mahon & Caramazza, 2008). The current studies seem to address some of these criticisms through demonstrating the perceptual nature of color knowledge, showing that object-interaction knowledge is motion based, and most importantly providing a potential resolution to the problem of abstract concepts.

7.1.1. Color Grounding

In Chapter 4 it is shown that color imagery can influence subsequent color perception and in Chapter 5 it is shown that object recognition can be primed using known color associates. Together these findings show in two different ways that the activation of color knowledge has perceptual consequences similar to that of color perception. This provides new evidence that color knowledge is grounded within perceptual color processing systems, as this similarity is likely attributable to the overlap in neural processing of color knowledge and color perception proposed by prior studies (Chapter 1.2.2). Unfortunately some of these studies have employed inappropriate or suboptimal experimental designs for the investigation of potential interactions between knowledge and perceptual-based processing, which is likely the cause of much of the conflicting evidence within the color grounding literature.

Various methodologies have been used to investigate the neural processing of color knowledge. For example, in an experiment conducted by Howard et al. (1998) participants made judgments on the relative color brightness of known

objects. Consequently, it seems likely that their participants may have focused entirely on the relative luminance of the objects, disregarding the colors entirely. Shuren et al. (1996) employed a similar color brightness judgment task, as well as a color naming task wherein participants were required to recall the canonical color of various known objects. Also used by Goldenberg et al. (1995) and Martin and colleagues (1999; 1995), these kinds of naming tasks obviously require knowledge of object-color associations, but do not necessarily require any perceptual color processing; performance may be entirely based upon associative links between the names of the objects and their colors. The biggest problem with these kinds of semantic methodologies is that they fail to include any actual perception of color, making it impossible to determine if color knowledge and color perception involve similar neural mechanisms. However, the studies within this thesis include the use of both components, allowing for the observation of direct interactions between color knowledge and perceptual-based processing. The findings of these studies are discussed below.

Chapter 4 shows how color knowledge can interact with color perception. In this study participants were required to generate the visual mental image of a color upon seeing a corresponding word cue. This was followed by a binocular rivalry stimulus (Chapter 2.3) wherein the previously imagined color and its opposite were perceptually presented to different eyes. As mental imagery is based upon knowledge of prior perceptual stimuli (Chapter 1.2.1), and the previously imagined color tended to perceptually dominate during rivalry, this result seems to show that color knowledge can directly interact with perceptual color processing.

Chapter 5 shows how color perception can interact with color knowledge. In this study the participants passively viewed six differently colored Gaussian stimuli. This was followed by an object recognition task (Chapter 2.1) using achromatic fruit stimuli, some of which were strongly associated with a specific color. As the only possible link between the pure-color Gaussian stimuli and the achromatic fruit stimuli is knowledge of these color associations gained from prior experience, and the recognition of these color diagnostic fruits was primed by their known color associates, this result seems to show that color perception can directly interact with color knowledge processing.

Based upon these findings, the processing of color knowledge and color perception appear to be highly interactive. This high degree of interactivity is likely the result of these two processes sharing similar neural mechanisms, as the previous neuroimaging and behavioral research have suggested (Chapter 1.2.2). Additional support for this conclusion has been provided by those prior studies using methodologies allowing for the direct comparison of color knowledge and perceptual color processing (see Hsu et al., 2011). When combined these current and previous findings offer compelling evidence that color is grounded within perceptual processing systems.

Additional support for this conclusion comes from perceptual learning research. Numerous studies have demonstrated that perceptual learning appears to be specific to various stimulus features including retinotopic location and orientation (Ahissar & Hochstein, 1997; Crist, Kapadia, Westheimer, & Gilbert, 1997; Fiorentini & Berardi, 1980; Nishina, Seitz, Kawato, & Watanabe, 2007; Seitz et al., 2005). Specificity for such basic stimulus features implicates the involvement

of the low-level visual systems which process them (Ahissar & Hochstein, 1996; Fahle, 2005; Watanabe et al., 2002), and likely occurs by way of changes in the physical connections between neurons within these areas. Synaptic changes are widely believed to be the underlying mechanism of all kinds of learning (Fanselow & Poulos, 2005; Geinisman, 2000; Gilbert, Sigman, & Crist, 2001), and evidence showing that perceptual learning can also be color specific (Özgen, 2004) provides a clear mechanism through which color perception may directly influence color knowledge. The proposition that physical links between neurons processing very basic stimulus features can occur has the potential to explain the current results and is the fundamental idea of the theory of modality grounded cognition.

7.1.2. Manipulable Object Concepts

It is well known that the perception of manipulable objects and their associated actions involve complex patterns of activity throughout the brain (Chapter 1.2.3). These patterns of activity are known to involve processing within both ventral and dorsal stream areas (Chapter 1.1.1). Evidence of a correspondingly large degree of overlap in their processing has been found using visually presented tools and hands (Bracci, 2011; Bracci et al., 2010). As described in Bracci, Cavina-Pratesi, Ietswaart, Caramazza, and Peelen (2012), visually presented hands and tools activate highly overlapping regions within the left lateral occipitotemporal cortex. This neural area is found within the ventral processing stream, which is known to process visual shape information. Based on this finding of a neural overlap between hand and tool concepts, and the previous finding that tool images can prime the mimicry of associated tool-use hand postures (Bub &

Masson, 2006), it was predicted that the visual presentation of hands depicting the canonical posture required for functional tool-use could prime the recognition of corresponding tool objects. The current data do not support this prediction.

In Chapter 6 the non-animated hand postures were found to be insufficient for the priming of visual recognition for tools; only the animated hand postures showed any indication that this kind of thematic priming may be possible. This appears to indicate that the most important visual component of manipulable object concepts may be the information regarding the motions associated with their canonical use. Consequently, such concepts are not grounded in the same visual areas as non-manipulable object concepts; these concepts are most likely grounded within the motion-sensitive areas of the dorsal stream. Some support for this conclusion has been provided by neuroimaging studies (Buxbaum et al., 2006; Choi et al., 2001; Creem-Regehr & Lee, 2005; Fang & He, 2005; Frey, 2007; Hermsdörfer et al., 2007; Mahon et al., 2010; Vingerhoets, 2008), but how and why the motor cortex will show activity when no actual motion is being perceived is unclear.

Implied motion may offer an explanation. It may be the case that because tools are so strongly associated with certain kinds of motion their mere perception implies movement. This could explain the previously discussed evidence of activity within motor areas during the perception of non-moving tools, as it has been shown that implied motions are also processed by motor cortex areas (Kourtzi & Kanwisher, 2000; Krekelberg, Vatakis, & Kourtzi, 2005; Winawer, Huk, & Boroditsky, 2008). However, the still-frame photographic stimuli used in these studies tend to depict actors undergoing real motion and include various motion

cues (e.g. motion blur), yet the tool stimuli used in the current study do not. The backgrounds were removed from all of the photographs, and none of the tool stimuli were shown being manipulated by an actor. Therefore, it seems unlikely that implied motion can explain these data.

Mirror neuron research can perhaps offer a better explanation (Chapter 6.5.1). It has traditionally been thought that mirror neurons are innate or hardwired within the brain (Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), however evidence has started to build against this assumption. Tool-use mirror neurons have now been found in monkey and human subjects (Arbib, Bonaiuto, Jacobs, & Frey, 2009; Ferrari, Rozzi, & Fogassi, 2005; Rochat et al., 2010; van Elk, van Schie, & Bekkering, 2011). These studies do not support the innateness assumption of mirror neurons, because experience is obviously required to understand how to properly use tools. In a recent review by Cook (2012) it was argued that these kinds of studies have demonstrated the fact that mirror neurons gain their properties from prior sensorimotor experiences. Based on this argument it seems rather likely that these sensorimotor experiences could include strong links between an object's canonical motion and shape information, thus resulting in the reciprocal activation of one kind of information when the other becomes activated. This may be the mechanism through which manipulable object knowledge can be grounded within motion processing areas but accessible through shape perception.

7.1.3. Abstract Concepts

In Chapter 3 it is demonstrated for the first time that a voluntarily generated

mental imagery stimulus can become associated with a visual perceptual stimulus using a classical conditioning methodology, and in Chapter 4 it is demonstrated that the generation of color imagery can influence subsequent color perception. These novel findings provide compelling new evidence of the perceptual nature of voluntary mental imagery, and correspond well with recent research in this field (Chapter 1.2.1). Despite the arguments of many early associative learning and imagery researchers (Pylyshyn, 1973, 1981; Skinner, 1977; Watson, 1913), the current findings clearly show that a stimulus does not need to be physically present in order for it to undergo classical conditioning. This has profound implications for theories of associative learning – which are discussed in chapters 3.5.2 and 7.5.1 – and potentially provides a resolution to a major problem with the theory of modality grounded cognition: how abstract concepts are represented within the brain (Chapter 1.2).

Abstract concepts, such as love or justice, have no inherent sensory or motor information. This makes them hard to reconcile with the theory of modality grounded cognition, which states that object knowledge is stored within the same neural areas that are involved in the perception or interaction with that object. However, recent evidence has suggested that abstract concepts may be grounded within modality specific systems (see Casasanto, 2011). For example, Casasanto and colleagues (2009; 2011; 2012) have found differences between right and left-handers in the meanings of positive and negative abstract concepts; right-handers associated “good” concepts (e.g. honesty) with their right side and bad concepts (e.g. deceit) with their left side, while left-handers had the opposite pairings. The participants appeared to have embodied these abstract concepts by “mapping”

them relative to their own bodies. This appears to show that abstract concepts can involve activity within perceptual and motor areas, yet how they come to be grounded within these modality-specific systems remains unclear.

We propose that the modality grounding of abstract concepts occurs through simple associative learning. As demonstrated in the classic studies by Ivan Pavlov (see Pavlov, 2003), a perceptual stimulus can gain new meaning by being paired with another one that is inherently meaningful. If this basic principle of learning is applied to abstract concepts it would suggest that their meaning arises from the formation of associative links with multiple objects or events. Consequently, the neural representation of an abstract concept should involve a complex pattern of activity determined by its associated objects or events. The current findings support this potential framework through which abstract concepts gain their meaning by showing that associative links can form between stimuli that are never physically presented together.

This possibility seems especially likely as previous research has suggested that abstract concepts may gain their meaning by being situated within an inherently meaningful context (Barsalou & Wiemer-Hastings, 2005; Pecher et al., 2011). As no stimulus is experienced in isolation, it is highly likely that the neural representation of every concept includes information regarding its associated context. As current research has shown that similar concepts are represented by overlapping patterns of neural activity (Chapter 1.1) the grounding of concept knowledge within modality specific systems does not require or suggest that concepts include unique and discrete information regarding their meaning. Many concepts may simply consist of combinations of various aspects of other concepts

(e.g. platypus).

Associative links have been observed to rapidly and automatically form between objects and their associated perceptual and motor-based information, even when that information does not directly arise from the object itself. This simple observation appears to be applicable to both abstract and concrete concepts, and is in fact central to models of spreading activation (Collins & Loftus, 1975), and thematic categorization (Chapter 1.1.2). The theory of modality grounded cognition should therefore be improved by taking into account the information gained from situational context.

7.2. Applications

Though the primary aim of this thesis was to address theoretical issues of modality grounded cognition, the presented findings have some clear real-world applications. In particular, the results of Studies 1 and 3 show great potential for advancements in the applied sciences. Though it is quite probable these findings could be applied in numerous ways, the two most obvious applications consist of the advancement of computer vision technology and the improvement of current treatment methods for anxiety disorders. A detailed discussion of how the current findings are suited for such applications has been provided.

7.2.1. Treatments of Anxiety

The current findings provide new insight and suggestions for potential treatment methods of various anxiety disorders and phobias. In Chapters 3 and 4 it is demonstrated that mental imagery has many of the same qualities as visual

perceptual stimuli. These findings implicate the involvement of low-level visual processing areas, which further supports previous mental imagery research suggesting that visual imagery and visual perception involve largely similar neural processing (Chapter 1.2.1). Regarding treatments of anxiety, these conclusions indicate that associative learning may offer the best explanation of highly effective treatment methodologies, and also some suggestions for their improvement.

Anxiety disorders are often modeled on fear learning (Lissek et al., 2005; Milad et al., 2006; Rauch, Shin, & Phelps, 2006; Rosen & Schulkin, 1998; Watson & Rayner, 1920), a type of associative learning wherein a pleasant or neutral stimulus will come to elicit fearful responses after being paired with an aversive stimulus (Öhman & Mineka, 2001). After undergoing this form of associative learning anxiety sufferers tend to engage in inappropriately fearful behaviors during mundane events. Often these behavioral symptoms are preceded or amplified by distressing mental images (Hirsch, Mathews, Clark, Williams, & Morrison, 2006; Holmes, Geddes, Colom, & Goodwin, 2008; Holmes & Mathews, 2010; Pitman et al., 1990). For most individuals this imagery tends to be automatically cued by external stimuli and are related to the individual's specific fears or concerns (Albright, 2012; Brewin, Gregory, Lipton, & Burgess, 2010; Dadds, Hawes, Schaefer, & Vaka, 2004; Hirsch & Holmes, 2007; Holmes & Mathews, 2010).

Distressing mental imagery has been identified as playing a key role in the maintenance of many anxiety disorders (Hackmann, Clark, & McManus, 2000; Hirsch & Holmes, 2007). Accordingly, the most effective treatment methods tend to focus on this anxiety producing imagery (Edwards, 2007; Holmes & Mathews, 2010). One such treatment is cognitive behavior therapy with imagery rescripting

(Arntz, Tiesema, & Kindt, 2007; Holmes, Arntz, & Smucker, 2007; Smucker, Dancu, Foa, & Niederee, 1995), wherein patients are directed to focus on and then transform the content of their emotionally distressing mental imagery into something pleasant or less upsetting. This kind of treatment method seems to be more effective than verbal techniques (Kosslyn et al., 2001; Kreiman et al., 2000) and is generally found to be effective for anxiety sufferers (Bradley, Greene, Russ, Dutra, & Westen, 2005; Foa & Meadows, 1997; Harvey, 2003), though there is still much room for improvement. An explanation of the inner mechanisms driving these treatments would assist in development of more effective treatments.

As fear learning is the driving force of many anxiety disorders, fear extinction is likely the driving force of these imagery-based treatments. During fear extinction the learned association between the distressing stimulus and the previously neutral stimulus is “unlearned” (Hermans et al., 1994). Also known as counter-conditioning, during this extinction process the patient is exposed to the anxiety producing stimuli while in a setting that assists in the reduction of inappropriate behavioral symptoms (Holmes & Mathews, 2010; Hunt & Fenton, 2007). As extinction is merely a form of associative learning that results in the weakening of previously formed associative links, the underlying mechanism of effective treatments of anxiety appears to simply be the active and repeated demonstration that the patient’s fear-inducing stimuli are not necessarily associated with anxiety producing experiences. The more focused application of this fear extinction has the potential to improve their efficacy.

The current findings show that mental imagery and perception undergo largely the same mental processing, therefore it is likely that the effectiveness of

these imagery-based treatments could be enhanced by focusing on the low-level sensory aspects of the distressing mental imagery symptoms. More effective treatments could be produced that directly apply a fear extinction methodology to the individual stimulus features of the distressing mental imagery (e.g. shapes, colors, sounds, smells). Support for this proposal comes from the recent finding that the presentation of stimuli that engage low-level perceptual systems, not high-level semantic systems, can aid in preventing the formation of distressing flashbacks after experiencing a traumatic event (Holmes, James, Kilford, & Deepprose, 2010).

Suggesting that imagery-based treatments could be improved by focusing on the imagery's low-level perceptual qualities is especially exciting given that previous work has shown ways to modify mental imagery strength (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). This modifiability enables imagery-based treatments to be catered to the specific needs of each individual undergoing such treatments, such as reducing the vividness of exceptionally distressing mental images. If applied, these practices have the potential to produce far better treatment outcomes for sufferers of anxiety.

7.2.2. Computer Vision

Despite great advancements in computer science and technology the human visual recognition system remains vastly superior to that of any artificial systems developed thus far. Humans and most other animals have the ability to quickly and accurately recognize objects despite large changes in their illumination, size, orientation, surface features, and even shape. The creation of

artificial visual systems that match or surpass these capabilities is a very attractive goal as they would have numerous potential applications including the development of advanced visual systems for medical professionals, robotic vision for industrial and military use, the production of visual prostheses, and for various entertainment purposes. Perhaps the greatest difficulty these computer scientists and engineers face in accomplishing their goal is due to the fact they are attempting to emulate something that is not currently well understood. Accordingly, discoveries within the fields of vision science, neuroscience, and cognitive psychology can help to direct efforts toward the development of advanced computer vision systems. This thesis offers some suggestions in this regard.

In Chapter 5 the importance of color towards the fast and accurate recognition of certain objects was shown. These objects consisted of different kinds of fruits that are widely known to be high in color diagnosticity (Chapter 1.2.2). As color is clearly an important visual feature for objects such as these, arguments have been made to include color within computer models of object recognition (Mel, 1997; Swain & Ballard, 1991). Unfortunately mainstream computational approaches generally place little to no emphasis on object color information (Dalal & Triggs, 2005; Leibe et al., 2008; Lowe, 1999, 2000; Paragios, Chen, & Faugeras, 2010; Szeliski, 2010; Zhu, Yeh, Cheng, & Avidan, 2006). Consequently, the currently presented findings suggest that object recognition by computers could be improved by taking the diagnostic information provided by object colors into account. Yet color is obviously only diagnostic for certain kinds of objects. Therefore computational object recognition models could be improved through the addition of a module that determines if color information should be

utilized based on early estimates of the object's category – only if it contains color diagnostic objects should the object's color be utilized during recognition.

In Chapter 6 it is found that the recognition of manipulable objects can be primed using stimuli depicting the visual motion and posture associated with their use. Yet stimuli that only depicted the visual posture of the hands – not their movement – were found to be ineffective as primes. This finding has relevance to the great deal of research that has been conducted regarding how humans interact with objects and whether these forms of interaction can assist in object recognition. In general it has been shown that action and object recognition can be improved when contextual factors such as body shape and movement are taken into consideration (Gupta & Davis, 2007; Gupta, Kembhavi, & Davis, 2009; Yao & Fei-Fei, 2010). The current data expand upon these findings by suggesting that actual visual motion, not implied motion or hand or body postures, is the most important visual feature associated with the recognition of manipulable objects. Perhaps computational object recognition could therefore be improved by producing algorithms that primarily focus on the movements of objects and their effecters.

7.3. Future Research

The findings presented within this thesis offer some suggestions for future vision science studies. While there are numerous lines of research that could be conducted based upon the currently presented findings, a few important issues have been identified that necessitate investigation. These issues include whether there are any important differences between mental imagery and perception

regarding associative learning, exactly how color interacts with other surface features for object recognition, and exactly what kind of visual motion information is most strongly associated with manipulable objects.

7.3.1. Associative Learning for Mental Imagery

Associative learning can occur for mental imagery stimuli (Chapter 3). This finding is supported by an increasing large body of cognitive neuroscientific research that has shown perceptual systems are not only involved in the processing of incoming sensory signals but also in processing the sensory qualities of previously perceived stimuli that are brought to mind (Chapter 1.2.1). However, many of these prior researchers have not fully embraced, or even acknowledged, the theory of modality grounded cognition. Regardless, these prior studies and those contained within the current thesis have demonstrated that perceptual processing and the knowledge based processing of mental imagery are largely overlapping. Unfortunately the extent of this overlap remains unclear.

While much has been learned about associative learning for perceptual stimuli (De Houwer et al., 2001; I. Martin & Levey, 1978; Milad et al., 2006), relatively little is known about associative learning for mental imagery. It seems rather likely that the strength of the associative links developed using mental imagery may be different from that of perceptual stimuli. As mental imagery appears to act like weak perception (Pearson et al., 2008), it seems highly probable that the strength of these links will be similarly weak. Yet it is also known that individuals can differ greatly in their ability to generate mental images (Cui et al., 2007; Kosslyn et al., 1984; Pearson et al., 2011). Therefore, it seems possible

that highly skilled imagers may have the ability to form associative links with mental imagery that are as strong or stronger than when using perceptual stimuli. Future studies should be conducted to measure the relative strength of the associative links formed using mental imagery and to determine if this strength correlates with an individual's mental imagery ability.

Another potential line of research lies in the determination of whether or not there are any limits to the kinds of mental imagery that can undergo associative learning. Generating a mental image is fundamentally different from the observation of a perceptual stimulus. Focused effort is required to voluntarily create and maintain a mental image, whereas perception is largely passive and will occur automatically upon stimulus sensation (Albright, 2012). Consequently, highly complex or detailed mental images may be too difficult to maintain for associative learning purposes. Additionally, as mental imagery research is still in its infancy it remains to be seen whether mentally generated stimuli can possess all the sensory qualities found in normal perceptual stimuli. It may be the case that certain perceptual features of mental imagery can undergo associative learning (e.g. shape, orientation, and color), while others cannot. A more complete understanding of how mental imagery is processed within perceptual systems would aid in addressing these open issues.

7.3.2. Bayesian Models and Color Associate Priming

In Chapter 5 it is predicted that the strongest color associate priming effects would be observed when the high spatial-frequencies were removed from the target photographs. This prediction was based upon previous research (Laws &

Hunter, 2006; J. W. Tanaka & Presnell, 1999; Yip & Sinha, 2002) showing that the inclusion of an object's surface features, such as color or luminance, will most greatly facilitate object recognition when the object's shape information has been blurred or degraded (Chapter 2.1.1). However, color associate priming was found for low spatial-frequency only photographs and normal photographs, which contain all spatial-frequencies (including high). Furthermore, a larger amount of significant effects were found using the normal photographs than the low spatial-frequency photographs. As the strongest color-associate priming was found for the normal photographs, which have fully intact shape and texture information, these findings cannot be explained by the Bayesian models our predictions were based on.

Bayesian models of object perception (Kersten, 2003; Kersten, Mamassian, & Yuille, 2004; Mamassian, Landy, & Maloney, 2002) assert that incoming visual information is compared to visual object knowledge in order to determine the most probable identity of the object being perceived. This process of comparison attempts to match across all of the perceived object's visual features, such as shape, luminance, texture, and color. If one or more of these visual features are degraded or not present within the object's image (e.g. shape) a greater amount of emphasis will be placed upon other visual features (e.g. color). Therefore it was predicted that removing the high spatial-frequency shape and texture information would allow the color primes to exert a stronger facilitatory influence on visual recognition of the color-diagnostic fruits used in the current study.

As explained in Chapter 5.5.2 the current data do not fit with this prediction. This result appears to suggest that the processing involved in color associate priming is different from that of normal object recognition. Neuroimaging studies

are required to determine exactly how similar these two neural processes are, but the current findings seem to indicate that color associate priming is tuned to low spatial-frequencies; it is driven by the objects' low spatial-frequency luminance information. In this form of priming perceptual colors appear to be maximally influential when the objects' low spatial-frequencies remain intact. As low spatial-frequencies are known to typically be processed before high spatial-frequencies during object recognition (Navon, 1977; Parker, Lishman, & Hughes, 1992; Schyns & Oliva, 1994), a possible explanation for this result may be that color associate priming exerts the majority of its influence during the earliest stages of object recognition. If evidence were found in support of this explanation it would suggest that spatial frequency information plays a very important role in the organization of object concepts. Since the current study offers only tentative evidence of this possibility further investigation is required.

7.3.3. Visual Motion Information

In Chapter 6 marginally significant functional-interaction priming effects were found for the animated pantomime-hand primes, while the non-animated primes did not appear to show any effects whatsoever. This appears to indicate that manipulable object concepts may be more grounded within systems that process visual-motion information than those that process visual-form. Future studies could test this suggestion by using prime stimuli consisting only of visual-motion, such as dot-motion stimuli (Britten, Shadlen, Newsome, & Movshon, 1992; Smith & Ratcliff, 2004). However, this priming may instead be driven by a combination of factors, such as visual shape and motion. If so, then significant

effects should only be observable when using more complex stimuli, such as the point-light walkers described by Johansson (1973). Evidence of functional-interaction priming using such stimuli has the potential to conclusively explain the role of visual-motion information on the grounding of manipulable object concepts.

Additionally, the lack of significant effects observed in this study may have simply been due to the age of the participants. Mounoud et al. (2007) showed that age correlates negatively with these kinds of pantomime tool-recognition priming effects. Therefore, perhaps the use of a younger group of participants would produce significant effects for both the animated and the non-animated pantomime hand primes used in this study. As these non-animated primes inherently convey less information than the animated primes it seems rather likely that their effects would correlate differently with participant age. It may very well be that animated pantomime primes can be effective for participants of all ages while non-animated pantomime primes are only effective for the youngest of participants. Developmental studies investigating this potential interaction between visual-motion information and participant age would help to explain how manipulable object concepts change over an individual's lifetime.

7.4. General Conclusions

Object concepts are perceptually based. In many ways this thesis has demonstrated that the neural processing of visual perception and visual knowledge are directly interactive. The results of four independently designed and conducted studies demonstrate that the prior knowledge of visual stimuli can undergo

associative learning with perceptual stimuli, visual color knowledge can influence perceptual color processing, color-diagnostic object concepts can be activated through the perception of their associated colors, and manipulable object concepts might be able to become activated through the visual perception of associated movements. Together these findings have provided a compelling argument for the grounding of object knowledge within modality specific systems.

While the idea that knowledge and perception share largely the same neural mechanisms is not at all new (Epicurus, 1987), in recent years there has been an explosion of interest in the theory of modality grounded cognition. Unfortunately many of these studies have used inappropriate or sub-optimal methodologies. Yet the aim of this thesis was not to conduct a comprehensive critical review of the previous literature, as many such reviews have recently been published (Barsalou, 2008, 2010; Pezzulo et al., 2011). Instead the goal of this thesis was to address some of the contentious issues with the theory of modality grounded cognition and to provide a resolution to what is perhaps the largest issue that is preventing widespread acceptance of the theory – abstract concepts.

The theory of modality grounded cognition – also known as embodied cognition – appears to offer an accurate description of the nature and organization of concept knowledge within the human brain. Mainstream acceptance of this theory has the potential to unify what are commonly thought to be disparate findings produced within various fields of scientific investigation. In particular, the theory of grounded cognition has clear applications within neuroscience, cognitive psychology, clinical psychology, and computer science. The primary contribution of

this thesis to research on modality grounded cognition is the description of a simple mechanism through which abstract concepts may gain their meaning.

REFERENCES

- Adams, F. (2010). Embodied cognition. *Phenomenology and the Cognitive Sciences*, 9(4), 619-628. doi: 10.1007/s11097-010-9175-x
- Ahissar, M., & Hochstein, S. (1996). Learning pop-out detection: Specificities to stimulus characteristics. *Vision Research*, 36(21), 3487-3500.
- Ahissar, M., & Hochstein, S. (1997). Task difficulty and the specificity of perceptual learning. *Nature*, 387(6631), 401-406.
- Albright, T. D. (2012). On the perception of probable things: Neural substrates of associative memory, imagery, and perception. *Neuron*, 74(2), 227-245.
- Allen, G. (1879). *The colour-sense: Its origin and development*. London: Trübner & Co.
- Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In S. K. Newman & R. Epstein (Eds.), *Current perspectives in dysphasia* (pp. 207-244). New York: Churchill Livingstone.
- Almeida, J., Mahon, B. Z., & Caramazza, A. (2010). The role of the dorsal visual processing stream in tool identification. *Psychological Science*, 21(6), 772-778. doi: 10.1177/0956797610371343
- Almeida, J., Mahon, B. Z., Nakayama, K., & Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proceedings of the National Academy of Sciences*, 105(39), 15214-15218. doi: 10.1073/pnas.0805867105
- Alpers, G., & Pauli, P. (2006). Emotional pictures predominate in binocular rivalry. *Cognition & Emotion*, 20(5), 596-607.
- Anelli, F., Nicoletti, R., Kalkan, S., Sahin, E., & Borghi, A. M. (2012, 10-15 June 2012). *Human and robotics hands grasping danger*. Paper presented at the Neural Networks (IJCNN), The 2012 International Joint Conference on.
- Annett, M. (1959). The classification of instances of four common class concepts by children and adults. *British Journal of Educational Psychology*, 29(3), 223-236. doi: 10.1111/j.2044-8279.1959.tb01503.x
- Arbib, M. A., Bonaiuto, J. B., Jacobs, S., & Frey, S. H. (2009). Tool use and the distalization of the end-effector. *Psychological Research*, 73(4), 441-462. doi: 10.1007/s00426-009-0242-2
- Arévalo, A., Perani, D., Cappa, S. F., Butler, A., Bates, E., & Dronkers, N. (2007). Action and object processing in aphasia: From nouns and verbs to the effect of manipulability. *Brain and Language*, 100(1), 79-94.
- Arntz, A., Tiesema, M., & Kindt, M. (2007). Treatment of PTSD: A comparison of imaginal exposure with and without imagery rescripting. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 345-370. doi: 10.1016/j.jbtep.2007.10.006
- Assmus, A., Giessing, C., Weiss, P. H., & Fink, G. R. (2007). Functional interactions during the retrieval of conceptual action knowledge: An fMRI study. *Journal of Cognitive Neuroscience*, 19(6), 1004-1012.
- Bajo, M. T. (1988). Semantic facilitation with pictures and words. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 14(4), 579-589.
- Balsam, P. D., Drew, M. R., & Gallistel, C. R. (2010). Time and associative learning. *Comparative Cognition & Behavior Reviews*, 5, 1-22. doi: 10.3819/ccbr.2010.50001
- Barenholtz, E., & Tarr, M. J. (2006). Reconsidering the role of structure in vision. In B. M. Arthur & H. R. Brian (Eds.), *Psychology of Learning and Motivation* (Vol. Volume 47, pp. 157-180): Academic Press.
- Barlow, H. B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology. *Perception*, 1(4), 371-394.

-
- Barrett, S. E., & Rugg, M. D. (1990). Event-related potentials and the semantic matching of pictures. *Brain and Cognition*, 14(2), 201-212. doi: 10.1016/0278-2626(90)90029-n
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22(4), 577-660.
- Barsalou, L. W. (2003). Abstraction in perceptual symbol systems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 358(1435), 1177-1187. doi: 10.1098/rstb.2003.1319
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59, 617-645. doi: 10.1146/annurev.psych.59.103006.093639
- Barsalou, L. W. (2009). Simulation, situated conceptualization, and prediction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 364(1521), 1281-1289. doi: 10.1098/rstb.2008.0319
- Barsalou, L. W. (2010). Grounded cognition: Past, present, and future. *Topics in Cognitive Science*, 2(4), 716-724. doi: 10.1111/j.1756-8765.2010.01115.x
- Barsalou, L. W., Simmons, W. K., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences*, 7(2), 84-91.
- Barsalou, L. W., & Wiemer-Hastings, K. (2005). Situating abstract concepts. In D. Pecher & R. Zwaan (Eds.), *Grounding cognition: The role of perception and action in memory, language, and thought* (pp. 129-163). New York: Cambridge University Press.
- Bartolomeo, P., Bachoud-Lévi, A. C., & Denes, G. (1997). Preserved imagery for colours in a patient with cerebral achromatopsia. *Cortex*, 33(2), 369-378.
- Barton, J. J. S., & Cherkasova, M. (2003). Face imagery and its relation to perception and covert recognition in prosopagnosia. *Neurology*, 61(2), 220-225. doi: 10.1212/01.wnl.0000071229.11658.f8
- Beauchamp, M. S., & Martin, A. (2007). Grounding object concepts in perception and action: Evidence from fMRI studies of tools. *Cortex*, 43(3), 461-468.
- Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., & Saxe, R. (2008). Concepts are more than percepts: The case of action verbs. *The Journal of Neuroscience*, 28(44), 11347-11353. doi: 10.1523/jneurosci.3039-08.2008
- Behrmann, M. (2000). The mind's eye mapped onto the brain's matter. *Current Directions in Psychological Science*, 9(2), 50-54. doi: 10.1111/1467-8721.00059
- Belongie, S., Malik, J., & Puzicha, J. (2002). Shape matching and object recognition using shape contexts. *Pattern Analysis and Machine Intelligence, IEEE Transactions on*, 24(4), 509-522.
- Besner, D., Twilley, L., McCann, R. S., & Seergobin, K. (1990). On the association between connectionism and data: Are a few words necessary? *Psychological Review*, 97(3), 432-446.
- Biederman, I. (1987). Recognition-by-components: a theory of human image understanding. *Psychological Review*, 94(2), 115-147.
- Biederman, I. (1995). Visual Object Recognition. In S. M. Kosslyn & D. N. Osherson (Eds.), *Visual cognition: An invitation to cognitive science* (pp. 121-165). Cambridge, MA, US: MIT press.
- Biederman, I., & Ju, G. (1988). Surface versus edge-based determinants of visual recognition. *Cognitive Psychology*, 20(1), 38-64. doi: 10.1016/0010-0285(88)90024-2
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145-167.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3(1), 13-21. doi: 10.1038/nrn701
- Blake, R., & Tong, F. (2008). Binocular rivalry. *Scholarpedia*, 3(12), 1578. doi: 10.4249/scholarpedia.1578
- Blake, R., Yu, K., Lokey, M., & Norman, H. (1998). Binocular rivalry and motion perception. *Journal of Cognitive Neuroscience*, 10(1), 46-60.
-

-
- Blakemore, C., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *The Journal of Physiology*, 203(1), 237-260.
- Borghi, A. M., Bonfiglioli, C., Lugli, L., Ricciardelli, P., Rubichi, S., & Nicoletti, R. (2007). Are visual stimuli sufficient to evoke motor information?: Studies with hand primes. *Neuroscience Letters*, 411(1), 17-21.
- Borghi, A. M., & Riggio, L. (2009). Sentence comprehension and simulation of object temporary, canonical and stable affordances. *Brain Research*, 1253, 117-128. doi: <http://dx.doi.org/10.1016/j.brainres.2008.11.064>
- Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y., & Detre, J. A. (2005). Distinctions between manipulation and function knowledge of objects: Evidence from functional magnetic resonance imaging. *Cognitive Brain Research*, 23(2-3), 361-373.
- Bowers, J. S. (2002). Challenging the widespread assumption that connectionism and distributed representations go hand-in-hand. *Cognitive Psychology*, 45(3), 413-445.
- Bowers, J. S. (2009). On the biological plausibility of grandmother cells: Implications for neural network theories in psychology and neuroscience. *Psychological Review*, 116(1), 220-251. doi: 10.1037/a0014462
- Bowmaker, J. K. (1998). Evolution of colour vision in vertebrates. *Eye*, 12(3b), 541-547.
- Bracci, S. (2011). *Neural correlates of hand-tool interaction*. Northumbria University.
- Bracci, S., Cavina-Pratesi, C., Ietswaart, M., Caramazza, A., & Peelen, M. V. (2012). Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. *Journal of Neurophysiology*, 107(5), 1443-1456.
- Bracci, S., Ietswaart, M., Peelen, M. V., & Cavina-Pratesi, C. (2010). Dissociable neural responses to hands and non-hand body parts in human left extrastriate visual cortex. *Journal of Neurophysiology*, 103(6), 3389-3397. doi: 10.1152/jn.00215.2010
- Bradley, R., Greene, J., Russ, E., Dutra, L., & Westen, D. (2005). A multidimensional meta-analysis of psychotherapy for PTSD. *American Journal of Psychiatry*, 162, 214-227.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433-436.
- Bramão, I., Faísca, L., Forkstam, C., Inácio, F., Araújo, S., Petersson, K. M., & Reis, A. (2012). The interaction between surface color and color knowledge: Behavioral and electrophysiological evidence. *Brain and Cognition*, 78(1), 28-37.
- Bramão, I., Faísca, L., Forkstam, C., Reis, A., & Petersson, K. M. (2010). Cortical brain regions associated with color processing: An fMRI study. *Open Neuroimaging Journal*, 4, 164-173. doi: 10.2174/1874440001004010164
- Bramão, I., Faísca, L., Petersson, K. M., & Reis, A. (2010). The influence of surface color information and color knowledge information in object recognition. *The American Journal of Psychology*, 123(4), 437-446.
- Bramão, I., Inácio, F., Faísca, L., Reis, A., & Petersson, K. M. (2011). The influence of color information on the recognition of color diagnostic and noncolor diagnostic objects. *The Journal of general psychology*, 138(1), 49-65.
- Bramão, I., Reis, A., Petersson, K. M., & Faísca, L. (2011). The role of color information on object recognition: A review and meta-analysis. *Acta Psychologica*, 138(1), 244-253. doi: 10.1016/j.actpsy.2011.06.010
- Brewin, C. R., Gregory, J. D., Lipton, M., & Burgess, N. (2010). Intrusive images in psychological disorders: Characteristics, neural mechanisms, and treatment implications. *Psychological Review*, 117(1), 210-232. doi: 10.1037/a0018113
-

-
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *The Journal of Neuroscience*, 12(12), 4745-4765.
- Brown, C., & Hagoort, P. (1993). The processing nature of the N400: Evidence from masked priming. *Journal of Cognitive Neuroscience*, 5(1), 34-44. doi: 10.1162/jocn.1993.5.1.34
- Bruzzo, A., Borghi, A. M., & Ghirlanda, S. (2008). Hand-object interaction in perspective. *Neuroscience Letters*, 441(1), 61-65. doi: <http://dx.doi.org/10.1016/j.neulet.2008.06.020>
- Bub, D. N., & Masson, M. E. J. (2006). Gestural knowledge evoked by objects as part of conceptual representations. *Aphasiology*, 20(9), 1112-1124.
- Bub, D. N., & Masson, M. E. J. (2010). Grasping beer mugs: On the dynamics of alignment effects induced by handled objects. *Journal of Experimental Psychology: Human Perception and Performance*, 36(2), 341-358.
- Bub, D. N., & Masson, M. E. J. (2012). On the dynamics of action representations evoked by names of manipulable objects. *Journal of Experimental Psychology-General*, 141(3), 502.
- Bub, D. N., Masson, M. E. J., & Cree, G. S. (2008). Evocation of functional and volumetric gestural knowledge by objects and words. *Cognition*, 106(1), 27-58.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., . . . Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: an FMRI study. *Journal of Cognitive Neuroscience*, 16(1), 114-126. doi: 10.1162/089892904322755601
- Burt, J. S. (1994). Identity primes produce facilitation in a colour naming task. *The Quarterly Journal of Experimental Psychology*, 47(4), 957-1000.
- Buxbaum, L. J., Johnson-Frey, S. H., & Bartlett-Williams, M. (2005). Deficient internal models for planning hand-object interactions in apraxia. *Neuropsychologia*, 43(6), 917-929. doi: 10.1016/j.neuropsychologia.2004.09.006
- Buxbaum, L. J., Kyle, K. M., Tang, K., & Detre, J. A. (2006). Neural substrates of knowledge of hand postures for object grasping and functional object use: Evidence from fMRI. *Brain Research*, 1117(1), 175-185. doi: 10.1016/j.brainres.2006.08.010
- Buxbaum, L. J., Veramontil, T., & Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: Knowing 'what for' but not 'how'. *Neurocase*, 6(2), 83-97.
- Cabeza, R., & Nyberg, L. (1997). Imaging Cognition: An Empirical Review of PET Studies with Normal Subjects. *Journal of Cognitive Neuroscience*, 9(1), 1-26. doi: 10.1162/jocn.1997.9.1.1
- Cabeza, R., & Nyberg, L. (2000). Imaging Cognition II: An Empirical Review of 275 PET and fMRI Studies. *Journal of Cognitive Neuroscience*, 12(1), 1-47. doi: 10.1162/08989290051137585
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, 16(19), 1905-1910.
- Cant, J. S., Large, M. E., McCall, L., & Goodale, M. A. (2008). Independent processing of form, colour, and texture in object perception. *Perception*, 37(1), 57-78.
- Carr, T. H., McCauley, C., Sperber, R. D., & Parmelee, C. M. (1982). Words, pictures, and priming: On semantic activation, conscious identification, and the automaticity of information processing. *Journal of Experimental Psychology: Human Perception and Performance*, 8(6), 757-777.
- Casasanto, D. (2009). Embodiment of abstract concepts: Good and bad in right-and left-handers. *Journal of experimental psychology. General*, 138(3), 351-367.
- Casasanto, D. (2011). Different bodies, different minds: The body specificity of language and thought. *Current Directions in Psychological Science*, 20(6), 378-383.
-

-
- Casasanto, D., & Chrysikou, E. G. (2011). When left is “right”: Motor fluency shapes abstract concepts. *Psychological Science*, 22(4), 419-422.
- Casasanto, D., & Henetz, T. (2012). Handedness shapes children’s abstract concepts. *Cognitive Science*, 36(2), 359-372.
- Chainay, H., & Humphreys, G. W. (2001). The real-object advantage in agnosia: Evidence for a role of surface and depth information in object recognition. *Cognitive Neuropsychology*, 18(2), 175-191.
- Chang, S., Lewis, D. E., & Pearson, J. (in press). The functional effects of colour perception and colour imagery. *Journal of Vision*.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, 2(10), 913-919. doi: 10.1038/13217
- Chao, L. L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience*, 11(1), 25-35.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, 12(4), 478-484.
- Choi, S., Na, D. L., Kang, E., Lee, K., Lee, S., & Na, D. (2001). Functional magnetic resonance imaging during pantomiming tool-use gestures. *Experimental Brain Research*, 139(3), 311-317.
- Chwilla, D. J., Brown, C. M., & Hagoort, P. (1995). The N400 as a function of the level of processing. *Psychophysiology*, 32(3), 274-285.
- Collins, A. M., & Loftus, E. F. (1975). A spreading-activation theory of semantic processing. *Psychological Review*, 82(6), 407-428. doi: 10.1037/0033-295x.82.6.407
- Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: a dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, 108(1), 204-256.
- Connell, L. (2007). Representing object colour in language comprehension. *Cognition*, 102(3), 476-485.
- Cook, R. (2012). The ontogenetic origins of mirror neurons: Evidence from 'tool-use' and 'audiovisual' mirror neurons. *Biol Lett*, 8(5), 856-859. doi: 10.1098/rsbl.2012.0192
- Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., & Committeri, G. (2010). Where does an object trigger an action? An investigation about affordances in space. *Experimental Brain Research*, 207(1-2), 95-103.
- Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia*, 40(5), 492-502.
- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. A. (1998). Visuomotor priming. *Visual Cognition*, 5(1-2), 109-125. doi: 10.1080/713756780
- Craighero, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *NeuroReport*, 8(1), 347-349.
- Creem-Regehr, S. H., & Lee, J. N. (2005). Neural representations of graspable objects: Are tools special? *Cognitive Brain Research*, 22(3), 457-469.
- Crist, R. E., Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. *Journal of Neurophysiology*, 78(6), 2889-2894.
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: Individual variability can be measured objectively. *Vision Research*, 47(4), 474-478.
-

-
- Culham, J. C., Danckert, S. L., DeSouza, J. F. X., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, 153(2), 180-189.
- D'Ausilio, A., Pulvermüller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The motor somatotopy of speech perception. *Current Biology*, 19(5), 381-385. doi: 10.1016/j.cub.2009.01.017
- D'Zmura, M., & Lennie, P. (1986). Mechanisms of color constancy. *Journal of the Optical Society of America A*, 3(10), 1662-1672.
- Dadds, M., Bovbjerg, D., Redd, W., & Cutmore, T. (1997). Imagery in human classical conditioning. *Psychological Bulletin*, 122, 89-210.
- Dadds, M., Hawes, D., Schaefer, B., & Vaka, K. (2004). Individual differences in imagery and reports of aversions. *Memory*, 12(4), 462-466. doi: 10.1080/09658210444000070
- Dakin, S. C., Hess, R. F., Ledgeway, T., & Achtman, R. L. (2002). What causes nonmonotonic tuning of fMRI response to noisy images? *Current Biology*, 12(14), R476-R477.
- Dalal, N., & Triggs, B. (2005, 25-25 June 2005). *Histograms of oriented gradients for human detection*. Paper presented at the Computer Vision and Pattern Recognition, 2005. CVPR 2005. IEEE Computer Society Conference on.
- Damian, M. F., & Rahman, R. A. (2003). Semantic priming in the name retrieval of objects and famous faces. *British Journal of Psychology*, 94(4), 517-527.
- De Houwer, J., Thomas, S., & Baeyens, F. (2001). Associative learning of likes and dislikes: A review of 25 years of research on human evaluative conditioning. *Psychological Bulletin*, 127, 853-869.
- De Vreese, L. P. (1991). Two systems for colour-naming defects: Verbal disconnection vs colour imagery disorder. *Neuropsychologia*, 29(1), 1-18. doi: 10.1016/0028-3932(91)90090-u
- Decety, J., & Grèzes, J. (2006). The power of simulation: Imagining one's own and other's behavior. *Brain Research*, 1079(1), 4-14. doi: 10.1016/j.brainres.2005.12.115
- Dekker, T., Mareschal, D., Sereno, M. I., & Johnson, M. H. (2011). Dorsal and ventral stream activation and object recognition performance in school-age children. *NeuroImage*, 57(3), 659-670. doi: 10.1016/j.neuroimage.2010.11.005
- den Heyer, K., Briand, K., & Dannenbring, G. (1983). Strategic factors in a lexical-decision task: Evidence for automatic and attention-driven processes. *Memory & Cognition*, 11(4), 374-381. doi: 10.3758/bf03202452
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91(1), 176-180.
- Edwards, D. (2007). Restructuring implicational meaning through memory-based imagery: Some historical notes. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 306-316. doi: 10.1016/j.jbtep.2007.10.001
- Ellis, R., & Tucker, M. (2000). Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology*, 91(4), 451-471.
- Epicurus. (1987). Sensation, imagination, and memory. In A. A. Long & D. N. Sedley (Eds.), *The Hellenistic Philosophers* (Vol. 1, pp. 72-101). New York: Cambridge.
- Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: recognition, navigation, or encoding? *Neuron*, 23, 115-125.
- Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, 392(6676), 598-601.
- Estes, Z., Golonka, S., & Jones, L. L. (2011). Thematic thinking the apprehension and consequences of thematic relations. In B. H. Ross (Ed.), *The Psychology of Learning and Motivation* (Vol. 54, pp. 249-294): Elsevier.
-

-
- Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, 23(3), 171-179.
- Fagioli, S., Ferlazzo, F., & Hommel, B. (2007). Controlling attention through action: Observing actions primes action-related stimulus dimensions. *Neuropsychologia*, 45(14), 3351-3355. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2007.06.012>
- Fagioli, S., Hommel, B., & Schubotz, R. I. (2007). Intentional control of attention: Action planning primes action-related stimulus dimensions. *Psychological Research*, 71(1), 22-29.
- Fahle, M. (2005). Perceptual learning: Specificity versus generalization. *Current Opinion in Neurobiology*, 15(2), 154-160.
- Faillenot, I., Toni, I., Decety, J., Gregoire, M. C., & Jeannerod, M. (1997). Visual pathways for object-oriented action and object recognition: functional anatomy with PET. *Cerebral Cortex*, 7(1), 77-85.
- Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, 8(10), 1380-1385.
- Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned fMRI adaptation in human visual cortex. *Journal of Neurophysiology*, 94(6), 4188-4195. doi: 10.1152/jn.00378.2005
- Fanselow, M. S., & Poulos, A. M. (2005). The neuroscience of mammalian associative learning. *Annual Review of Psychology*, 56(1), 207-234. doi: 10.1146/annurev.psych.56.091103.070213
- Farah, M. J. (1984). The neurological basis of mental imagery: A componential analysis. *Cognition*, 18(1-3), 245-272. doi: 10.1016/0010-0277(84)90026-x
- Farah, M. J., Levine, D. N., & Calvanio, R. (1988). A case study of mental imagery deficit. *Brain and Cognition*, 8(2), 147-164. doi: 10.1016/0278-2626(88)90046-2
- Farah, M. J., Rochlin, R., & Klein, K. L. (1994). Orientation invariance and geometric primitives in shape recognition. *Cognitive Science*, 18(2), 325-344.
- Farivar, R. (2009). Dorsal-ventral integration in object recognition. *Brain Research Reviews*, 61(2), 144-153. doi: 10.1016/j.brainresrev.2009.05.006
- Farivar, R., Blanke, O., & Chaudhuri, A. (2009). Dorsal-ventral integration in the recognition of motion-defined unfamiliar faces. *The Journal of Neuroscience*, 29(16), 5336-5342. doi: 10.1523/jneurosci.4978-08.2009
- Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: The neural correlates of the experience of agency. *NeuroImage*, 15(3), 596-603.
- Fazio, R. H., Sanbonmatsu, D. M., Powell, M. C., & Kardes, F. R. (1986). On the automatic activation of attitudes. *Journal of Personality and Social Psychology*, 50(2), 229-238. doi: 10.1037/0022-3514.50.2.229
- Ferrari, P. F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience*, 17(2), 212-226. doi: 10.1162/0898929053124910
- Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature*, 287, 43-44.
- Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S., & Dolan, R. J. (1995). The mind's eye--precuneus activation in memory-related imagery. *NeuroImage*, 2(3), 195-200. doi: 10.1006/nimg.1995.1025
- Foa, E. B., & Meadows, E. A. (1997). Psychosocial treatments for posttraumatic stress disorder: A critical review. *Annual Review of Psychology*, 48, 449-480.
- Fodor, J. A. (1975). *The Language of Thought*. New York: Crowell
- Fodor, J. A. (1988). *Concepts: Where Cognitive Science Went Wrong*. Oxford University Press.
-

-
- Fodor, J. A., & Pylyshyn, Z. W. (1988). Connectionism and cognitive architecture: A critical analysis. *Cognition*, 28(1–2), 3-71. doi: 10.1016/0010-0277(88)90031-5
- Franklin, M. S., Dien, J., Neely, J. H., Huber, E., & Waterson, L. D. (2007). Semantic priming modulates the N400, N300, and N400RP. *Clinical Neurophysiology*, 118(5), 1053-1068.
- Frey, S. H. (2007). What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex*, 43(3), 368-375. doi: 10.1016/s0010-9452(08)70462-3
- Frey, S. H., Funnell, M. G., Gerry, V. E., & Gazzaniga, M. S. (2005). A dissociation between the representation of tool-use skills and hand dominance: Insights from left-and right-handed callosotomy patients. *Journal of Cognitive Neuroscience*, 17(2), 262-272.
- Fried, I., MacDonald, K. A., & Wilson, C. L. (1997). Single neuron activity in human hippocampus and amygdala during recognition of faces and objects. *Neuron*, 18(5), 753-765.
- Fukushima, K. (1980). Neocognitron: A self-organizing neural network model for a mechanism of pattern recognition unaffected by shift in position. *Biological cybernetics*, 36(4), 193-202.
- Gallese, V. (2001). The shared manifold hypothesis. From mirror neurons to empathy. *Journal of consciousness studies*, 8, 33-50.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, 22(3-4), 455-479.
- Gallivan, J. P., McLean, D. A., Valyear, K. F., & Culham, J. C. (2013). Decoding the neural mechanisms of human tool use. *Elife*, 2, e00425. doi: 10.7554/eLife.00425
- Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, 10(2), 175-180. doi: 10.1093/cercor/10.2.175
- Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: an fMRI study. *Cognitive Brain Research*, 20(2), 226-241. doi: 10.1016/j.cogbrainres.2004.02.012
- Gao, X. P., Xin, J. H., Sato, T., Hansuebsai, A., Scalzo, M., Kajiwar, K., . . . Billger, M. (2007). Analysis of cross-cultural color emotion. *Color Research & Application*, 32(3), 223-229.
- Garbarini, F., & Adenzato, M. (2004). At the root of embodied cognition: Cognitive science meets neurophysiology. *Brain and Cognition*, 56(1), 100-106. doi: <http://dx.doi.org/10.1016/j.bandc.2004.06.003>
- Gegenfurtner, K. R. (2003). Cortical mechanisms of colour vision. *Nature Reviews Neuroscience*, 4(7), 563-572.
- Geinisman, Y. (2000). Structural synaptic modifications associated with hippocampal LTP and behavioral learning. *Cerebral Cortex*, 10(10), 952-962. doi: 10.1093/cercor/10.10.952
- Genç, E., Bergmann, J., Tong, F., Blake, R., Singer, W., & Kohler, A. (2011). Callosal connections of primary visual cortex predict the spatial spreading of binocular rivalry across the visual hemifields. *Frontiers in Human Neuroscience*, 5, 161.
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2000). Categorization and category effects in normal object recognition - A PET Study. *Neuropsychologia*, 38(13), 1693-1703. doi: 10.1016/s0028-3932(00)00082-8
- Gerlach, C., Law, I., Gade, A., & Paulson, O. B. (2002). The role of action knowledge in the comprehension of artefacts - A PET study. *NeuroImage*, 15(1), 143-152. doi: 10.1006/nimg.2002.0969
- Gerlach, C., Law, I., & Paulson, O. B. (2002). When action turns into words. Activation of motor-based knowledge during categorization of manipulable objects. *Journal of Cognitive Neuroscience*, 14(8), 1230-1239. doi: 10.1162/089892902760807221
-

-
- Gianelli, C., Dalla Volta, R., Barbieri, F., & Gentilucci, M. (2008). Automatic grasp imitation following action observation affects estimation of intrinsic object properties. *Brain Research*, 1218, 166-180. doi: <http://dx.doi.org/10.1016/j.brainres.2008.04.046>
- Gibbs Jr, R. W. (2005). *Embodiment and Cognitive Science*. New York, NY: Cambridge University Press.
- Gibson, J. J. (1978). The ecological approach to the visual perception of pictures. *Leonardo*, 11(3), 227-235.
- Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. Dallas, TX: Houghton Mifflin.
- Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron*, 31(5), 681-697.
- Glenberg, A. M. (1997). What memory is for. *Behavioral and Brain Sciences*, 20(1), 1-55.
- Goldberg, R. F., Perfetti, C. A., & Schneider, W. (2006). Perceptual knowledge retrieval activates sensory brain regions. *The Journal of Neuroscience*, 26(18), 4917-4921.
- Goldenberg, G., Hartmann, K., & Schlott, I. (2003). Defective pantomime of object use in left brain damage: Apraxia or asymbolia? *Neuropsychologia*, 41(12), 1565-1573.
- Goldenberg, G., Mullbacher, W., & Nowak, A. (1995). Imagery without perception - A case study of anosognosia for cortical blindness. *Neuropsychologia*, 33(11), 1373-1382.
- Golonka, S., & Estes, Z. (2009). Thematic relations affect similarity via commonalities. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35(6), 1454.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20-25. doi: 10.1016/0166-2236(92)90344-8
- Grafton, S. T., Fadiga, L., Arbib, M. A., & Rizzolatti, G. (1997). Premotor cortex activation during observation and naming of familiar tools. *NeuroImage*, 6(4), 231-236. doi: 10.1006/nimg.1997.0293
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human brain mapping*, 12(1), 1-19.
- Grèzes, J., & Decety, J. (2002). Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia*, 40(2), 212-222.
- Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: an fMRI study of implicit processing. *European Journal of Neuroscience*, 17(12), 2735-2740.
- Grill-Spector, K., Henson, R. N., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10(1), 14-23. doi: 10.1016/j.tics.2005.11.006
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, 24(1), 187-203. doi: 10.1016/s0896-6273(00)80832-6
- Gross, C. G. (2002). Genealogy of the "grandmother cell". *Neuroscientist*, 8(5), 512-518.
- Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, 35(1), 96-111.
- Grossberg, S., & Mingolla, E. (1985). Neural dynamics of perceptual grouping: Textures, boundaries, and emergent segmentations. *Perception & Psychophysics*, 38(2), 141-171.
- Gupta, A., & Davis, L. S. (2007, 17-22 June 2007). *Objects in action: An approach for combining action understanding and object perception*. Paper presented at the Computer Vision and Pattern Recognition, 2007. CVPR '07. IEEE Conference on.
- Gupta, A., Kembhavi, A., & Davis, L. S. (2009). Observing human-object interactions: Using spatial and functional compatibility for recognition. *Pattern Analysis and Machine Intelligence, IEEE Transactions on*, 31(10), 1775-1789. doi: 10.1109/TPAMI.2009.83
-

- Hackmann, A., Clark, D. M., & McManus, F. (2000). Recurrent images and early memories in social phobia. *Behaviour Research and Therapy*, 38, 601-610.
- Hamm, J. P., Johnson, B. W., & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology*, 113(8), 1339-1350. doi: 10.1016/s1388-2457(02)00161-x
- Handy, T. C., Grafton, S. T., Shroff, N. M., Ketay, S., & Gazzaniga, M. S. (2003). Graspable objects grab attention when the potential for action is recognized. *Nature Neuroscience*, 6(4), 421-427.
- Hansen, T., Olkkonen, M., Walter, S., & Gegenfurtner, K. R. (2006). Memory modulates color appearance. *Nature Neuroscience*, 9(11), 1367-1368. doi: http://www.nature.com/neuro/journal/v9/n11/supinfo/n11794_S1.html
- Hare, M., Jones, M., Thomson, C., Kelly, S., & McRae, K. (2009). Activating event knowledge. *Cognition*, 111(2), 151.
- Harvey, A. (2003). Cognitive behaviour therapy for posttraumatic stress disorder. *Clinical Psychology Review*, 23(3), 501-522. doi: 10.1016/s0272-7358(03)00035-7
- Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory*. New York: Wiley & Sons Inc.
- Helbig, H. B., Graf, M., & Kiefer, M. (2006). The role of action representations in visual object recognition. *Experimental Brain Research*, 174(2), 221-228.
- Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, 70(1), 53-81. doi: 10.1016/s0301-0082(03)00086-8
- Hering, E. (1920). *Grundzüge der Lehre vom Lichtsinn*. Berlin: Springer-Verlag.
- Hermans, D., De Houwer, J., & Eelen, P. (1994). The affective priming effect: Automatic activation of evaluative information in memory. *Cognition & Emotion*, 8(6), 515-533. doi: 10.1080/02699939408408957
- Hermisdörfer, J., Terlinden, G., Mühlau, M., Goldenberg, G., & Wohlschläger, A. M. (2007). Neural representations of pantomimed and actual tool use: Evidence from an event-related fMRI study. *NeuroImage*, 36, T109-T118. doi: <http://dx.doi.org/10.1016/j.neuroimage.2007.03.037>
- Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, 21(7), 1229-1243.
- Hirsch, C., & Holmes, E. (2007). Mental imagery in anxiety disorders. *Psychiatry*, 6(4), 161-165. doi: 10.1016/j.mppsy.2007.01.005
- Hirsch, C., Mathews, A., Clark, D., Williams, R., & Morrison, J. (2006). The causal role of negative imagery in social anxiety: A test in confident public speakers. *Journal of Behavior Therapy and Experimental Psychiatry*, 37(2), 159-170. doi: 10.1016/j.jbtep.2005.03.003
- Holcomb, P. J. (1988). Automatic and attentional processing: An event-related brain potential analysis of semantic priming. *Brain and Language*, 35(1), 66-85. doi: 10.1016/0093-934x(88)90101-0
- Hollins, M. (1980). The effect of contrast on the completeness of binocular rivalry suppression. *Attention, Perception, & Psychophysics*, 27(6), 550-556.
- Holmes, E. A., Arntz, A., & Smucker, M. R. (2007). Imagery rescripting in cognitive behaviour therapy: Images, treatment techniques and outcomes. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 297-305. doi: 10.1016/j.jbtep.2007.10.007
- Holmes, E. A., Geddes, J. R., Colom, F., & Goodwin, G. M. (2008). Mental imagery as an emotional amplifier: Application to bipolar disorder. *Behaviour Research and Therapy*, 46(12), 1251-1258. doi: 10.1016/j.brat.2008.09.005

-
- Holmes, E. A., & Mathews, A. (2010). Mental imagery in emotion and emotional disorders. *Clinical Psychology Review, 30*(3), 349-362. doi: 10.1016/j.cpr.2010.01.001
- Howard, R. J., ffytche, D. H., Barnes, J., McKeefry, D., Ha, Y., Woodruff, P. W., . . . Brammer, M. (1998). The functional anatomy of imagining and perceiving colour. *NeuroReport, 9*(6), 1019-1023.
- Hsu, N. S., Frankland, S. M., & Thompson-Schill, S. L. (2012). Chromaticity of color perception and object color knowledge. *Neuropsychologia, 50*(2), 327-333. doi: 10.1016/j.neuropsychologia.2011.12.003
- Hsu, N. S., Kraemer, D. J. M., Oliver, R. T., Schlichting, M. L., & Thompson-Schill, S. L. (2011). Color, context, and cognitive style: Variations in color knowledge retrieval as a function of task and subject variables. *Journal of Cognitive Neuroscience, 23*(9), 2544-2557. doi: 10.1162/jocn.2011.21619
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields in functional architecture of monkey striate cortex. *The Journal of Physiology, 195*, 215-243.
- Humphrey, G. K., Goodale, M. A., Jakobson, L. S., & Servos, P. (1994). The role of surface information in object recognition: Studies of a visual form agnostic and normal subjects. *Perception, 23*(12), 1457-1481.
- Hunt, M., & Fenton, M. (2007). Imagery rescripting versus in vivo exposure in the treatment of snake fear. *Journal of Behavior Therapy and Experimental Psychiatry, 38*(4), 329-344. doi: 10.1016/j.jbtep.2007.09.001
- Hurlbert, A. C., & Ling, Y. (2005). If it's a banana, it must be yellow: The role of memory colors in color constancy. *Journal of Vision, 5*(8), 787. doi: 10.1167/5.8.787
- Huth, A. G., Nishimoto, S., Vu, A. T., & Gallant, J. L. (2012). A continuous semantic space describes the representation of thousands of object and action categories across the human brain. *Neuron, 76*(6), 1210-1224. doi: <http://dx.doi.org/10.1016/j.neuron.2012.10.014>
- Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology, 60*(1), 653-670. doi: doi:10.1146/annurev.psych.60.110707.163604
- Jackson, P. L., Meltzoff, A. N., & Decety, J. (2006). Neural circuits involved in imitation and perspective-taking. *NeuroImage, 31*(1), 429-439.
- Jacobs, G. H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews, 68*(3), 413-471. doi: 10.1111/j.1469-185X.1993.tb00738.x
- Jaeger, W., Krastel, H., & Braun, S. (1988). [Cerebral achromatopsia (symptoms, course, differential diagnosis and strategy of the study). I]. *Klin Monbl Augenheilkd, 193*(6), 627-634. doi: 10.1055/s-2008-1050309
- Jeannerod, M. (1995). Mental imagery in the motor context. *Neuropsychologia, 33*(11), 1419-1432. doi: 10.1016/0028-3932(95)00073-c
- Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in Neurosciences, 18*(7), 314-320. doi: 10.1016/0166-2236(95)93921-j
- Jirak, D., Menz, M. M., Buccino, G., Borghi, A. M., & Binkofski, F. (2010). Grasping language—A short story on embodiment. *Consciousness and Cognition, 19*(3), 711-720.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Attention, Perception, & Psychophysics, 14*(2), 201-211.
- Johnson-Frey, S. H. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences, 8*(2), 71-78.
- Jones, M. K. (1974). Imagery as a mnemonic aid after left temporal lobectomy: Contrast between material-specific and generalized memory disorders. *Neuropsychologia, 12*(1), 21-30.
- Joseph, J. E. (1997). Color processing in object verification. *Acta Psychologica, 97*(1), 95-127.
-

-
- Joseph, J. E., & Proffitt, D. R. (1996). Semantic versus perceptual influences of color in object recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 22(2), 407.
- Kalénine, S., Bonthoux, F., & Borghi, A. M. (2009). How action and context priming influence categorization: A developmental study. *British Journal of Developmental Psychology*, 27(3), 717-730.
- Kan, I. P., Barsalou, L. W., Solomon, K. O., Minor, J. K., & Thompson-Schill, S. L. (2003). Role of mental imagery in a property verification task: fMRI evidence for perceptual representations of conceptual knowledge. *Cognitive Neuropsychology*, 20(3), 525-540. doi: 10.1080/02643290244000257
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17(11), 4302-4311.
- Kaya, N., & Epps, H. H. (2004). Relationship between color and emotion: A study of college students. *College Student Journal*, 38, 396-405.
- Kellenbach, M. L., Brett, M., & Patterson, K. (2001). Large, colorful, or noisy? Attribute- and modality-specific activations during retrieval of perceptual attribute knowledge. *Cognitive, Affective, & Behavioral Neuroscience*, 1(3), 207-221.
- Kellenbach, M. L., Brett, M., & Patterson, K. (2003). Actions speak louder than functions: The importance of manipulability and action in tool representation. *Journal of Cognitive Neuroscience*, 15(1), 30-46.
- Kemmerer, D., & Gonzalez-Castillo, J. (2010). The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain and Language*, 112(1), 54-76. doi: <http://dx.doi.org/10.1016/j.bandl.2008.09.010>
- Keogh, R., & Pearson, J. (2011). Mental imagery and visual working memory. *PLoS ONE*, 6(12), e29221. doi: 10.1371/journal.pone.0029221
- Kersten, D. (2003). Bayesian models of object perception. *Current Opinion in Neurobiology*, 13(2), 150-158. doi: 10.1016/s0959-4388(03)00042-4
- Kersten, D., Mamassian, P., & Yuille, A. (2004). Object perception as Bayesian inference. *Annual Review of Psychology*, 55, 271-304.
- Keysers, C. (2009). Mirror neurons. *Current Biology*, 19(21), R971-R973. doi: <http://dx.doi.org/10.1016/j.cub.2009.08.026>
- Keysers, C., & Gazzola, V. (2010). Social neuroscience: Mirror neurons recorded in humans. *Current Biology*, 20(8), R353-R354.
- Klatzky, R. L., Pellegrino, J. W., McCloskey, B. P., & Lederman, S. J. (1993). Cognitive representations of functional interactions with objects. *Memory & Cognition*, 21(3), 294-303.
- Knauff, M., Kassubek, J., Mulack, T., & Greenlee, M. W. (2000). Cortical activation evoked by visual mental imagery as measured by fMRI. *NeuroReport*, 11(18), 3957-3962.
- Kosslyn, S. M., Brunn, J., Cave, K. R., & Wallach, R. W. (1984). Individual differences in mental imagery ability: A computational analysis. *Cognition*, 18(1), 195-243.
- Kosslyn, S. M., Ganis, G., & Thompson, W. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, 2, 635-642.
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., . . . Alpert, N. M. (1999). The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science*, 284(5411), 167-170. doi: 10.1126/science.284.5411.167
-

-
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental images in primary visual cortex. *Nature*, 378(6556), 496-498. doi: 10.1038/378496a0
- Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience*, 12(1), 48-55.
- Kovács, I., Papathomas, T. V., Yang, M., & Fehér, Á. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences*, 93(26), 15508-15511.
- Kreiman, G., Koch, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, 408(6810), 357-361.
- Krekelberg, B., Vatakis, A., & Kourtzi, Z. (2005). Implied motion from form in the human visual cortex. *Journal of Neurophysiology*, 94(6), 4373-4386.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective ratings of pictures and instruction manual. Technical Report A-8*. University of Florida, Gainesville, FL.
- Large, M. E., Kiss, I., & McMullen, P. A. (2004). Electrophysiological correlates of object categorization: Back to basics. *Cognitive Brain Research*, 20(3), 415-426. doi: 10.1016/j.cogbrainres.2004.03.013
- Laws, K. R., & Hunter, M. Z. (2006). The impact of colour, spatial resolution, and presentation speed on category naming. *Brain and Cognition*, 62(2), 89-97. doi: 10.1016/j.bandc.2006.03.002
- Leibe, B., Leonardis, A., & Schiele, B. (2008). Robust object detection with interleaved categorization and segmentation. *International journal of computer vision*, 77(1), 259-289.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, 3(7), 254-264.
- Lewis, D. E., O'Reilly, M. J., Khuu, S. K., & Pearson, J. (2013). Conditioning the mind's eye: Associative learning with voluntary mental imagery. *Clinical Psychological Science*. doi: 10.1177/2167702613484716
- Lewis, D. E., Pearson, J., & Khuu, S. K. (2013). The color "Fruit": Object memories defined by color. *PLoS ONE*, 8(5), e64960. doi: 10.1371/journal.pone.0064960
- Lin, E. L., & Murphy, G. L. (2001). Thematic relations in adults' concepts. *Journal of Experimental Psychology: General*, 130(1), 3.
- Ling, S., Pearson, J., & Blake, R. (2009). Dissociation of Neural Mechanisms Underlying Orientation Processing in Humans. *Current Biology*, 19(17), 1458-1462. doi: 10.1016/j.cub.2009.06.069
- Lissek, S., Powers, A., McClure, E., Phelps, E., Woldehawariat, G., Grillon, C., & Pine, D. (2005). Classical fear conditioning in the anxiety disorders: a meta-analysis. *Behaviour Research and Therapy*, 43(11), 1391-1424. doi: 10.1016/j.brat.2004.10.007
- Liuzza, M. T., Setti, A., & Borghi, A. M. (2012). Kids observing other kids' hands: Visuomotor priming in children. *Consciousness and Cognition*, 21(1), 383-392. doi: 10.1016/j.concog.2011.09.015
- Lo Sciuto, L. A., & Hartley, E. L. (1963). Religious affiliation and open-mindedness in binocular resolution. *Perceptual and Motor Skills*, 17(2), 427-430.
- Logothetis, N. K., & Sheinberg, D. L. (1996). Visual object recognition. *Annual Review of Neuroscience*, 19(1), 577-621.
- Longo, M. R. (2009). What's embodied and how can we tell? *European Journal of Social Psychology*, 39(7), 1207-1209.
-

-
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., . . . Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: An fMRI study. *Journal of Cognitive Neuroscience*, 11(5), 491-501.
- Lowe, D. G. (1999). *Object recognition from local scale-invariant features*. Paper presented at the Computer Vision, 1999. The Proceedings of the Seventh IEEE International Conference on.
- Lowe, D. G. (2000). *Towards a computational model for object recognition in IT cortex*. Paper presented at the Biologically Motivated Computer Vision.
- Lu, A., Xu, G., Jin, H., Mo, L., Zhang, J., & Zhang, J. X. (2010). Electrophysiological evidence for effects of color knowledge in object recognition. *Neuroscience Letters*, 469(3), 405-410. doi: 10.1016/j.neulet.2009.12.039
- Luzzatti, C., & Davidoff, J. (1994). Impaired retrieval of object-colour knowledge with preserved colour naming. *Neuropsychologia*, 32(8), 933-950. doi: 10.1016/0028-3932(94)90044-2
- Maeda, F., Kleiner-Fisman, G., & Pascual-Leone, A. (2002). Motor facilitation while observing hand actions: Specificity of the effect and role of observer's orientation. *Journal of Neurophysiology*, 87(3), 1329-1335.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology-Paris*, 102(1-3), 59-70. doi: 10.1016/j.jphysparis.2008.03.004
- Mahon, B. Z., & Caramazza, A. (2009). Concepts and categories: A cognitive neuropsychological perspective. *Annual Review of Psychology*, 60(1), 27-51. doi: 10.1146/annurev.psych.60.110707.163532
- Mahon, B. Z., & Caramazza, A. (2011). What drives the organization of object knowledge in the brain? *Trends in Cognitive Sciences*, 15(3), 97-103. doi: 10.1016/j.tics.2011.01.004
- Mahon, B. Z., Schwarzbach, J., & Caramazza, A. (2010). The representation of tools in left parietal cortex is independent of visual experience. *Psychological Science*, 21(6), 764-771.
- Mamassian, P., Landy, M. S., & Maloney, L. T. (2002). Bayesian modelling of visual perception. In R. P. N. Rao, B. A. Olshausen & M. S. Lewicki (Eds.), *Probabilistic models of the brain: Perception and neural function* (pp. 13-36). Cambridge, MA.: MIT Press.
- Mapelli, D., & Behrmann, M. (1997). The role of color in object recognition: Evidence from visual agnosia. *Neurocase*, 3(4), 237-247. doi: 10.1080/13554799708405007
- Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 200(1140), 269-294.
- Martin, A. (1998). Organization of semantic knowledge and the origin of words in the brain. In N. Jablonski & L. Aiello (Eds.), *The Origins and Diversification of Language* (pp. 69-98). San Francisco: California Academy of Sciences.
- Martin, A. (2001). Functional neuroimaging of semantic memory. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging of cognition* (pp. 153-186). Cambridge, MA: MIT Press.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, 58(1), 25-45. doi: 10.1146/annurev.psych.57.102904.190143
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270(5233), 102-105.
- Martin, I., & Levey, A. B. (1978). Evaluative conditioning. *Advances in Behavior Research and Therapy*, 1, 57-101.
-

-
- Masson, M. E. J., Bub, D. N., & Breuer, A. T. (2011). Priming of reach and grasp actions by handled objects. *Journal of Experimental Psychology-Human Perception and Performance*, 37(5), 1470.
- Mast, F. W., Tartaglia, E., & Herzog, M. New percepts via mental imagery? *Front Psychol*, 3, 360.
- McClain, L. (1983). Color priming affects Stroop interference. *Perceptual and Motor Skills*, 56(2), 643-651.
- McClelland, J. L., & Rumelhart, D. E. (1987). *Parallel distributed processing: Explorations in the microstructure of cognition. Volume 2. Psychological and biological models*. Cambridge: MIT Press.
- McPherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, 36(01), 53-65. doi: doi:null
- McRae, K., & Boisvert, S. (1998). Automatic semantic similarity priming. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 24(3), 558.
- McRae, K., & Matsuki, K. (2009). People use their knowledge of common events to understand language, and do so as quickly as possible. *Language and linguistics compass*, 3(6), 1417-1429.
- Meadows, J. C. (1974). Disturbed perception of colours associated with localized cerebral lesions. *Brain*, 97(4), 615-632.
- Mel, B. W. (1997). SEEMORE: Combining color, shape, and texture histogramming in a neurally inspired approach to visual object recognition. *Neural computation*, 9(4), 777-804.
- Mellet, E., Petit, L., Mazoyer, B., Denis, M., & Tzourio, N. (1998). Reopening the mental imagery debate: Lessons from functional anatomy. *NeuroImage*, 8(2), 129-139. doi: 10.1006/nimg.1998.0355
- Meteyard, L., Cuadrado, S. R., Bahrami, B., & Vigliocco, G. (2012). Coming of age: A review of embodiment and the neuroscience of semantics. *Cortex*, 48(7), 788-804. doi: <http://dx.doi.org/10.1016/j.cortex.2010.11.002>
- Meteyard, L., Zokaei, N., Bahrami, B., & Vigliocco, G. (2008). Visual motion interferes with lexical decision on motion words. *Current Biology*, 18(17), R732-R733.
- Meyer, V., & Yates, A. J. (1955). Intellectual changes following temporal lobectomy for psychomotor epilepsy: Preliminary communication. *Journal of Neurology, Neurosurgery, and Psychiatry*, 18(1), 44-52.
- Miceli, G., Fouch, E., Capasso, R., Shelton, J. R., Tomaiuolo, F., & Caramazza, A. (2001). The dissociation of color from form and function knowledge. *Nature Neuroscience*, 4(6), 662-667. doi: 10.1038/88497
- Milad, M., Rauch, S., Pitman, R., & Quirk, G. (2006). Fear extinction in rats: Implications for human brain imaging and anxiety disorders. *Biological Psychology*, 73(1), 61-71. doi: 10.1016/j.biopsycho.2006.01.008
- Milner, A. D., & Goodale, M. A. (1998). The visual brain in action. *PSYCHE*, 4(12).
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, 6(0), 414-417. doi: 10.1016/0166-2236(83)90190-X
- Miyashita, Y. (1993). Inferior temporal cortex: where visual perception meets memory. *Annual Review of Neuroscience*, 16(1), 245-263.
- Mizelle, J. C., & Wheaton, L. A. (2010). The neuroscience of storing and molding tool action concepts: How "plastic" is grounded cognition? *Front Psychol*, 1. doi: 10.3389/fpsyg.2010.00195
- Moll, J., de Oliveira-Souza, R., Passman, L. J., Cunha, F. C., Souza-Lima, F., & Andreiuolo, P. A. (2000). Functional MRI correlates of real and imagined tool-use pantomimes. *Neurology*, 54(6), 1331-1336.
-

-
- Mounoud, P., Duscherer, K., Moy, G., & Perraudin, S. (2007). The influence of action perception on object recognition: A developmental study. *Developmental Science*, 10(6), 836-852. doi: 10.1111/j.1467-7687.2007.00624.x
- Movshon, J. A., Thompson, I. D., & Tolhurst, D. J. (1978a). Receptive field organization of complex cells in the cat's striate cortex. *The Journal of Physiology*, 283(1), 79-99.
- Movshon, J. A., Thompson, I. D., & Tolhurst, D. J. (1978b). Spatial summation in the receptive fields of simple cells in the cat's striate cortex. *The Journal of Physiology*, 283(1), 53-77.
- Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology*, 20(8), 750-756. doi: <http://dx.doi.org/10.1016/j.cub.2010.02.045>
- Mummery, C. J., Shallice, T., & Price, C. J. (1999). Dual-process model in semantic priming: A functional imaging perspective. *NeuroImage*, 9(5), 516-525. doi: 10.1006/nimg.1999.0434
- Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology*, 83(5), 2580-2601.
- Murphy, G. L. (2002). *The big book of concepts*: MIT Press.
- Nagai, J., & Yokosawa, K. (2003). What regulates the surface color effect in object recognition: Color diagnosticity or category. *Technical Report on Attention and Cognition*, 28, 1-4.
- Naor-Raz, G., Tarr, M. J., & Kersten, D. (2003). Is color an intrinsic property of object representation? *Perception*, 32(6), 667-680.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9, 353-383.
- Neely, J. H. (1977). Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited-capacity attention. *Journal of Experimental Psychology: General*, 106(3), 226-254.
- Neely, J. H., Keefe, D. E., & Ross, K. L. (1989). Semantic priming in the lexical decision task: Roles of prospective prime-generated expectancies and retrospective semantic matching. *Journal of experimental psychology. Learning, memory, and cognition*, 15(6), 1003-1019.
- Nigam, A., Hoffman, J. E., & Simons, R. F. (1992). N400 to semantically anomalous pictures and words. *Journal of Cognitive Neuroscience*, 4(1), 15-22. doi: 10.1162/jocn.1992.4.1.15
- Nishina, S., Seitz, A. R., Kawato, M., & Watanabe, T. (2007). Effect of spatial distance to the task stimulus on task-irrelevant perceptual learning of static Gabors. *Journal of Vision*, 7(13).
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, 12, 1013-1023.
- Ohgami, Y., Matsuo, K., Uchida, N., & Nakai, T. (2004). An fMRI study of tool-use gestures: Body part as object and pantomime. *NeuroReport*, 15(12), 1903-1906.
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108(3), 483-522.
- Oliver, R. T., & Thompson-Schill, S. L. (2003). Dorsal stream activation during retrieval of object size and shape. *Cognitive, Affective, & Behavioral Neuroscience*, 3(4), 309-322.
- Olkkonen, M., Hansen, T., & Gegenfurtner, K. (2008). Color appearance of familiar objects: Effects of object shape, texture, and illumination changes. *Journal of Vision*, 8(5), 1-16. doi: 10.1167/8.5.13
- Olman, C. A., Ugurbil, K., & Kersten, D. (2004). The role of feature density in determining V1 BOLD fMRI sensitivity to spatial phase structure. *Journal of Vision*, 4(8), 544. doi: 10.1167/4.8.544
-

-
- Oppenheim, A. V., & Lim, J. S. (1981). The importance of phase in signals. *Proceedings of the IEEE*, 69(5), 529-541. doi: 10.1109/proc.1981.12022
- Orlov, T., Makin, T. R., & Zohary, E. (2010). Topographic representation of the human body in the occipitotemporal cortex. *Neuron*, 68(3), 586-600. doi: 10.1016/j.neuron.2010.09.032
- Özgen, E. (2004). Language, learning, and color perception. *Current Directions in Psychological Science*, 13(3), 95-98.
- Paragios, N., Chen, Y., & Faugeras, O. D. (2010). *Handbook of Mathematical Models in Computer Vision*: Springer Publishing Company, Incorporated.
- Parker, D. M., Lishman, J. R., & Hughes, J. (1992). Temporal integration of spatially filtered visual images. *Perception*, 21(2), 147-160.
- Pavlov, I. P. (2003). *Conditioned Reflexes* (G. V. Anrep Ed.): Courier Dover Publications.
- Pearson, J., & Brascamp, J. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences*, 12(9), 334-341.
- Pearson, J., & Clifford, C. W. G. (2005a). Suppressed patterns alter vision during binocular rivalry. *Current Biology*, 15(23), 2142-2148.
- Pearson, J., & Clifford, C. W. G. (2005b). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. *Psychological Science*, 16(7), 516-519.
- Pearson, J., Clifford, C. W. G., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Current Biology*, 18(13), 982-986. doi: 10.1016/j.cub.2008.05.048
- Pearson, J., Rademaker, R. L., & Tong, F. (2011). Evaluating the mind's eye. *Psychological Science*, 22(12), 1535-1542. doi: 10.1177/0956797611417134
- Pecher, D., Boot, I., & Van Dantzig, S. (2011). Abstract concepts: Sensory-motor grounding, metaphors, and beyond. In B. Ross (Ed.), *The Psychology of Learning and Motivation* (Vol. 54, pp. 217-248). Burlington: Academic Press.
- Péran, P., Démonet, J. F., Cherubini, A., Carbebat, D., Caltagirone, C., & Sabatini, U. (2010). Mental representations of action: The neural correlates of the verbal and motor components. *Brain Research*, 1328, 89-103.
- Pérez-Carpinell, J., de Fez, M. D., Baldoví, R., & Soriano, J. C. (1998). Familiar objects and memory color. *Color Research & Application*, 23(6), 416-427. doi: 10.1002/(sici)1520-6378(199812)23:6<416::aid-col10>3.0.co;2-n
- Pezzulo, G., Barsalou, L. W., Cangelosi, A., Fischer, M. H., Spivey, M., & McRae, K. (2011). The mechanics of embodiment: A dialogue on embodiment and computational modeling. *Front Psychol*, 2. doi: 10.3389/fpsyg.2011.00005
- Phillips, J. C., & Ward, R. (2002). SR correspondence effects of irrelevant visual affordance: Time course and specificity of response activation. *Visual Cognition*, 9(4-5), 540-558.
- Pinker, S. (1984). Visual cognition: An introduction. *Cognition*, 18(1), 1-63.
- Pitman, R. K., Orr, S. P., Forgue, D. F., Altman, B., de Jong, J. B., & Herz, L. R. (1990). Psychophysiologic responses to combat imagery of Vietnam veterans with posttraumatic stress disorder versus other anxiety disorders. *Journal of Abnormal Psychology*, 99(1), 49-54. doi: 10.1037/0021-843x.99.1.49
- Plaut, D. C., & McClelland, J. L. (2010). Locating object knowledge in the brain: Comment on Bowers's (2009) attempt to revive the grandmother cell hypothesis. *Psychological Review*, 117(1), 284-288. doi: 10.1037/a0017101
- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage*, 10(1), 15-35.
- Posner, M., & Snyder, C. R. R. (1975). Facilitation and inhibition in the processing of signals. In P. M. A. Rabbitt & S. Dornic (Eds.), *Attention and Performance V*. New York: Academic Press.
-

-
- Price, C. J., & Humphreys, G. W. (1989). The effects of surface detail on object categorization and naming. *The Quarterly Journal of Experimental Psychology Section A*, 41(4), 797-828. doi: 10.1080/14640748908402394
- Proverbio, A. M., Burco, F., del Zotto, M., & Zani, A. (2004). Blue piglets? Electrophysiological evidence for the primacy of shape over color in object recognition. *Cognitive Brain Research*, 18(3), 288-300. doi: 10.1016/j.cogbrainres.2003.10.020
- Pulvermuller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6(7), 576-582.
- Pylyshyn, Z. W. (1973). What the mind's eye tells the mind's brain: A critique of mental imagery. *Psychological Bulletin*, 80(1), 1-24. doi: 10.1037/h0034650
- Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, 88(1), 16-45. doi: 10.1037/0033-295x.88.1.16
- Quiroga, R. Q., Kreiman, G., Koch, C., & Fried, I. (2008). Sparse but not 'grandmother-cell' coding in the medial temporal lobe. *Trends in Cognitive Sciences*, 12(3), 87-91.
- Quiroga, R. Q., Mukamel, R., Isham, E. A., Malach, R., & Fried, I. (2008). Human single-neuron responses at the threshold of conscious recognition. *Proceedings of the National Academy of Sciences*, 105(9), 3599-3604.
- Quiroga, R. Q., Reddy, L., Kreiman, G., Koch, C., & Fried, I. (2005). Invariant visual representation by single neurons in the human brain. *Nature*, 435(7045), 1102-1107.
- Rademaker, R. L., & Pearson, J. (2012). Training visual imagery: Improvements of metacognition, but not imagery strength. *Front Psychol*, 3, 224. doi: 10.3389/fpsyg.2012.00224
- Randerath, J., Goldenberg, G., Spijkers, W., Li, Y., & Hermsdörfer, J. (2010). Different left brain regions are essential for grasping a tool compared with its subsequent use. *NeuroImage*, 53(1), 171-180. doi: <http://dx.doi.org/10.1016/j.neuroimage.2010.06.038>
- Rauch, S., Shin, L., & Phelps, E. (2006). Neurocircuitry models of posttraumatic stress disorder and extinction: Human neuroimaging research—past, present, and future. *Biological Psychiatry*, 60(4), 376-382. doi: 10.1016/j.biopsych.2006.06.004
- Regan, B. C., Julliot, C., Simmen, B., Vienot, F., Charles-Dominique, P., & Mollon, J. D. (2001). Fruits, foliage and the evolution of primate colour vision. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 356(1407), 229-283.
- Rice, N. J., Valyear, K. F., Goodale, M. A., Milner, A. D., & Culham, J. C. (2007). Orientation sensitivity to graspable objects: An fMRI adaptation study. *NeuroImage*, 36, Supplement 2(0), T87-T93. doi: 10.1016/j.neuroimage.2007.03.032
- Rich, A. N., Williams, M. A., Puce, A., Syngienotis, A., Howard, M., McGlone, F., & Mattingley, J. B. (2006). Neural correlates of imagined and synaesthetic colours. *Neuropsychologia*, 44(14), 2918-2925.
- Richter, T., & Zwaan, R. A. (2009). Processing of color words activates color representations. *Cognition*, 111(3), 383-389.
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, 2, 1019-1025.
- Riesenhuber, M., & Poggio, T. (2000). Models of object recognition. *Nature Neuroscience*, 3, 1199-1204.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27(1), 169-192. doi: doi:10.1146/annurev.neuro.27.070203.144230
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3(2), 131-141.
-

-
- Rochat, M. J., Caruana, F., Jezzini, A., Intskirveli, I., Grammont, F., Gallese, V., . . . Umiltà, M. A. (2010). Responses of mirror neurons in area F5 to hand and tool grasping observation. *Experimental Brain Research*, 204(4), 605-616.
- Rogers, T. T., & Patterson, K. (2007). Object categorization: Reversals and explanations of the basic-level advantage. *Journal of Experimental Psychology: General*, 136(3), 451-469. doi: 10.1037/0096-3445.136.3.451
- Rolls, E. T. (1994). Brain mechanisms for invariant visual recognition and learning. *Behavioural Processes*, 33(1), 113-138.
- Rosch, E., Mervis, C. B., Gray, W. D., Johnson, D. M., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology*, 8(3), 382-439. doi: [http://dx.doi.org/10.1016/0010-0285\(76\)90013-X](http://dx.doi.org/10.1016/0010-0285(76)90013-X)
- Rosen, J. B., & Schulkin, J. (1998). From normal fear to pathological anxiety. *Psychological Review*, 105(2), 325-350.
- Rossell, S. L., Price, C. J., & Nobre, A. C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia*, 41(5), 550-564. doi: 10.1016/s0028-3932(02)00181-1
- Rossion, B., & Pourtois, G. (2004). Revisiting Snodgrass and Vanderwart's object pictorial set: The role of surface detail in basic-level object recognition. *Perception*, 33(2), 217-236.
- Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience*, 4(5), 546-550.
- Rueschemeyer, S. A., Pfeiffer, C., & Bekkering, H. (2010). Body schematics: On the role of the body schema in embodied lexical-semantic representations. *Neuropsychologia*, 48(3), 774-781. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2009.09.019>
- Rueschemeyer, S. A., van Rooij, D., Lindemann, O., Willems, R. M., & Bekkering, H. (2009). The function of words: Distinct neural correlates for words denoting differently manipulable objects. *Journal of Cognitive Neuroscience*, 22(8), 1844-1851. doi: 10.1162/jocn.2009.21310
- Rumelhart, D. E., Hinton, G. E., & McClelland, J. L. (1986). A general framework for parallel distributed processing. *Parallel distributed processing*, 1(2), 45-76.
- Rumelhart, D. E., & McClelland, J. L. (1986). *Parallel distributed processing: Explorations in the microstructure of cognition. Volume 1. Foundations*. Cambridge: MIT Press.
- Sack, A. T., Camprodon, J. A., Pascual-Leone, A., & Goebel, R. (2005). The dynamics of interhemispheric compensatory processes in mental imagery. *Science*, 308(5722), 702-704. doi: 10.1126/science.1107784
- Sakai, K., & Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. *Nature*, 354, 152-155.
- Sakuraba, S., Sakai, S., Yamanaka, M., Yokosawa, K., & Hirayama, K. (2012). Does the human dorsal stream really process a category for tools? *The Journal of Neuroscience*, 32(11), 3949-3953.
- Sanocki, T., Bowyer, K. W., Heath, M. D., & Sarkar, S. (1998). Are edges sufficient for object recognition? *Journal of Experimental Psychology: Human Perception and Performance*, 24(1), 340-349.
- Sasaki, Y., Nanez, J. E., & Watanabe, T. (2010). Advances in visual perceptual learning and plasticity. *Nature Reviews Neuroscience*, 11(1), 53-60. doi: http://www.nature.com/nrn/journal/v11/n1/supinfo/nrn2737_S1.html
- Schacter, D. L. (1992). Priming and multiple memory systems: Perceptual mechanisms of implicit memory. *Journal of Cognitive Neuroscience*, 4(3), 244-256. doi: 10.1162/jocn.1992.4.3.244
- Schacter, D. L., & Buckner, R. L. (1998). Priming and the brain. *Neuron*, 20(2), 185-195.
-

-
- Schneider, G. E. (1969). Two visual systems. *Science*, 163, 895-902. doi: 10.1126/science.163.3870.895
- Schupp, H. T., Lutzenberger, W., Birbaumer, N., Miltner, W., & Braun, C. (1994). Neurophysiological differences between perception and imagery. *Cognitive Brain Research*, 2(2), 77-86. doi: 10.1016/0926-6410(94)90004-3
- Schyns, P. G., & Oliva, A. (1994). From blobs to boundary edges: Evidence for time-and spatial-scale-dependent scene recognition. *Psychological Science*, 5(4), 195-200. doi: 10.1111/j.1467-9280.1994.tb00500.x
- Seitz, A. R., Yamagishi, N., Werner, B., Goda, N., Kawato, M., & Watanabe, T. (2005). Task-specific disruption of perceptual learning. *Proceedings of the National Academy of Sciences of the United States of America*, 102(41), 14895-14900.
- Serre, T., Wolf, L., Bileschi, S., Riesenhuber, M., & Poggio, T. (2007). Robust object recognition with cortex-like mechanisms. *Pattern Analysis and Machine Intelligence, IEEE Transactions on*, 29(3), 411-426.
- Sherwood, R., & Pearson, J. (2010). Closing the mind's eye: Incoming luminance signals disrupt visual imagery. *PLoS ONE*, 5(12), e15217. doi: 10.1371/journal.pone.0015217
- Shibata, K., Watanabe, T., Sasaki, Y., & Kawato, M. (2011). Perceptual learning incepted by decoded fMRI neurofeedback without stimulus presentation. *Science*, 334(6061), 1413-1415. doi: 10.1126/science.1212003
- Shuren, J. E., Brott, T. G., Schefft, B. K., & Houston, W. (1996). Preserved color imagery in an achromatopsic. *Neuropsychologia*, 34(6), 485-489. doi: 10.1016/0028-3932(95)00153-0
- Simmons, S., & Estes, Z. (2008). Individual differences in the perception of similarity and difference. *Cognition*, 108(3), 781-795. doi: 10.1016/j.cognition.2008.07.003
- Simmons, W. K., Ramjee, V., Beauchamp, M. S., McRae, K., Martin, A., & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, 45(12), 2802-2810. doi: 10.1016/j.neuropsychologia.2007.05.002
- Skinner, B. F. (1977). Why I am not a cognitive psychologist. *Behaviorism*, 5(2), 1-10.
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. *Cerebral Cortex*, 15(10), 1570-1583. doi: 10.1093/cercor/bhi035
- Smiley, S. S., & Brown, A. L. (1979). Conceptual preference for thematic or taxonomic relations: A nonmonotonic age trend from preschool to old age. *Journal of Experimental Child Psychology*, 28(2), 249-257.
- Smith, P. L., & Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends in Neurosciences*, 27(3), 161-168.
- Smucker, M. R., Dancu, C., Foa, E. B., & Niederee, J. L. (1995). Imagery rescripting: A new treatment for survivors of childhood sexual abuse suffering from posttraumatic stress. *Journal of Cognitive Psychotherapy*, 9(1), 3-17.
- Sparing, R., Mottaghy, F. M., Ganis, G., Thompson, W. L., Töpper, R., Kosslyn, S. M., & Pascual-Leone, A. (2002). Visual cortex excitability increases during visual mental imagery—a TMS study in healthy human subjects. *Brain Research*, 938(1-2), 92-97. doi: 10.1016/s0006-8993(02)02478-2
- Spunt, R. P., Falk, E. B., & Lieberman, M. D. (2010). Dissociable neural systems support retrieval of how and why action knowledge. *Psychological Science*, 21(11), 1593-1598.
- Sterzer, P., Kleinschmidt, A., & Rees, G. (2009). The neural bases of multistable perception. *Trends in Cognitive Sciences*, 13(7), 310-318.
- Sumner, P., & Mollon, J. D. (2000a). Catarrhine photopigments are optimized for detecting targets against a foliage background. *Journal of Experimental Biology*, 203(13), 1963-1986.
-

-
- Sumner, P., & Mollon, J. D. (2000b). Chromaticity as a signal of ripeness in fruits taken by primates. *Journal of Experimental Biology*, 203(13), 1987-2000.
- Surridge, A. K., Osorio, D., & Mundy, N. I. (2003). Evolution and selection of trichromatic vision in primates. *Trends in Ecology & Evolution*, 18(4), 198-205. doi: 10.1016/s0169-5347(03)00012-0
- Swain, M. J., & Ballard, D. H. (1991). Color indexing. *International journal of computer vision*, 7(1), 11-32.
- Szeliski, R. (2010). *Computer Vision: Algorithms and Applications*: Springer.
- Taira, M., Mine, S., Georgopoulos, A. P., Murata, A., & Sakata, H. (1990). Parietal cortex neurons of the monkey related to the visual guidance of hand movement. *Experimental Brain Research*, 83(1), 29-36.
- Tanaka, J. W., & Presnell, L. M. (1999). Color diagnosticity in object recognition. *Perception & Psychophysics*, 61(6), 1140-1153.
- Tanaka, K. (1997). Mechanisms of visual object recognition: monkey and human studies. *Current Opinion in Neurobiology*, 7(4), 523-529.
- Taylor, D. A. (1977). Time course of context effects. *Journal of Experimental Psychology: General*, 106(4), 404-426. doi: 10.1037/0096-3445.106.4.404
- Therriault, D., Yaxley, R., & Zwaan, R. (2009). The role of color diagnosticity in object recognition and representation. *Cognitive Processing*, 10(4), 335-342. doi: 10.1007/s10339-009-0260-4
- Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: inferring "how" from "where". *Neuropsychologia*, 41(3), 280-292.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, 94(26), 14792-14797.
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, 10(11), 502-511.
- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, 21, 753-759.
- Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. *Quarterly Journal of Experimental Psychology*, 14(1), 23-37.
- Tsuchiya, N., & Koch, C. (2004). Continuous flash suppression. *Journal of Vision*, 4(8), 61-61.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), 1096-1101. doi: 10.1038/nn1500
- Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology-Human Perception and Performance*, 24(3), 830-846.
- Tucker, M., & Ellis, R. (2004). Action priming by briefly presented objects. *Acta Psychologica*, 116(2), 185-203. doi: 10.1016/j.actpsy.2004.01.004
- Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science*, 247(4940), 301-306. doi: 10.1126/science.2296719
- Tweedy, J. R., & Lapinski, R. H. (1981). Facilitating word recognition: Evidence for strategic and automatic factors. *The Quarterly Journal of Experimental Psychology Section A*, 33(1), 51-59. doi: 10.1080/14640748108400768
- Ullman, S. (1989). Aligning pictorial descriptions: an approach to object recognition. *Cognition*, 32(3), 193-254.
- Ullman, S., & Power, G. J. (1997). High-level vision: Object-recognition and visual cognition. *Optical Engineering*, 36(11), 3224-3224.
-

-
- Umiltà, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., . . . Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences*, 105(6), 2209-2213. doi: 10.1073/pnas.0705985105
- Uttl, B., Graf, P., & Santacruz, P. (2006). Object color affects identification and repetition priming. *Scandinavian Journal of Psychology*, 47(5), 313-325. doi: 10.1111/j.1467-9450.2006.00532.x
- Vainio, L., Ellis, R., & Tucker, M. (2007). The role of visual attention in action priming. *The Quarterly Journal of Experimental Psychology*, 60(2), 241-261.
- Vainio, L., Ellis, R., Tucker, M., & Symes, E. (2006). Manual asymmetries in visually primed grasping. *Experimental Brain Research*, 173(3), 395-406.
- Vainio, L., Symes, E., Ellis, R., Tucker, M., & Ottoboni, G. (2008). On the relations between action planning, object identification, and motor representations of observed actions and objects. *Cognition*, 108(2), 444-465. doi: <http://dx.doi.org/10.1016/j.cognition.2008.03.007>
- Valyear, K. F., Culham, J. C., Sharif, N., Westwood, D., & Goodale, M. A. (2006). A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: A human fMRI study. *Neuropsychologia*, 44(2), 218-228.
- van Elk, M., van Schie, H. T., & Bekkering, H. (2011). Imitation of hand and tool actions is effector-independent. *Experimental Brain Research*, 214(4), 539-547.
- Vingerhoets, G. (2008). Knowing about tools: Neural correlates of tool familiarity and experience. *NeuroImage*, 40(3), 1380-1391. doi: 10.1016/j.neuroimage.2007.12.058
- Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., & Fink, G. R. (2004). Neural correlates of first-person perspective as one constituent of human self-consciousness. *Journal of Cognitive Neuroscience*, 16(5), 817-827.
- Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: Perspective matters. *Neuropsychologia*, 41(8), 941-951. doi: 10.1016/S0028-3932(02)00319-6
- Wadsworth, H. M., & Kana, R. K. (2011). Brain mechanisms of perceiving tools and imagining tool use acts: A functional MRI study. *Neuropsychologia*, 49(7), 1863-1869. doi: 10.1016/j.neuropsychologia.2011.03.010
- Wagner, A. D., Desmond, J. E., Domb, J. B., Glover, G. H., & Gabrieli, J. D. E. (1997). Semantic repetition priming for verbal and pictorial knowledge: A functional MRI study of left inferior prefrontal cortex. *Journal of Cognitive Neuroscience*, 9(6), 714-726. doi: 10.1162/jocn.1997.9.6.714
- Walker, P. (1978). Binocular rivalry: central or peripheral selective processes? *Psychological Bulletin*, 85(2), 376-389.
- Watanabe, T., Náñez, J. E., Koyama, S., Mukai, I., Liederman, J., & Sasaki, Y. (2002). Greater plasticity in lower-level than higher-level visual motion processing in a passive perceptual learning task. *Nature Neuroscience*, 5(10), 1003-1009.
- Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, 20(2), 158-177. doi: 10.1037/h0074428
- Watson, J. B., & Rayner, R. (1920). Conditioned emotional reactions. *Journal of Experimental Psychology*, 3(1), 1-14.
- Waydo, S., Kraskov, A., Quiroga, R. Q., Fried, I., & Koch, C. (2006). Sparse representation in the human medial temporal lobe. *The Journal of Neuroscience*, 26(40), 10232-10234.
- West, W. C., & Holcomb, P. J. (2002). Event-related potentials during discourse-level semantic integration of complex pictures. *Cognitive Brain Research*, 13(3), 363-375. doi: 10.1016/s0926-6410(01)00129-x
-

-
- Wheaton, L. A., & Hallett, M. (2007). Ideomotor apraxia: A review. *Journal of the neurological sciences*, 260(1), 1-10.
- Wheatstone, C. (1838). Contributions to the physiology of vision. Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, 128, 371-394.
- Wiedermann, J. (2012). Mirror neurons, embodied cognitive agents and imitation learning. *Computing and Informatics*, 22(6), 545-559.
- Willems, R. M., & Hagoort, P. (2007). Neural evidence for the interplay between language, gesture, and action: A review. *Brain and Language*, 101(3), 278-289. doi: 10.1016/j.bandl.2007.03.004
- Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: Neural evidence from right-and left-handers. *Psychological Science*, 21(1), 67-74.
- Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2009). Body-specific motor imagery of hand actions: Neural evidence from right-and left-handers. *Frontiers in Human Neuroscience*, 3. doi: 10.3389/neuro.09.039.2009
- Williams, J. H. G., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience & Biobehavioral Reviews*, 25(4), 287-295. doi: [http://dx.doi.org/10.1016/S0149-7634\(01\)00014-8](http://dx.doi.org/10.1016/S0149-7634(01)00014-8)
- Wilson, H. R., Blake, R., & Lee, S. H. (2001). Dynamics of travelling waves in visual perception. *Nature*, 412, 907-910.
- Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, 9(4), 625-636. doi: 10.3758/bf03196322
- Winawer, J., Huk, A. C., & Boroditsky, L. (2008). A motion aftereffect from still photographs depicting motion. *Psychological Science*, 19(3), 276-283.
- Witzel, C., Valkova, H., Hansen, T., & Gegenfurtner, K. (2011). Object knowledge modulates colour appearance. *i-Perception*, 2(1), 13-49.
- Wurm, L. H., Legge, G. E., Isenberg, L. M., & Luebker, A. (1993). Color improves object recognition in normal and low vision. *Journal of Experimental Psychology: Human Perception and Performance*, 19(4), 899-911. doi: 10.1037/0096-1523.19.4.899
- Yakovlev, V., Fusi, S., Berman, E., & Zohary, E. (1998). Inter-trial neuronal activity in inferior temporal cortex: a putative vehicle to generate long-term visual associations. *Nature Neuroscience*, 1(4), 310-317.
- Yao, B., & Fei-Fei, L. (2010, 13-18 June 2010). *Modeling mutual context of object and human pose in human-object interaction activities*. Paper presented at the Computer Vision and Pattern Recognition (CVPR), 2010 IEEE Conference on.
- Yee, E., Ahmed, S. Z., & Thompson-Schill, S. L. (2012). Colorless green ideas (can) prime furiously. *Psychological Science*, 23(4), 364-369.
- Yee, E., Chrysikou, E. G., Hoffman, E., & Thompson-Schill, S. L. (2013). Manual experience shapes object representations. *Psychological Science*, 24. doi: 10.1177/0956797612464658
- Yip, A. W., & Sinha, P. (2002). Contribution of color to face recognition. *Perception*, 31(8), 995-1004.
- Young, G. (2006). Are different affordances subserved by different neural pathways? *Brain and Cognition*, 62(2), 134-142. doi: <http://dx.doi.org/10.1016/j.bandc.2006.04.002>
- Yu, K., & Blake, R. (1992). Do recognizable figures enjoy an advantage in binocular rivalry? *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 1158-1173.
- Zhu, Q., Yeh, M., Cheng, K., & Avidan, S. (2006). *Fast human detection using a cascade of histograms of oriented gradients*. Paper presented at the Computer Vision and Pattern Recognition, 2006 IEEE Computer Society Conference on.
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APPENDIX A

Published version of Study 1: Associative Learning with Mental Imagery

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Conditioning the Mind's Eye: Associative Learning With Voluntary Mental Imagery

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Abstract

Many treatments for anxiety utilize associative learning theory and involve mental imagery components. However, the roles associative learning and imagery play in anxiety disorders and their treatments are still largely unknown. Here we show that voluntary mental imagery can undergo associative learning in the same manner as normal sensory perception. After conditioning voluntary mental images with emotion-evoking stimuli, perceptual stimuli of the same content were found to produce the associated emotional response—indicating generalization from imagery to perception. This associative learning with imagery was found to be orientation selective and could not be accounted for by alternative, non-imagery-based interpretations of the data. These results support pictorial theories of mental imagery by indicating the interchangeability of imagery and perception in associative learning and demonstrate that voluntary mental images can drive associative learning, providing a mechanistic account of clinical practice involving mental imagery.

Keywords

mental imagery, associative learning, learning, classical conditioning, Pavlovian conditioning, anxiety disorders

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In recent times the field of learning has seen rapid growth in the areas of fear and hedonic processes (Lissek et al., 2005), perceptual learning (Sasaki, Nanez, & Watanabe, 2010), motor learning (Jeannerod, 1995), and learning driven by neural-feedback signals (Shibata, Watanabe, Sasaki, & Kawato, 2011). The learning paradigms of conditioning, counterconditioning, and extinction form the backbone of the underlying mechanisms of many psychological disorders and their treatments (Milad, Rauch, Pitman, & Quirk, 2006; Myers & Davis, 2002; Rauch, Shin, & Phelps, 2006). Many behavioral interventions for psychological disorders rely on counterconditioning or extinction-like approaches as part of cognitive behavioral therapy (CBT) to produce behavior change. Exposure, for example, is a key component of many effective treatment strategies for anxiety disorders. A clinically anxious individual may receive real or imagined exposure to his or her feared stimulus or situation with the goal of reducing fear and anxiety (Holmes & Mathews, 2010; Hunt & Fenton, 2007). Progress in understanding the many aspects of learning has led to great improvements in the

treatment of many mental illnesses, such as anxiety disorders and various phobias, which are often modeled on fear learning (Lissek et al., 2005; Milad et al., 2006; Rauch et al., 2006; Watson & Rayner, 1920).

Treatments for disorders of anxiety often focus on their imagery-like symptoms (Edwards, 2007; Holmes & Mathews, 2010). One such treatment is CBT with imagery rescripting (Arntz, Tiesema, & Kindt, 2007; Holmes, Arntz, & Smucker, 2007; Smucker, Dancu, Foa, & Niederee, 1995), wherein patients are directed to focus on and then transform the content of their distressing mental imagery. Though such techniques have been effective for anxiety sufferers, current imagery-based treatments show room for improvement (Bradley, Greene, Russ, Dutra, & Westen, 2005; Foa & Meadows, 1997; Harvey, 2003). A greater understanding of the mechanisms of these disorders and

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their treatment options is pivotal for the development of new treatment methods that more directly address their underlying causes.

Mental imagery, a perceptual-like experience without corresponding sensory input, is typically based on the memories of previously perceived stimuli. The generation of mental images can be voluntary, explicitly crafted by the observer, or involuntary, automatically cued by some external stimulus (Albright, 2012; Brewin, Gregory, Lipton, & Burgess, 2010; Holmes & Mathews, 2010). For anxiety sufferers these images are typically involuntary and related to the individual's specific fears or concerns (Brewin et al., 2010; Dadds, Hawes, Schaefer, & Vaka, 2004; Hirsch & Holmes, 2007). Such imagery is predominantly visual, but can also be auditory and tactile (Ehlers & Steil, 1995). Instances of distressing mental imagery tend to precede or amplify other nonimagery symptoms (Hirsch, Mathews, Clark, Williams, & Morrison, 2006; Holmes, Geddes, Colom, & Goodwin, 2008; Holmes & Mathews, 2010; Pitman et al., 1990), indicating that they play a key role in the maintenance of the disorder. Unfortunately, a comprehensive understanding of what mental imagery is and how it fits into current theories of associative learning is still missing.

Associative learning has been well documented with various perceptual stimuli (De Houwer, Thomas, & Baeyens, 2001; Martin & Levey, 1978; Milad et al., 2006). A review by Dadds, Boybjerg, Redd, and Cutmore (1997) suggested that mental imagery and perception are highly similar processes that might play interchangeable roles in associative learning. This view has gained support from the finding that the processes involved in imagery and perception can share similar patterns of neural activity (Behrmann, 2000; Slotnick, Thompson, & Kosslyn, 2005). More recently, it has been found that repeated generation of a mental imagery stimulus will subsequently improve an observer's ability to discriminate between perceptual stimuli (Tartaglia, Bamert, Mast, & Herzog, 2009), but repeated training of imagery does not lead to improvements in imagery itself (Rademaker & Pearson, 2012). In general, the evidence seems to indicate that mental imagery can act like perception (Kosslyn, Ganis, & Thompson, 2001; Pearson, Clifford, & Tong, 2008) and the relative strength of imagery is closely tied to the observer's subjective reports of its vividness (Pearson, Rademaker, & Tong, 2011).

In the current study we sought to determine whether voluntary mental imagery could undergo associative learning as visual perception does. Specifically, we first sought to verify that our task could produce significant associative learning effects for perceptual stimuli (Experiment 1); we then utilized this same task to associate specific content of mental imagery with a set of emotion-evoking photographs (Experiment 2). The formation of these kinds of associations can result in evaluative

conditioning (De Houwer et al., 2001; Martin & Levey, 1978), wherein the perceptual or imagery content will gain new emotional significance subsequently inducing fear-indicant responses, much like the original emotion-evoking photographs.

To test the emotional valence of the voluntarily generated mental images, we used an affective priming method (Fazio, Sanbonmatsu, Powell, & Kardes, 1986; Hermans, De Houwer, & Eelen, 1994). If the imagery patterns become associated with a specific emotion, they should facilitate the recognition of subsequently presented photographs with matching emotional content. The magnitude of this facilitation should be indicative of the strength of associative learning with imagery.

In addition, we sought to determine whether this associative learning can occur without color information (Experiment 3). It has been suggested that various colors can have strong emotional associations (Gao et al., 2007; Kaya & Epps, 2004). Hence, we investigated associative learning with the same paradigm using achromatic imagery. Two additional tests were also conducted to rule out a potential nonmental imagery account of our results.

Finally, we assessed the orientation specificity of the associative learning with mental imagery (Experiment 4). Evidence shows that neurons within low-level visual cortex are sensitive to slight spatial rotations of visual stimuli, whereas activity in higher-level brain areas appears to be relatively insensitive (Blakemore & Campbell, 1969; Fang, Murray, Kersten, & He, 2005; Hubel & Wiesel, 1968). To show that associative learning for mental imagery is similarly orientation specific would indicate that such learning is contingent on activity within these low-level visual areas, such as primary visual cortex. Consequently, this would improve our understanding of the mechanisms underlying disorders involving mental imagery symptomatology. This would also suggest that the effectiveness of treatments for anxiety might be enhanced by focusing on the low-level sensory aspects of the distressing imagery symptoms. In addition, showing that imagery and perception have shared neural processing in relation to associative learning in early visual cortex would provide compelling evidence that visual mental imagery can be pictorial in nature.

Materials and Method

Participants

A total of 143 University of New South Wales students were recruited for the current study ($n_{\text{Experiment 1}} = 79$, $n_{\text{Experiment 2}} = 30$, $n_{\text{Experiment 3}} = 19$, $n_{\text{Experiment 4}} = 15$). All participants were students from the University of New South Wales who gave written, informed consent before the start of each experimental session. New participants were

recruited for each experiment via Web advertisements. Fewer participants were recruited for each successive experiment in an attempt to produce a more conservative replication of the original results and efficient use of resources. Course credit or money was awarded upon completion of the study. The current study received ethical approval from the local committee.

Stimuli

All stimuli were created and presented using Psychtoolbox (Brainard, 1997) for Matlab (Version 7.10.0 R2010a) on a Mac mini computer and displayed on a 27 × 35.5 cm Philips 109P4 monitor at a resolution of 1152 × 870 at 75 Hz. Stimuli were presented on a black background with a circular fixation mark (diameter = 0.62°) in the center of the screen.

In Experiments 1, 2, and 4, two different Gabor patterns ($\sigma = 4^\circ$; SF = 1 cycles/degree) were used as conditioned stimuli: a red vertical pattern (CIE color space $x = 0.6$, $y = 0.37$) and a green horizontal pattern (CIE $x = 0.27$, $y = 0.62$). In Experiment 3, the achromatic imagery experiment, both Gabor patterns were grayscale (contrast = 100%; max luminance = 45.0 cd/m²). In all experiments the background was black (max luminance = 0.01 cd/m²), as background luminance has been shown to attenuate imagery generation (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). Photographs from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008) were used as unconditioned stimuli. These photographs were split into two categories based on their rating norms. "Pleasant" IAPS photos were those rated low on arousal and high on pleasantness. "Aversive" IAPS photos were those rated high on arousal and low on pleasantness. Photos rated high on both arousal and pleasantness were not used, as they are mostly sexually explicit in nature. Photos rated low on both scales were not used as they had no emotional content. In the associative learning phase a set of 12 photos (6 pleasant, 6 aversive) was used, and in the test phase a different set of 12 was used.

In Experiment 4, the orientation specificity experiment, the two original Gabor patterns (red = 90°, green = 0°) were accompanied by similar patterns that had been rotated 22° and 45°. Also, the number of IAPS photos was increased; 12 photographs were added to the associative learning phase (6 pleasant, 6 aversive) and 36 were added to the test phases (18 pleasant, 18 aversive). These additional photos were added to accommodate an increase in the total number of trials.

Procedure

All participants were seated in a dark room with their heads stabilized on a headrest 57 cm from the monitor.

Participants undergoing associative learning for mental imagery had previously been shown both Gabor patterns and instructed to imagine them when a corresponding letter cue was shown. In Experiments 2 and 4 the letter cue "R" corresponded to the red vertical Gabor and "G" corresponded to the green horizontal Gabor. In Experiment 3, the achromatic imagery experiment, the letter cue "V" corresponded to the vertical Gabor and "H" corresponded to the horizontal Gabor. Participants were instructed to fixate on a circular fixation mark in the center of the screen for the duration of the experimental session. Figure 1 shows the trial designs for the two associative learning phases and three test phases used in the current study.

It is important to note that voluntary mental imagery was used only in the associative learning phase and not in the test phase. Hence, any effect of learning in this design is inherently a generalization, or crossover, from an imagined representation to a perceptual one.

Associative learning phase. At the start of each experimental session participants completed multiple trials of the associative learning task. As shown in Figure 1a, the perceptual trials started with the presentation of one of the two randomly chosen perceptual Gabors for 1.5 s, followed immediately by the emotional photograph for 1.5 s. The screen then remained blank for a 2-s intertrial interval. As shown in Figure 1b, the mental imagery trials started with the presentation of one of the two randomly chosen letter cues for 1.5 s. This was followed by a blank screen for 5.5 s, during which the participants were to imagine the pattern indicated by the letter cue. Then either a pleasant or aversive photograph was displayed for 1.5 s, followed by a 2-s intertrial interval wherein the screen remained blank. In both learning tasks the participants were required to press the space bar as soon as the photograph was presented to help them maintain vigilance. This kind of associative learning technique is commonly used across the literature to associate emotional content with neutral sensory stimuli (De Houwer et al., 2001).

Throughout the associative learning phase the relationship between the Gabor patterns and their associated emotion-evoking photographs remained constant. The stimulus associations were counterbalanced across participants: For half of the participants the vertical Gabor patterns were paired with aversive photos and the horizontal Gabors with pleasant photos, and vice versa for the other half. Each Gabor was paired with all of its corresponding emotion-evoking photographs an equal number of times. These Gabor-photograph pairs were presented in a random order.

In Experiment 1 a total of 40 associative learning trials were conducted. In Experiments 2 and 3 a total of 84 learning trials with mental imagery were conducted. In Experiment 4 the number of learning trials was increased

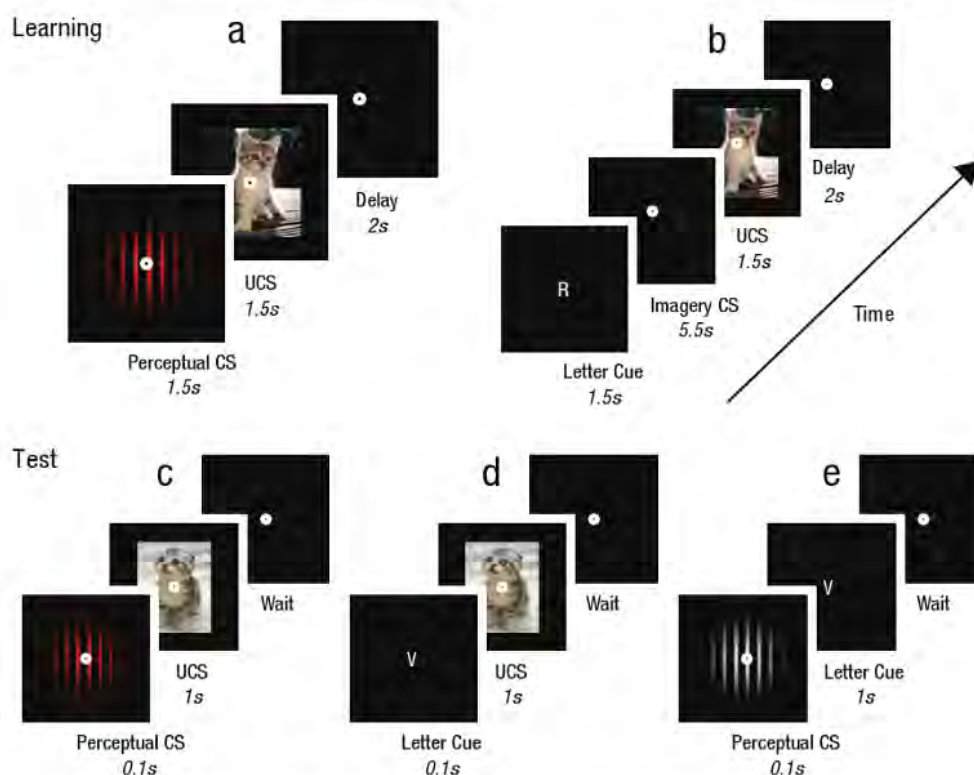


Fig. 1. Experimental timelines. (a) Experiment 1: associative learning with perceptual stimuli. (b) Experiments 2, 3, and 4: associative learning with mental imagery. (c) All Experiments: test of association between perceptual Gabor and emotional photograph. (d) Experiment 3: test of association between letter cue and emotional photograph. (e) Experiment 3: test of association between perceptual Gabor and letter cue.

Note: Photographs shown above are not actual International Affective Picture System photographs, as they are not to be used outside experimental settings.

to 144, with 102 trials at the beginning of the study and another 42 halfway through the test phase. This “top-up” was done to accommodate for any potential extinction due to the increased number of test trials.

Gabor pattern: test phase. Participants in all experiments then completed 120 trials of a choice reaction time task on a new set of emotion-evoking photographs to test the strength of the previously learned associations. Figure 1c shows the design of a Gabor pattern test trial. One of the two previously imagined Gabor patterns was presented for 100 ms, immediately followed by the presentation of an IAPS photograph for 1 s. Participants were required to judge the emotional content of the photographs upon their presentation as quickly and accurately as possible. They could judge the photos as either “Pleasant” or “Aversive” by pushing either the 1 or 3 button on the keyboard. Participants were instructed to respond as fast as possible without sacrificing accuracy. If

conditioning did occur, then reaction times should be faster when the pattern’s associated emotion accurately predicts the emotional content of the subsequent photograph.

In Experiment 4 the number of Gabor test trials was increased to 288, split evenly among the six Gabor pattern orientations (red 90°, red 68°, red 45°, green 0°, green 22°, and green 45°) and presented in random order.

Letter cue: test phase. Participants in Experiment 3 completed an additional priming task to test the strength of any learned associations between the emotional content and the letter cues used in the associative learning task. As Figure 1d shows, this letter cue test phase was identical to the Gabor test phase except that the Gabor patterns were replaced with their corresponding letter cues. The order of test phase presentation was counterbalanced between participants, with half of the

participants completing the Gabor test first and the other half completing the letter cue test first.

Gabor cue: test phase. Participants in Experiment 3 also completed a third test to directly measure the strength of any learned association between the Gabors and their corresponding letter cues. Figure 1e shows the trial design for testing the priming from the Gabor patterns for the letter cues. Participants completed a total of 40 trials, consisting of 10 presentations for each combination of Gabor and letter cue. In each trial one of the two previously imagined Gabor patterns was *physically* presented for 100 ms, followed immediately by one of the two letter cues for 1 s. Upon presentation of a letter cue, participants were required to press the corresponding key on the keyboard as quickly and accurately as possible. This Gabor cue test was always completed last.

Data preparation

Incorrect emotionality judgments were removed from the data set, as were individual participant reaction times that

were shorter than 250 ms, longer than 2,500 ms, or beyond 2.5 *SD* from that participant's mean. In addition, 2 outlying participants were excluded from analysis in Experiment 3 due to having average mismatch-match scores beyond 2.5 *SD* of the overall group mean.

To measure the strength of associative learning for the voluntary mental imagery, each participant's reaction-time data were split into matched and mismatched trials. Matched trials included the stimulus pairs that were presented during the associative learning, whereas mismatched trials consisted of stimulus pairs that were not. If matched trials produced significantly faster reaction times, this would be indicative of affective priming, suggesting that the previously neutral Gabor patterns had gained emotional content due to associative learning.

Results

Experiment 1: perceptual stimuli

Figure 2a shows the data from the Gabor pattern test phase following associative learning with perceptual

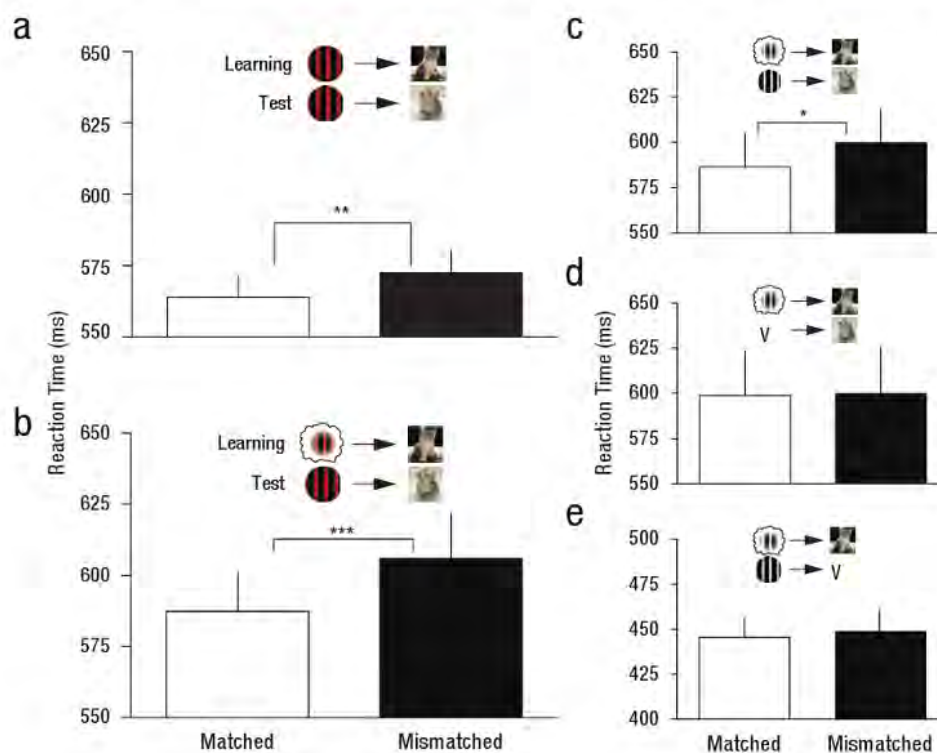


Fig. 2. Mean reaction times for matched and mismatched stimuli during the test phases. Data indicate associative learning effects from sensory stimuli and imagined stimuli. (a) Experiment 1: Gabor-photo test preceded by perceptual conditioning ($n = 79$). (b) Experiment 2: Gabor-photo test preceded by imagery conditioning ($n = 30$). (c) Experiment 3: Achromatic Gabor-photo test preceded by achromatic imagery conditioning ($n = 17$). (d) Experiment 3: cue-photo test preceded by achromatic imagery conditioning ($n = 17$). (e) Experiment 3: achromatic Gabor-cue test preceded by achromatic imagery conditioning ($n = 17$).

Note: Photographs shown above are not actual International Affective Picture System photographs, as they are not to be used outside experimental settings. Error bars show ± 1 SEM.

* $p < .05$. ** $p < .005$. *** $p < .001$.

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Gabor patterns. A paired-samples comparison shows that reaction times were significantly faster when the preceding pattern's associated emotion matched the emotional photograph ($M = 563.9$ ms, $SEM = 7.84$ ms) than when it was mismatched ($M = 572.5$ ms, $SEM = 8.05$ ms), $t(78) = 3.29$, $p = .002$, $\eta^2 = .12$. This shows that our task can produce associative learning for perceptual stimuli.

Experiment 2: mental imagery

Figure 2b shows the data from the Gabor pattern test phase following associative learning with mental imagery. A paired-samples comparison shows that reaction times were significantly faster when the preceding pattern's associated emotion matched the emotional content of the photograph ($M = 587.44$ ms, $SEM = 13.95$ ms) than when it was mismatched ($M = 606$ ms, $SEM = 15.82$ ms), $t(29) = 4.14$, $p < .001$, $\eta^2 = .37$. This finding suggests that associative learning can occur between mentally generated stimuli and the emotional content of photographs.

Experiment 3: achromatic mental imagery

Figure 2c shows the data from the Gabor test phase following associative learning with achromatic mental imagery. A paired-samples comparison shows significantly faster reaction times when the pattern's previously associated emotion matched the emotional photograph ($M = 586.7$ ms, $SEM = 18.05$ ms) than when it was mismatched ($M = 599.7$ ms, $SEM = 18.6$ ms), $t(16) = 2.50$, $p = .023$, $\eta^2 = .28$. These data once again show a significant effect of associative learning with mental imagery. In addition, this replication provides further evidence that mental imagery can undergo associative learning, and also suggests that color information is not necessary for such associative learning.

However, one possible alternative explanation of the data is that during the test phase the perceptual Gabor patterns induced a representation of the corresponding letter cues, and these letter cues were actually driving the affective priming shown in Figure 2c. To assess this alternative account, each participant as part of Experiment 3 completed two additional test phases. These tests measured the strength of the associations between the letter cues and the photographs, and between the perceptual Gabor patterns and the letter cues. If *both* tests show significant priming, this would suggest an alternative explanation of our data and that mental imagery did not necessarily undergo associative learning.

Figure 2d shows the data from the letter cue test phase following associative learning with achromatic mental imagery. This test was conducted to determine if there was any direct link between the imagery cues and the

emotion-evoking photographs. Associative learning found in this task would be attributable to either conditioning between the cue and the emotional photographs, or indirect association via the mental imagery Gabors. However, a paired-samples comparison showed no significant difference in the reaction times between matched ($M = 598.9$ ms, $SEM = 24.44$ ms) and mismatched pairs ($M = 599.9$ ms, $SEM = 25.69$ ms), $t(16) = 0.21$, $p = .838$. These data indicate that the letter cues did not undergo significant associative learning according to our measure.

Figure 2e shows the data from the Gabor-cue test phase following associative learning with achromatic mental imagery. This test was conducted to determine if the Gabor patterns were associatively linked to the letter cues. A paired-samples comparison showed no significant difference in reaction times between the matched ($M = 445.7$ ms, $SEM = 10.73$ ms) and mismatched conditions ($M = 449.1$ ms, $SEM = 11.78$ ms), $t(16) = 0.43$, $p = .675$. This indicates that participants did not reliably associate the Gabor patterns with their letter cues, despite being shown physical versions of the Gabors at the start of the experiment and being instructed to imagine them when the appropriate letter cue was shown.

Experiment 4: orientation specificity of mental imagery

Figure 3 shows the mean reaction-time differences between the matched and mismatched trials for Gabor

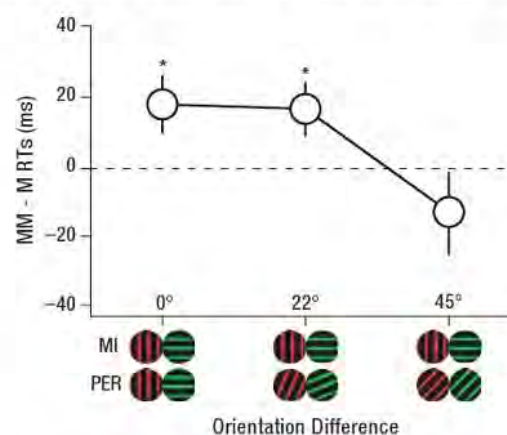


Fig. 3. Reaction time difference between mismatched and matched pairs using Gabors rotated 0°, 22°, and 45° from those used in the associative learning phase.

Note: MI = mental imagery Gabors used in the associative learning phase. PER = perceptual Gabors used the test phase. Error bars show between subjects ± 1 SEM. Significant differences shown indicate paired-samples analyses between matched and mismatched conditions for individual orientations ($n = 15$).

* $p < .05$.

patterns rotated 0°, 22°, and 45°. A significant change was found across the three levels of orientation, repeated measures ANOVA, $F(2, 28) = 4.11$, $p = .042$, $\eta^2 = .23$, $n = 15$. Post hoc analyses showed that the difference scores for Gabors rotated 0° ($M = 18.05$ ms, $SEM = 7.89$ ms) and 22° ($M = 16.76$ ms, $SEM = 7.43$ ms) were significantly greater than Gabor patterns rotated 45° ($M = -12.06$ ms, $SEM = 11.75$ ms), $p < .05$. These results show that the associative learning was specific to the given spatial orientation of the Gabor patterns.

We then sought to determine if a significant amount of associative learning had occurred in any of the three orientation conditions. For each test pattern orientation, the matched and mismatched reaction times were compared in the same manner as the previous experiments. Reaction times for 0° rotated Gabors were significantly faster for matched pairs ($M = 640.98$ ms, $SEM = 13.52$ ms) than mismatched pairs ($M = 659.03$ ms, $SEM = 16.51$ ms), $t(14) = 2.29$, $p = .038$, $\eta^2 = .27$, providing yet another replication of our findings from Experiments 2 and 3. Reaction times for 22° rotated Gabors were also significantly faster for matched pairs ($M = 646.86$ ms, $SEM = 12.13$ ms) than mismatched pairs ($M = 663.62$ ms, $SEM = 16.45$ ms), $t(14) = 2.26$, $p = .041$, $\eta^2 = .27$, indicating a degree of generalization between similarly oriented Gabors. However, when the patterns were rotated 45°, the reaction times for matched pairs ($M = 656.66$ ms, $SEM = 17.26$ ms) were not significantly different from mismatched pairs ($M = 644.60$ ms, $SEM = 13.13$ ms), $t(14) = 1.03$, $p = .322$. In addition, these data also show that the Gabor pattern colors were unable to independently elicit the learned emotion, as only the spatial orientation changed and not the colors. This result supports that of Experiment 3 (achromatic stimuli), suggesting that associative learning with mental imagery can be feature specific in the domain of vision.

General Discussion

We have shown evidence that associative learning can occur for voluntary mental imagery. Perceptual Gabor patterns were found to elicit a measurable emotional response after voluntary mental imagery of the same Gabors was subjected to associative learning. Hence, by definition, our dependent measure includes generalization from an internally generated mental image to sensory perception. The observed effects were substantial across all studies, similar to previous findings of associative learning with perceptual stimuli (De Houwer et al., 2001; Martin & Levey, 1978; Milad et al., 2006).

Our results cannot be accounted for by associative learning involving the imagery cues, as opposed to the imagery content. We tested an alternative hypothesis consisting of associative learning for the imagery cues in

conjunction with the test phase Gabor patterns inducing recall of these imagery letter cues. This compound-alternative hypothesis was not supported by our two control experiments.

If this nonimagery hypothesis were valid, then the imagery cues should be able to prime the emotion-evoking IAPS images, and the perceptual Gabors should be able to prime the imagery cues. However, we found that the imagery cues did not prime the emotion-evoking photographs (Figure 2d), and the perceptual Gabor patterns did not prime the imagery cues (Figure 2e), thus ruling out this alternative account. In addition, the failure of this alternative account may be explained by the temporal relationships between the stimuli. It has been shown that the strength of a learned association between two stimuli is negatively correlated with the temporal distance and number of stimuli presented between them (Balsam, Drew, & Gallistel, 2010). Hence, the lack of associative learning for the letter cues may simply be due to the large amount of time between the cues and the emotion-evoking photographs.

In primates, a strong candidate for the neural mechanism of associative learning is the inferior temporal (IT) cortex (Jones, 1974; Meyer & Yates, 1955; Miyashita, 1993; Sakai & Miyashita, 1991; Yakovlev, Fusi, Berman, & Zohary, 1998). Both single cell physiology and human neuropsychological studies demonstrating that damage to the IT cortex can lead to impairments in visual recognition and learning together suggest associative learning occurs in high-level IT cortex. Here, we have demonstrated that the content of voluntary mental imagery can undergo a form of associative learning that is selective for spatial orientation. These findings support previous research showing orientation specificity for mental imagery (Pearson et al., 2008), though the present findings show a broader degree of orientation tuning than previously reported. Orientation specificity has been shown to be a hallmark of early levels of processing in the visual cortex (Blakemore & Campbell, 1969; Hubel & Wiesel, 1968; Ling, Pearson, & Blake, 2009). Our findings show that associative learning with voluntary mental imagery is sensitive to spatial orientation, indicating the involvement of these early visual processing areas. This is a rather surprising finding as associative learning is thought to involve processing within higher-level areas (Jones, 1974; Meyer & Yates, 1955; Miyashita, 1993; Sakai & Miyashita, 1991; Yakovlev et al., 1998).

Mental imagery and perception are similar processes

These results provide further evidence that mental imagery and sensory perception can involve overlapping mechanisms. However, imagery is an inherently private

affair, making it difficult to study using traditional research methods, which has resulted in many compelling criticisms of the research. The founder of the behaviorism movement, John B. Watson (1913), argued that mental imagery plays no role in thought or behavior—the generation of mental images simply does not occur. This idea was revisited by B. F. Skinner (1977), who claimed that everything required to explain human behavior can be found within the environment. Zenon Pylyshyn (1973, 1981) conceded that mental imagery can occur but argued that the term is misleading, as what people refer to as imagery is actually the generation of verbal descriptions and not pictorial representations.

With the advent of modern brain imaging techniques it has become possible to observe the neural processes involved in mental imagery tasks. Studies using functional magnetic resonance imaging (Ganis, Thompson, & Kosslyn, 2004; Knauff, Kassubek, Mulack, & Greenlee, 2000; Mellet, Petit, Mazoyer, Denis, & Tzourio, 1998; O'Craven & Kanwisher, 2000), single cell neurophysiology (Kreiman, Koch, & Fried, 2000), and transcranial magnetic stimulation (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Sparing et al., 2002) have provided a wealth of neural evidence that common brain areas can be used for both visual imagery and visual perception. In addition, individuals with cortical damage specific to perceptual areas tend to experience deficits in the ability to generate mental imagery (Barton & Cherkasova, 2003; Farah, 1984; Farah, Levine, & Calvanio, 1988), but this is not always the case (Bridge, Harrold, Holmes, Stokes, & Kennard, 2012). For normal observers, perception has been shown to interfere with concurrent mental image generation (Pearson et al., 2008; Sherwood & Pearson, 2010), and the content of mental imagery has been shown to bias subsequent visual perception in a manner specific to early sensory processes (Pearson et al., 2008). The current study builds on this literature by showing that mental imagery can be used in place of perceptual stimuli in an associative learning task, and that this learning is specific to the spatial orientation of the imagined stimuli. Taken together, these studies provide compelling evidence that mental imagery can indeed be pictorial.

Clinical relevance

Fear learning is a type of associative learning wherein a neutral stimulus will come to display fear-indicant responses after being paired with an aversive stimulus (Öhman & Mineka, 2001). Influential models for numerous mental illnesses tend to include fear learning components, such as posttraumatic stress disorder, obsessive-compulsive disorder, and various phobias (Büchel & Dolan, 2000; Lissek et al., 2005; Milad et al., 2006; Rauch et al., 2006; Rosen & Schulkin, 1998; Watson & Rayner,

1920). These disorders often involve instances of intrusive and harmful mental imagery (Hackmann, Clark, & McManus, 2000; Hirsch & Holmes, 2007), which seem to cause or amplify the distress experienced (Hirsch et al., 2006; Holmes et al., 2008; Holmes & Mathews, 2010; Pitman et al., 1990). CBT and other treatments for anxiety often include mental imagery components (Holmes & Mathews, 2010), such as imaginal exposure or imagery rescripting (Arntz et al., 2007). Unfortunately the underlying mechanisms of these imagery-based treatments are not fully understood.

Our findings show that the content of voluntary mental imagery can gain new (emotional) meaning through association with emotion-evoking stimuli. Hence, the present data suggest that the efficacy of these imagery-based treatments can be explained in part by associative learning theory. These treatments involve the manipulation of mental imagery content to alter learned associations. In imaginal exposure, the distressing mental images are repeatedly generated in a nonaversive setting, resulting in the gradual decrease of anxiety symptoms (Tarrier et al., 1999). In addition, in imagery rescripting the patient actively attempts to change the content of their distressing mental images by associating them with pleasant or neutral mental images (Smucker et al., 1995). The orientation specificity observed in the current study suggests that the associative learning components of these treatments might involve activity within low-level sensory areas of the brain.

The effectiveness of imagery-based treatments for anxiety might actually be enhanced by focusing on the low-level sensory aspects of the distressing imagery symptoms as opposed to the semantic content. The orientation specificity observed in the current study supports this suggestion by providing evidence that it is the sensory content of the voluntary imagery that is driving the mechanisms of learning, which likely involves low-level sensory areas of the brain. Additional support comes from the recent demonstration that engaging low-level sensory systems, not high-level semantic systems, can help prevent the formation of distressing flashbacks after experiencing trauma (Holmes, James, Kilford, & Deerpore, 2010). Though this particular study did not use mental imagery stimuli, the current study and many others have shown that visual imagery can act in a similar manner to visual perception (Kosslyn et al., 2001; Pearson et al., 2008). Therefore, it seems likely that highly effective treatment methods could be developed that focus on engaging low-level sensory systems.

Conclusion

We have shown that associative learning can occur between a voluntarily generated mental image and the

emotional content of a photograph, providing further support for the pictorial theory of mental imagery. For the first time we have demonstrated that a stimulus not physically present can become emotionally charged after its voluntarily generated mental image is paired with an emotion-evoking photograph. Associative links will form between these sensory representations even though they are never physically presented together in the world. This novel finding adds to the previous research on associative learning for mental imagery (Dadds et al., 1997) by showing that mental images can be effectively used as conditioned stimuli, thus providing a unique contribution to the rapidly growing field of learning (Jeannerod, 1995; Lissek et al., 2005; Sasaki et al., 2010; Shibata et al., 2011).

It will be exciting for future work to compare the relative strength of associative learning with voluntary imagery and normal perception. There have been claims that triggering memories perceptually prior to learning regimes can boost memory reconsolidation, which in turn modulates the effects of associative learning (Monfils, Cowansage, Klann, & LeDoux, 2009; Schiller et al., 2009; Schiller & Phelps, 2011). If simply activating memories in this manner has the power to change the outcome of learning, it will be of particular interest to see if mental imagery, a process that inherently involves memory retrieval, initiates similar or even stronger reconsolidation of memories. The prospect that mental imagery could be utilized to simultaneously target memories and make them malleable and more receptive to long-term change is an exciting possibility as many psychological disorders are rooted in traumatic memories. Such breakthroughs would have a profound impact on the outcome of clinical practice that utilizes extinction-like paradigms.

Our findings suggest that the sensory components of imagery are instrumental to its role in associative learning. On a general level this has some interesting implications. All the characteristics known to modulate imagery should logically be applicable to regulating associative learning with mental imagery. For example, research has shown that uniform passive perception, simply being in a bright environment, disrupts the generation of mental images (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010); the brighter the environment, the greater the attenuation of imagery. It will be intriguing for future research to investigate the role of the perceptual environment in associative learning with mental imagery, and how this extends to clinical practice. For example, is imagery rescripting more effective in dark environments or with the eyes closed because imagery is stronger?

In summary, the current study demonstrates that voluntary mental imagery can drive the mechanisms of associative learning. This provides strong laboratory support for clinical practice that utilizes both mental imagery and regimes based on associative learning.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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References

- Albright, T. D. (2012). On the perception of probable things: Neural substrates of associative memory, imagery, and perception. *Neuron*, 74(2), 227–245.
- Arntz, A., Tiesema, M., & Kindt, M. (2007). Treatment of PTSD: A comparison of imaginal exposure with and without imagery rescripting. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 345–370. doi:10.1016/j.jbtep.2007.10.006
- Balsam, P. D., Drew, M. R., & Gallistel, C. R. (2010). Time and associative learning. *Comparative Cognition & Behavior Reviews*, 5, 1–22. doi:10.3819/ccbr.2010.50001
- Barton, J. J. S., & Cherkasova, M. (2003). Face imagery and its relation to perception and covert recognition in prosopagnosia. *Neurology*, 61(2), 220–225. doi:10.1212/01.wnl.0000071229.11658.f8
- Behrmann, M. (2000). The mind's eye mapped onto the brain's matter. *Current Directions in Psychological Science*, 9(2), 50–54. doi:10.1111/1467-8721.00059
- Blakemore, C., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology*, 203(1), 237–260.
- Bradley, R., Greene, J., Russ, E., Dutra, L., & Westen, D. (2005). A multidimensional meta-analysis of psychotherapy for PTSD. *American Journal of Psychiatry*, 162, 214–227.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Brewin, C. R., Gregory, J. D., Lipton, M., & Burgess, N. (2010). Intrusive images in psychological disorders: Characteristics, neural mechanisms, and treatment implications. *Psychological Review*, 117(1), 210–232. doi:10.1037/a0018115
- Bridge, H., Harrold, S., Holmes, E. A., Stokes, M., & Kennard, C. (2012). Vivid visual mental imagery in the absence of the primary visual cortex. *Journal of Neurology*, 259(6), 1062–1070. doi:10.1007/s00415-011-6299-z
- Büchel, C., & Dolan, R. J. (2000). Classical fear conditioning in functional neuroimaging. *Current Opinion in Neurobiology*, 10(2), 219–223.
- Dadds, M., Bovbjerg, D., Redd, W., & Cutmore, T. (1997). Imagery in human classical conditioning. *Psychological Bulletin*, 122, 89–210.
- Dadds, M., Hawes, D., Schaefer, B., & Vaka, K. (2004). Individual differences in imagery and reports of aversions. *Memory*, 12(4), 462–466. doi:10.1080/09658210444000070

- De Houwer, J., Thomas, S., & Baeyens, F. (2001). Associative learning of likes and dislikes: A review of 25 years of research on human evaluative conditioning. *Psychological Bulletin*, 127, 853–869.
- Edwards, D. (2007). Restructuring implicational meaning through memory-based imagery: Some historical notes. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 306–316. doi:10.1016/j.jbtep.2007.10.001
- Ehlers, A., & Steil, R. (1995). Maintenance of intrusive memories in posttraumatic stress disorder: A cognitive approach. *Behavioural and Cognitive Psychotherapy*, 23(03), 217–249. doi:10.1017/S135246580001585X
- Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned fMRI adaptation in human visual cortex. *Journal of Neurophysiology*, 94(6), 4188–4195. doi:10.1152/jn.00378.2005
- Farah, M. J. (1984). The neurological basis of mental imagery: A componential analysis. *Cognition*, 18(1–3), 245–272. doi:10.1016/0010-0277(84)90026-x
- Farah, M. J., Levine, D. N., & Calvanio, R. (1988). A case study of mental imagery deficit. *Brain and Cognition*, 8(2), 147–164. doi:10.1016/0278-2626(88)90046-2
- Fazio, R. H., Sanbonmatsu, D. M., Powell, M. C., & Kardes, F. R. (1986). On the automatic activation of attitudes. *Journal of Personality and Social Psychology*, 50(2), 229–238. doi:10.1037/0022-3514.50.2.229
- Foa, E. B., & Meadows, E. A. (1997). Psychosocial treatments for posttraumatic stress disorder: A critical review. *Annual Review of Psychology*, 48, 449–480.
- Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, 10(2), 175–180. doi:10.1093/cercor/10.2.175
- Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2004). Brain areas underlying visual mental imagery and visual perception: An fMRI study. *Cognitive Brain Research*, 20(2), 226–241. doi:10.1016/j.cogbrainres.2004.02.012
- Gao, X. P., Xin, J. H., Sato, T., Hansuebsai, A., Scalzo, M., Kajiura, K., . . . Billger, M. (2007). Analysis of cross-cultural color emotion. *Color Research & Application*, 32(3), 223–229.
- Hackmann, A., Clark, D. M., & McManus, F. (2000). Recurrent images and early memories in social phobia. *Behaviour Research and Therapy*, 38, 601–610.
- Harvey, A. (2003). Cognitive behaviour therapy for posttraumatic stress disorder. *Clinical Psychology Review*, 23(3), 501–522. doi:10.1016/s0272-7358(03)00035-7
- Hermans, D., De Houwer, J., & Eelen, P. (1994). The affective priming effect: Automatic activation of evaluative information in memory. *Cognition & Emotion*, 8(6), 515–533. doi:10.1080/02699939408408957
- Hirsch, C., & Holmes, E. (2007). Mental imagery in anxiety disorders. *Psychiatry*, 6(4), 161–165. doi:10.1016/j.imppsy.2007.01.005
- Hirsch, C., Mathews, A., Clark, D., Williams, R., & Morrison, J. (2006). The causal role of negative imagery in social anxiety: A test in confident public speakers. *Journal of Behavior Therapy and Experimental Psychiatry*, 37(2), 159–170. doi:10.1016/j.jbtep.2005.03.003
- Holmes, E. A., Arntz, A., & Smucker, M. R. (2007). Imagery rescripting in cognitive behaviour therapy: Images, treatment techniques and outcomes. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 297–305. doi:10.1016/j.jbtep.2007.10.007
- Holmes, E. A., Geddes, J. R., Colom, F., & Goodwin, G. M. (2008). Mental imagery as an emotional amplifier: Application to bipolar disorder. *Behaviour Research and Therapy*, 46(12), 1251–1258. doi:10.1016/j.brat.2008.09.005
- Holmes, E. A., James, E. L., Kilford, E. J., & Deerprouse, C. (2010). Key steps in developing a cognitive vaccine against traumatic flashbacks: Visuospatial Tetris versus verbal Pub Quiz. *PLoS ONE*, 5(11), e13706.
- Holmes, E. A., & Mathews, A. (2010). Mental imagery in emotion and emotional disorders. *Clinical Psychology Review*, 30(3), 349–362. doi:10.1016/j.cpr.2010.01.001
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields in functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215–243.
- Hunt, M., & Fenton, M. (2007). Imagery rescripting versus in vivo exposure in the treatment of snake fear. *Journal of Behavior Therapy and Experimental Psychiatry*, 38(4), 329–344. doi:10.1016/j.jbtep.2007.09.001
- Jeannerod, M. (1995). Mental imagery in the motor context. *Neuropsychologia*, 33(11), 1419–1432. doi:10.1016/0028-3932(95)00073-c
- Jones, M. K. (1974). Imagery as a mnemonic aid after left temporal lobectomy: Contrast between material-specific and generalized memory disorders. *Neuropsychologia*, 12(1), 21–30.
- Kaya, N., & Epps, H. H. (2004). Relationship between color and emotion: A study of college students. *College Student Journal*, 38, 396–405.
- Keogh, R., & Pearson, J. (2011). Mental imagery and visual working memory. *PLoS ONE*, 6(12), e29221. doi:10.1371/journal.pone.0029221
- Knauff, M., Kassubek, J., Mulack, T., & Greenlee, M. W. (2000). Cortical activation evoked by visual mental imagery as measured by fMRI. *NeuroReport*, 11(18), 3957–3962.
- Kosslyn, S. M., Ganis, G., & Thompson, W. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, 2, 635–642.
- Kreiman, G., Koch, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, 408(6810), 357–361.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective ratings of pictures and instruction manual* Tech. Rep. A-8). Gainesville: University of Florida.
- Ling, S., Pearson, J., & Blake, R. (2009). Dissociation of neural mechanisms underlying orientation processing in humans. *Current Biology*, 19(17), 1458–1462. doi:10.1016/j.cub.2009.06.069
- Lissek, S., Powers, A., McClure, E., Phelps, E., Woldehawariat, G., Grillon, C., & Pine, D. (2005). Classical fear conditioning in the anxiety disorders: A meta-analysis. *Behaviour Research and Therapy*, 43(11), 1391–1424. doi:10.1016/j.brat.2004.10.007
- Martin, I., & Levey, A. B. (1978). Evaluative conditioning. *Advances in Behavior Research and Therapy*, 1, 57–101.

- Mellet, E., Petit, L., Mazoyer, B., Denis, M., & Tzourio, N. (1998). Reopening the mental imagery debate: Lessons from functional anatomy. *NeuroImage*, 8(2), 129–139. doi:10.1006/nimg.1998.0355
- Meyer, V., & Yates, A. J. (1955). Intellectual changes following temporal lobectomy for psychomotor epilepsy: Preliminary communication. *Journal of Neurology, Neurosurgery, and Psychiatry*, 18(1), 44–52.
- Milad, M., Rauch, S., Pitman, R., & Quirk, G. (2006). Fear extinction in rats: Implications for human brain imaging and anxiety disorders. *Biological Psychology*, 73(1), 61–71. doi:10.1016/j.biopsycho.2006.01.008
- Miyashita, Y. (1993). Inferior temporal cortex: Where visual perception meets memory. *Annual Review of Neuroscience*, 16(1), 245–263.
- Monfils, M. H., Cowansage, K. K., Klann, E., & LeDoux, J. E. (2009). Extinction-reconsolidation boundaries: Key to persistent attenuation of fear memories. *Science*, 324, 951–955.
- Myers, K. M., & Davis, M. (2002). Behavioral and neural analysis of extinction. *Neuron*, 36(4), 567–584.
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience*, 12, 1013–1023.
- Öhman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108(3), 483–522.
- Pearson, J., Clifford, C. W. G., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Current Biology*, 18(13), 982–986. doi:10.1016/j.cub.2008.05.048
- Pearson, J., Rademaker, R. L., & Tong, F. (2011). Evaluating the mind's eye. *Psychological Science*, 22(12), 1535–1542. doi:10.1177/0956797611417134
- Pitman, R. K., Orr, S. P., Forgue, D. F., Altman, B., de Jong, J. B., & Herz, L. R. (1990). Psychophysiologic responses to combat imagery of Vietnam veterans with posttraumatic stress disorder versus other anxiety disorders. *Journal of Abnormal Psychology*, 99(1), 49–54. doi:10.1037/0021-843x.99.1.49
- Pylyshyn, Z. W. (1973). What the mind's eye tells the mind's brain: A critique of mental imagery. *Psychological Bulletin*, 80(1), 1–24. doi:10.1037/h0034650
- Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, 88(1), 16–45. doi:10.1037/0033-295x.88.1.16
- Rademaker, R. L., & Pearson, J. (2012). Training visual imagery: Improvements of metacognition, but not imagery strength. *Frontiers in Psychology*, 3, 224. doi:10.3389/fpsyg.2012.00224
- Rauch, S., Shin, L., & Phelps, E. (2006). Neurocircuitry models of posttraumatic stress disorder and extinction: Human neuroimaging research—past, present, and future. *Biological Psychiatry*, 60(4), 376–382. doi:10.1016/j.biopsycho.2006.06.004
- Rosen, J. B., & Schulkin, J. (1998). From normal fear to pathological anxiety. *Psychological Review*, 105(2), 325–350.
- Sakai, K., & Miyashita, Y. (1991). Neural organization for the long-term memory of paired associates. *Nature*, 354, 152–155.
- Sasaki, Y., Nanez, J. E., & Watanabe, T. (2010). Advances in visual perceptual learning and plasticity. *Nature Reviews Neuroscience*, 11(1), 53–60. doi:10.1038/nrn2737
- Schiller, D., Monfils, M. H., Rao, C. M., Johnson, D. C., LeDoux, J. E., & Phelps, E. A. (2009). Preventing the return of fear in humans using reconsolidation update mechanisms. *Nature*, 463, 49–53. doi:10.1038/nature08637
- Schiller, D., & Phelps, E. A. (2011). Does reconsolidation occur in humans? *Frontiers in Behavioral Neuroscience*, 5. doi:10.3389/fnbeh.2011.00024
- Sherwood, R., & Pearson, J. (2010). Closing the mind's eye: Incoming luminance signals disrupt visual imagery. *PLoS ONE*, 5(12), e15217. doi:10.1371/journal.pone.0015217
- Shibata, K., Watanabe, T., Sasaki, Y., & Kawato, M. (2011). Perceptual learning incepted by decoded fMRI neurofeedback without stimulus presentation. *Science*, 334(6061), 1413–1415. doi:10.1126/science.1212003
- Skinner, B. F. (1977). Why I am not a cognitive psychologist. *Behaviorism*, 5(2), 1–10.
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. *Cerebral Cortex*, 15(10), 1570–1583. doi:10.1093/cercor/bhi035
- Smucker, M. R., Dancu, C., Foa, E. B., & Niederee, J. L. (1995). Imagery rescripting: A new treatment for survivors of childhood sexual abuse suffering from posttraumatic stress. *Journal of Cognitive Psychotherapy*, 9(1), 3–17.
- Sparing, R., Mottaghy, F. M., Ganis, G., Thompson, W. L., Töpper, R., Kosslyn, S. M., & Pascual-Leone, A. (2002). Visual cortex excitability increases during visual mental imagery—a TMS study in healthy human subjects. *Brain Research*, 938(1–2), 92–97. doi:10.1016/s0006-8993(02)02478-2
- Tarrier, N., Pilgrim, H., Sommerfield, C., Faragher, B., Reynolds, M., Graham, E., & Barrowclough, C. (1999). A randomized trial of cognitive therapy and imaginal exposure in the treatment of chronic posttraumatic stress disorder. *Journal of Consulting and Clinical Psychology*, 67(1), 13–18. doi:10.1037/0022-006x.67.1.13
- Tartaglia, E. M., Bamert, L., Mast, F. W., & Herzog, M. H. (2009). Human perceptual learning by mental imagery. *Current Biology*, 19(24), 2081–2085. doi:10.1016/j.cub.2009.10.060
- Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, 20(2), 158–177. doi:10.1037/h0074428
- Watson, J. B., & Rayner, R. (1920). Conditioned emotional reactions. *Journal of Experimental Psychology*, 3(1), 1–14.
- Yakovlev, V., Fusi, S., Berman, E., & Zohary, E. (1998). Inferential neuronal activity in inferior temporal cortex: A putative vehicle to generate long-term visual associations. *Nature Neuroscience*, 1(4), 310–317.

APPENDIX B

Soon to be published version of Study 2: Mental Imagery for Color

Chang, S., Lewis, D. E., & Pearson, J. (in press). The functional effects of colour perception and colour imagery. *Journal of Vision*.

Note of author contributions: Experiment 1 of this study was designed, programmed, and conducted by myself. Author S. Chang conducted Experiment 2 and finalized the manuscript for publication.

Running head: THE FUNCTIONAL EFFECTS OF COLOUR PERCEPTION AND COLOUR IMAGERY

The Functional Effects of Colour Perception and Colour Imagery

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THE FUNCTIONAL EFFECTS OF COLOUR PERCEPTION AND COLOUR IMAGERY

Functional brain imaging research and studies of brain-damaged patients have suggested that the mechanisms of colour perception and colour imagery have some degree of overlap. Previous research into colour imagery has focused on compound images consisting of both colour and form e.g. whole objects. Little is known regarding the characteristics of pure colour imagery- colour without any form structure. Binocular rivalry has been proven to be a successful method for assessing mental imagery indirectly, quantitatively, and reliably. Here we utilized this technique to assess pure colour imagery. Experiment 1 consisted of three conditions,, wherein participants were instructed to imagine pure colours, imagine pure colours in the presence of background luminance, or passively view weak perceptual colour patches, all prior to a brief rivalry display of pure colour patches wherein one of the matched the previously presented or imagined colour. Results indicate that perceptual dominance during rivalry was significantly biased by the participants' prior colour imagery and perception. However, the addition of background luminance attenuated this priming effect for imagery. In Experiment 2, we tested whether colour imagery was location-specific in retinotopic space. Colour imagery was only found to prime subsequent rivalry when the imagery and rivalry stimuli occurred at the same retinotopic location. These results demonstrate that imagery of pure colours without form structure can influence subsequent colour perception and can be localized within retinotopic space. These results are consistent with previous studies of mental imagery using compound visual stimuli, and demonstrate mental imagery of individual visual stimulus features can be assessed.

THE FUNCTIONAL EFFECTS OF COLOUR PERCEPTION AND COLOUR IMAGERY

1. Introduction

Colour plays an important role in visual memories. Strong memories of colour can develop for a wide range of objects or events through the learning of associations between visual features presented together within the environment. Recalling colour memories can have a powerful influence on the concurrent perception of colour (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Hering, 1920; Pérez-Carpinell, de Fez, Baldoví, & Soriano, 1998). Unlike colour constancy (D'Zmura & Lennie, 1986) colour memory effects can even be experienced if all objects in a scene are uniformly coloured or if an object is presented in isolation (Hering, 1920). Though the existence of these kinds of perceptual colour memories is generally agreed upon, their nature is not (for reviews see Barsalou, 2008; Bramao, Reis, Petersson, & Faisca, 2011). Regardless, previous research has clearly demonstrated that stored memories of colour can influence colour perception.

When asked to recall a particular colour memory people tend to use the sensory-based substrate of mental imagery to inspect the perceptual characteristics of that particular memory. Mental imagery is a perception-like experience based on memories, with no concurrent sensory input. As such, mental imagery can be generated without corresponding perceptual stimuli (Kosslyn, Ganis, & Thompson, 2001), allowing an individual to re-experience prior stimuli or simulate future events (Barsalou, 2009; Decety & Grèzes, 2006). Mental imagery can be pictorial in nature as evidenced by research showing that early visual areas, which are known to represent information pictorially/retinotopically, tend to be active during visual mental imagery (Kosslyn, Thompson, Kim, & Alpert, 1995; Slotnick, Thompson, & Kosslyn, 2005). Perception can also interfere with the ability to concurrently generate mental

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imagery (Keogh & Pearson, 2011; Pearson, Clifford, & Tong, 2008; Sherwood & Pearson, 2010) and imagery can influence subsequent perception in a manner specific to early visual cortex (Ishai & Sagi, 1995; Pearson, et al., 2008). Additionally, imagery can be dissociated from visual attention in a number of ways (Pearson, et al., 2008). When participants report the vividness of an individual trial, the higher the rating the higher the probability that mental image will bias subsequent rivalry (Pearson, Rademaker & Tong, 2011; Rademaker & Pearson, 2012). However, whether pure colour information can be voluntarily represented in pictorial/retinotopic mental imagery is unknown.

In mental imagery research, colour was initially treated as a 'side issue' of little importance to the models of mental imagery that were under debate. More recently colour imagery has become its own independent area of research (Bramão et al., 2011). Some studies using functional imaging methods have found that colour perception and colour imagery involve activity within the same neural areas (Hsu, Frankland, & Thompson-Schill, 2012; Hsu, Kraemer, Oliver, Schlichting, & Thompson-Schill, 2011; Simmons et al., 2007), while others have not (Bramão, Faisca, Forkstam, Reis, & Petersson, 2010; Chao & Martin, 1999; Lu et al., 2010; Miceli et al., 2001). Likewise, case studies of brain damaged patients with acquired achromatopsia have produced conflicting evidence that colour perception and colour imagery are sometimes independent, but can also overlap in function (e.g. Damasio, 1989; De Vreese, 1991; Goldenberg, Mullbacher, & Nowak, 1995; Shuren, Brott, Schefft, & Houston, 1996).

Various tasks have been employed to investigate colour imagery. These tasks

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can be divided into two basic categories, 'colour naming', which requires participants to imagine an object and report the name of its colour (e.g. Shuren et al., 1996) and 'colour comparison', which requires participants to imagine two objects and compare their colours (e.g. Howard et al., 1998). However, it is likely that both of these kinds of tasks can be performed using semantic object knowledge rather than visual imagery. In addition, these types of tasks are aimed at imagery of whole objects, such as the entire image of a raspberry, shape, surface texture, luminance and colour. Hence, even though the task directly queries the colour of the object, it remains unclear how separable the colour information is from composite object representations. To conclusively show that colour imagery is perceptual in nature would require demonstrating that it can influence perceptual colour processing in a manner specific to retinotopic visual cortex.

A recent study by Pearson et al. (2008) provided some evidence regarding the perceptual nature of voluntary mental imagery involving colour. Using imagery of red and green oriented Gabor patterns as stimuli, the authors demonstrated that such imagery could prime subsequent binocular rivalry perception, in a manner characteristic of early visual cortex. This priming was found to be orientation specific for the Gabor patterns, which is a characteristic known to be local to early visual cortex (Hubel & Wiesel, 1968; Tootell et al., 1998). However, the priming did not appear to be influenced by the colour of the imagined and rivalry Gabor patterns, as no effects were found when the colours were the same but the orientation differed. This lack of a colour effect seems to indicate either that participants simply could not imagine the Gabor colours, or that participants were focusing on the orientation of the Gabor patterns. Similar effects of orientation, but not colour, have also recently

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been found when mental images of these kinds of coloured Gabor patterns are used within an associative learning paradigm (Lewis, O'Reilly, Khuu, & Pearson, 2013). While these findings demonstrate the perceptual nature of visual imagery, they do not describe to perceptual contents of mental imagery in detail. A slightly modified methodology might allow for a more direct investigation of individual visual features, such as colour.

In the present study we sought to determine if the voluntary generation of pure colour imagery without any specific object form-structure could bias the subsequent perception of colour. This methodology allows for the direct investigation of colour imagery, as no other visual features are present. A binocular rivalry task was used, as it has previously been used to measure visual imagery multiple times (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010). Binocular rivalry has been demonstrated to be a reliable (Rademaker & Pearson, 2012) and indirect approach (Pearson et al., 2008), which has shown that imagery follows the known characteristics of early visual cortex. By replacing the coloured Gabor patterns used in previous studies with pure Gaussian colour patches, this task should allow for the measurement of purely colour-based effects of mental imagery stimuli.

In Experiment 1 we assessed to what extent voluntary colour imagery can bias subsequent colour perception in the form of biasing perceptual dominance during colour rivalry across three conditions. The first condition was conducted to determine if colour imagery could influence perception in optimal conditions. The second condition was conducted to determine if background luminance would interfere with

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colour imagery generation, as it has been shown to interfere with other kinds of compound mental imagery (Keogh & Pearson, 2011; Pearson et al., 2008; Sherwood & Pearson, 2010). The third condition was conducted to determine if a weak perceptual stimulus could have similar priming effects as colour imagery on subsequent perception, as suggested by previous research (Pearson et al., 2008).

In Experiment 2, we sought to determine if colour imagery was location specific in visual space. To assess the location specificity of colour imagery participants were instructed to imagine a colour patch at a particular location in visual space, subsequently the colour rivalry stimulus could appear at the same or at a different spatial location. If a difference were to be found between the same and different location conditions this would be indicative of location specificity for colour imagery. Location specificity for colour imagery would suggest that it involves activity in primary visual cortex, which is known to be retinotopic (Hubel & Wiesel, 1968).

By way of preview, the results of Experiment 1 indicate that colour imagery could bias the dominance in a subsequent colour rivalry display. This result was replicated using weak perceptual stimuli, which have been previously shown to act like mental imagery in this context (Pearson et al., 2008). However, we did not find any significant priming effects of voluntary imagery in the presence of background luminance. In Experiment 2 we show that pure colour imagery can be location specific, when assessed using colour rivalry.

2. Method

2.1 Participants

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Ten individuals (2 females) were recruited for this study ($n_{\text{Experiment 1}} = 9$; $n_{\text{Experiment 2}} = 6$). Authors AC and DL, and three other participants completed both experiments. All participants had normal or corrected to normal vision and gave written informed consent. This experiment was approved by UNSW Human Research Ethics Advisory Panel for Psychology.

2.2 Stimuli and Apparatus

Stimuli were displayed on a linearized Sony Trinitron G520 CRT monitor with 1280 × 960 resolution and 75-Hz refresh rate. Stimuli were generated using Matlab7.9.0 (R2009b) and the Psychophysics toolbox (Brainard, 1997; Pelli, 1997) running on an iMac computer with an Nvidia GeForce GT120 graphics chip. Luminance and CIE values of colours were measured using KONICA MINOLTA CS-100 photometer. In both experiments a circular bulls-eye fixation mark (diameter = 0.3° visual angle) was used to help participants maintain fixation.

In Experiment 1 the stimuli consisted of six different coloured Gaussian blobs (standard deviation $\approx .07^\circ$) presented at fixation. The CIE colour values of the Gaussians were as follows: red: $x = 0.633$, $y = 0.340$, max luminance = 2.22 cd/m², min luminance = 0.97 cd/m²; cyan: $x = 0.208$, $y = 0.326$, max luminance = 7.24 cd/m², min luminance = 1.18 cd/m²; green: $x = 0.274$, $y = 0.406$, max luminance = 7.58 cd/m², min luminance = 2.06 cd/m²; violet: $x = 0.293$, $y = 0.157$, max luminance = 2.88 cd/m², min luminance = 1.06 cd/m²; blue: $x = 0.142$, $y = 0.075$, max luminance = 1.01 cd/m², min luminance = 0.50 cd/m²; yellow: $x = 0.387$, $y = 0.521$, max luminance = 9.66 cd/m², min luminance = 1.27 cd/m². These Gaussian patches were split into three separate pairs of stimuli: red/cyan, green/violet, blue/yellow. The

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luminance values of the two colours in each pair were adjusted for each participant using an eye-dominance test adapted from previous studies to ensure they were perceptually balanced (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010). The procedure used for this perceptual balancing is described in greater detail within the first paragraph of the Procedure section. In the weak perception condition, the weak perceptual colour stimuli were presented at 30% of the luminance of the rivalry stimuli.

In Experiment 2 only the red and cyan Gaussians were used. These Gaussians were made smaller (mean diameter $\approx 2.7^\circ$) and presented either 2.6° to the left or right of fixation. Additionally, to indicate at which spatial location the participants should generate their mental imagery, a weak (low luminance) circle outline (diameter = 3°) was presented either to the left or right of fixation during the mental imagery interval. During this interval the circular fixation mark was replaced with a triangular one of equal size, which pointed towards the appropriate spatial location.

2.3 Procedure

For both experiments, participants were seated in a darkened room with their heads stabilized using a mirror stereoscope and chin rest. A specialized eye-dominance test was conducted to perceptually balance the vividness of the two colours in each pair. Relative luminance of the two coloured Gaussians was adjusted during this test in order to minimize any potential eye bias. For each eye-dominance trial, the two coloured Gaussians were briefly presented in a binocular rivalry display and participants were required to indicate the dominant colour by pressing different

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number keys. Then that same colour (the previously dominant one) was presented to one eye for 4s. After which the rivalry pair were presented again, if adapting to the previously dominant colour did not induce a change in rivalry dominance across the two presentations the relative luminance was adjusted accordingly. There were 30 trials in each eye-dominance session. The eye-dominance test was repeated until two eyes were balanced (the adaptation period led to a change in rivalry dominance on 90% of trials). This method of adjusting the stimuli is based upon previous research (for a detailed explanation of this eye-dominance test please refer to: Pearson et al., 2008).

In Experiment 1, each experimental session was broken into three blocks, one for each colour pair: red/cyan, green/violet, blue/yellow. Each block consisted of a total of sixty-three trials, split evenly into three conditions: imagery, background-luminance, and perception, in a random order. Participants were told which colour pair would be presented before each section began, and allowed to take breaks between the three sections. All participants completed a total of 4 experimental sessions.

As can be seen in Figure 1A, at the start of each trial of the imagery condition, a word cue was presented at fixation for 1s. This cue indicated which colour the participant should imagine during the subsequent 9s imagery interval. In the imagery condition the background remained black, but during the background luminance condition the luminance of the background ramped over a period of 2s, remained at full brightness for 5s, and then ramped off for 2s. After the imagery interval a coloured rivalry stimulus was presented for 1s followed by a 1s interval. Hence, there

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was a 2s response window for each the trial. Participants were required to report the colour that was most visible at rivalry stimulus onset by pressing the corresponding number keys on the keyboard within the response window, where "1" stood for red, green, or blue depending on the block being tested; "3" stood for cyan, violet or yellow depending on the block being tested; "2" stood for an equal mixture of the two colours. Participants were instructed to only indicate an equal mixture if the visibility of the two colours was perfectly balanced. Once a key was pressed, the response window ended and the 2s inter trial interval would start; if no key press was detected within the 2s, the program continued to the inter-trial interval.

In the weak perception condition, the word cue presented at fixation was "FOCUS". This word cue indicated to the participants that they should not attempt to generate any mental imagery during the imagery period. During this interval a perceptual Gaussian was presented at fixation. The Gaussian was ramped on for approximately 1s, remained at full brightness for 7s, and was then ramped off for about 1s. All other procedures were the same as the other two conditions.

As can be seen in Figure 2A, for Experiment 2 the same basic procedure was used with the following exceptions. Only the red/cyan colour pair and the imagery condition of Experiment 1 were used. The imagery cues were immediately followed by direction cues (a triangular fixation mark and circle outline), which indicated whether the participant should attempt to localize their colour imagery at either 2.6° visual angle to the left or right of fixation. This imagery interval was 9s. During the following binocular rivalry presentation the rivaling colour pair was either presented at the same location as the previous mental imagery or the opposite location with

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equal probability. Binocular rivalry was presented for 1s, followed by a 1s blank screen. The participants were allowed to make their responses either during the binocular rivalry or while the screen was blank (response window = 2s). All four combinations of imagery location and binocular rivalry location were tested an equal number of times during each experimental session. All other procedures were identical to Experiment 1.

Mock rivalry trials were included in both Experiment 1 and 2 to determine if the participants were influenced by a non-perceptual, cue-related bias. Such a non-perceptual bias would become apparent if participants indicated one colour being dominant in the fake rivalry (non-rivalrous) stimulus in which both colours were of equal strength and were not undergoing binocular rivalry. Mock rivalry stimuli were created by combining the two colours together, so that the left half of the mock stimulus was one colour and the right half was the other colour. This mock stimulus was presented simultaneously to both eyes, ensuring that the two colours were perfectly balanced and no actual rivalry could occur.

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Data from Experiment 1 are shown in Figure 1B. This figure illustrates the average perceptual bias for the three priming conditions, with 0.5 being chance-level performance, and numbers higher than 0.5 being indicative of positive priming effects. Percentages of equal colour mixed responses were very low (mean 0.5% of trials), and these responses were excluded from the data analysis. Imagery without an illuminated background was found to significantly bias perception, $t(8) = 3.46$, $p = .0086$. However, imagery with an illuminated background was not found to produce a bias significantly different from chance (0.5), $t(8) = 2.23$, $p = .056$, and were found to be significantly different from the non-illuminated condition $t(8) = 2.59$, $p = .032$. Weak perceptual primes, similar to the non-illuminated mental imagery, were also found to produce a significant perceptual bias $t(8) = 3.48$, $p = .0073$. These results appear to suggest that mental imagery of pure colours can have a priming effect on subsequent binocular rivalry, and weak perception of colour has a similar effect as mental imagery condition. Additionally, background luminance during mental imagery generation appears to attenuate this perceptual bias. These results suggest that it was perceptual processes occurring during the imagery generation period that are responsible for the observed priming effect on subsequent rivalry. In all conditions, as in previous studies (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Sherwood & Pearson, 2010), there were an equal number of both imagery cues, which were shuffled across each block of trials. Such randomized cues give us a measure of imagery strength independent of any effects of intermittent rivalry stabilization (Pearson & Brascamp, 2008) or any eye/luminance imbalance, and also avoided systematic influence of after images from binocular rivalry displays, if there were any.

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Figure 1C shows the perceptual bias for imagery separated into the three colour pairs of the rivalry stimuli. The perceptual biases are all significantly greater than chance level ($p < .05$). In addition, there is no significant difference in the magnitude of the colour priming effects between the three colour pairs ($F = 2.854, p = .09$). We also looked at rivalry dominance independent of the imagery cues. No significant difference was found between different colours ($F = 1.804, p = 0.19$).

Figure 1D shows the mock rivalry data for each individual participant in Experiment 1. The mock rivalry stimuli are non-ambiguous, stable stimuli, consisting of equal parts of the two colours in each pair. Therefore participant responses that indicated dominance of one of the two colours would likely show that their dominance judgments were being influenced by reading the word cues at the start of each trial. Such an influence would be suggestive of a non-perceptual or criterion bias. We analyzed this non-perceptual bias by coding veridical “mixed” responses to the mock trials as 0.5, while responses that matched the cued colour were coded as 1, and responses opposite to the cued colour were coded as 0. While a few participants do report some bias for the stable non-rivalrous mock trials, overall the decisional or criterion bias ($M_{imagery} = 0.51, M_{luminance} = 0.53, M_{perception} = 0.52$) are not statistically significant (t -tests: $ps > .05$). This result remains the same when the two authors’ data are excluded. These results suggest that a decisional or criterion bias is not responsible for the data in Experiment 1, and confirmed that the priming effect in binocular rivalry is likely due to colour imagery.

Figure 2E shows scatter plots of perceptual bias for imagery of the three colour pairs. Analysis shows that all three correlations were significant ($ps < .001$). This indicates that the imagery strength seems consistent across the different colour pairs.

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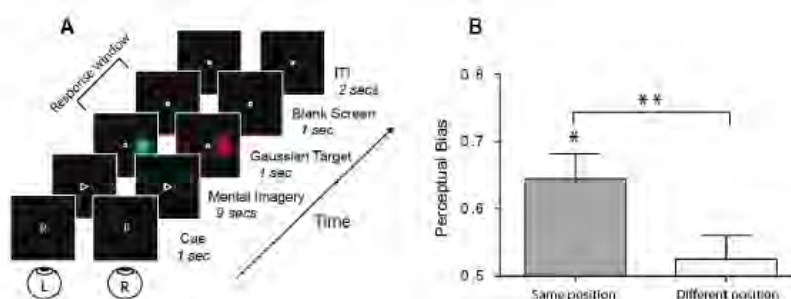


Figure 2: A: Individual trial timeline of Experiment 2. B: Average perceptual biases for the two conditions in Experiment 2. Error bars show +1 SEM.

** $p < .001$

In Experiment 2, we examined whether colour imagery had similar location-specificity to that previously demonstrated with compound coloured Gabor stimuli (Pearson et al., 2008). Figure 2B shows the data for imagery priming when imagery and subsequent rivalry are at the same and different locations. Analysis indicates that priming for same location condition is significantly greater than chance level, $t(5) = 3.94$, $p = .011$, replicating the results of Experiment 1. However, when the imagery and test stimuli were presented to different locations perceptual bias was not significantly different from chance, $t(5) = 0.75$, $p = .49$. A significant difference was also found between these two conditions, $t(5) = 4.23$, $p < .01$. These results appear to indicate that voluntarily generated pure colour imagery can be location-specific over a distance of at least $\sim 5^\circ$ of visual space.

4. Discussion

Here we have demonstrated that voluntary mental imagery of pure colour can

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bias subsequent colour perception. The generation of colour imagery was observed to bias perceptual dominance during a binocular rivalry task, wherein the previously imagined colour tended to be most visible. Increasing the luminance of the background during the imagery generation period or displaying the rivalry stimulus at a different visual location greatly attenuated this bias. These data suggest that the perceptual bias effect on subsequent rivalry is specifically due to low-level sensory processes occurring during the imagery period and not due to other factors such as voluntary control of the rivalry display. In addition, weak perceptual stimuli displayed bias-priming effects on subsequent rivalry much the same as voluntary imagery. The current results suggest that colour imagery and colour perception involve largely similar mental processing. These data are consistent with previous findings using compound multi-feature imagery stimuli (Pearson et al., 2008).

In previous research, mental imagery has mostly been treated as a general trait-like cognitive/perceptual process or ability, but potential complexities within the generation of mental imagery of various perceptual features have largely been ignored. In the current study we investigated one specific feature of visual imagery in isolation, colour. Previous studies on colour imagery used tasks such as colour naming and colour comparison in order to assess a participant's ability to perform colour imagery. It could be argued that in these experiments the mental imagery generated by the participants contained all the same sensory information as the physical objects such as shape, orientation, textures and luminance. However, whether colour information was a part of their mental imagery could not be confirmed, as these kinds of tasks could also be based entirely on semantic knowledge (McNorgan, 2012).

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Using the binocular rivalry method, colour could be treated as an independent perceptual element of visual imagery rather than integrated with other features. The use of binocular rivalry to study mental imagery was first employed by Pearson et al. (2008) to assess the perceptual nature of mental imagery. However, the stimuli used in this study, and others (Keogh & Pearson, 2011; Pearson et al., 2008; Pearson et al., 2011; Rademaker & Pearson, 2012; Sherwood & Pearson, 2010), consisted of Gabor patches that had multiple visual features including colour, orientation, and spatial frequency. By measuring the priming effects of our colour-only primes on perceptual dominance during binocular rivalry, we have shown that it is possible to not only generate mental imagery for colour but that this imagery can also influence colour perception.

Similar to colour imagery, the passive perception of weak (low-luminance) coloured Gaussians was found to also bias perceptual dominance during binocular rivalry. Previous work has shown that this perceptual priming of subsequent rivalry is contingent on the contrast and luminance of the prior stimulus (Pearson, et al., 2008; Brascamp, Knapen, Kanai, van Ee, & van den Berg., 2007). As the luminance of the prime stimulus is increased the facilitative priming effect turns into the opposite or suppressive effect on subsequent rivalry – biasing perception for the other pattern. These data suggest that voluntary imagery on the whole is acting much like weak or low luminance perceptual stimuli. It is an interesting question as to how weak perception and mental imagery can positively bias subsequent perception, and this phenomenon has been documented across a wide range of stimuli and situations (Koutstaal, Wagner, Rotte, Maril, Buckner, & Schacter, 2001; Pearson & Brascamp, 2008; Pearson et al., 2008; Schacter, Dobbins & Schnyer, 2004). However, the

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current study makes no attempt to explain this phenomenon. What is interesting here, is that the current study demonstrates what seems to be a form of perceptual priming in the absence of any incoming sensory information.

To rule out the possibility that the observed effects were caused by non-perceptual biases driven by the presentation of the word cues at the beginning of each test trial (Burt, 1994; McClain, 1983), a background luminance condition and mock trials were included. When the background luminance of the mental imagery period was increased the bias effect on subsequent rivalry was found to be greatly diminished. As the increased luminance only increased during the actual imagery generation period, and not during the rivalry or word cue presentation, this result does not appear to indicate the presence of non-perceptual biases. In addition, our non-rivalrous mock trials did not show any significant priming/decisional bias. These two findings suggest that the criterion for reporting dominance in rivalry was not strongly driven by the word cues.

The perceptual biases in Experiment 1 showed large individual differences in imagery strength (see Figure 2C), which indicate that participants probably differ in their colour imagery strength. Because of the method employed in previous colour imagery studies, they could not quantitatively evaluate mental imagery strength and hence, individual differences could not be analyzed. In the current data the strength of colour imagery does seem fairly stable between the different colour pairs. This appears to suggest that one common mechanism was used to generate imagery for all colour pairs. Yet we only tested colour imagery in set pairs, not individually, therefore it remains hard to draw strong conclusions about mechanistic differences

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between imagery of different colours.

Experiment 1 confirmed that individuals could generate a form of pure colour imagery. So why didn't the data in Pearson et al. (2008) or Lewis et al. (2013) show evidence on an effect of colour imagery? One answer could be that when colour is combined with orientation in an imagined or perceptual stimulus such as a coloured Gabor pattern, the effect of orientation is simply stronger than colour. Hence in a compound configuration orientation information will 'win' over colour. Future work should carefully titrate any differences in voluntary imagery across the different visual features.

Experiment 2 revealed that colour imagery is location specific, in a similar manner to visual perception. The perceptual bias observed in Experiment 1 was replicated in this experiment when the imagery and rivalry stimuli were presented at the same location, but the bias was lost when they were presented to different visual locations. The behavioral finding is also in line with findings from brain imaging studies. Tootell et al., (1998) used fMRI to show that early retinotopic visual cortex involving areas V2 and V3 were recruited during a mental imagery task. Other studies have shown that primary visual cortex (V1) is involved in visual imagery (Kosslyn et al., 1999; Kosslyn & Thompson, 2003). McNorgan (2012) in a meta-analysis concluded that V4 is the most likely candidate area responsible for the generation of colour imagery. Based on these brain-imaging data, we conclude that it may well be the retinotopic property of these visual areas that leads to the location specificity we see for colour imagery.

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In conclusion, the current study replicates the findings of previous studies of mental imagery that used compound visual stimuli (Lewis et al., 2013; Pearson et al., 2008; Pearson et al., 2011; Sherwood & Pearson, 2010) by using pure colour stimuli. These results demonstrate that imagery of pure colours (without form structure) can influence subsequent colour perception locally in retinotopic space. Like other forms of visual imagery, it appears that mental imagery of colour can be pictorial/retinotopic in nature. It will be interesting for future research to utilize this method with other visual features to probe the unitary versus compound nature of visual imagery.

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References

- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59, 617-645. doi: 10.1146/annurev.psych.59.103006.093639
- Barsalou, L. W. (2009). Simulation, situated conceptualization, and prediction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 364(1521), 1281-1289. doi: 10.1098/rstb.2008.0319
- Brainard, D. H. (1997) The Psychophysics Toolbox, *Spatial Vision* 10:433-436.
- Bramão, I., Faisca, L., Forkstam, C., Reis, A., & Petersson, K. M. (2010). Cortical brain regions associated with color processing: an fMRI study. *Open Neuroimaging Journal*, 4, 164-173. doi: 10.2174/1874440001004010164
- Bramão, I., Reis, A., Petersson, K. M., & Faisca, L. (2011). The role of color information on object recognition: A review and meta-analysis. *Acta Psychologica*, 138(1), 244-253. doi: DOI 10.1016/j.actpsy.2011.06.010
- Brascamp, J. W., Knapen, T. H. J., Kanai, R., van Ee, R., & van den Berg, A. V. (2007). Flash suppression and flash facilitation in binocular rivalry. *Journal of Vision*, 7(12). doi: Doi 10.1167/7.12.12
- Burt, J. S. (1994). Identity Primes Produce Facilitation in a Color Naming Task. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, 47(4), 957-1000.
- Chao, L. L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience*, 11(1), 25-35.
- Damasio, A. R. (1989). Time-Locked Multiregional Retroactivation - a Systems-Level Proposal for the Neural Substrates of Recall and Recognition. *Cognition*, 33(1-2), 25-62.
- De Vreese, L. P. (1991). Two systems for colour-naming defects: Verbal disconnection vs colour imagery disorder. *Neuropsychologia*, 29(1), 1-18. doi: 10.1016/0028-3932(91)90090-U
- Decety, J., & Grèzes, J. (2006). The power of simulation: Imagining one's own and other's behavior. *Brain Research*, 1079(1), 4-14. doi: 10.1016/j.brainres.2005.12.115
- D'Zmura, M., & Lennie, P. (1986). Mechanisms of color constancy. *Journal of the Optical Society of America A*, 3(10), 1662-1672.
- Goldenberg, G., Mullbacher, W., & Nowak, A. (1995). Imagery without Perception - a Case-Study of Anosognosia for Cortical Blindness. *Neuropsychologia*, 33(11), 1373-1382.
- Hansen, T., Olkkonen, M., Walter, S., & Gegenfurtner, K. R. (2006). Memory modulates color appearance. *Nature Neuroscience*, 9(11), 1367-1368. doi: http://www.nature.com/neuro/journal/v9/n11/supinfo/nn1794_S1.html
- Hering, E. (1920). *Grundzüge der Lehre vom Lichtsinn*. Berlin: Springer-Verlag.
- Howard, R. J., Ffytche, D. H., Barnes, J., McKeefry, D., Ha, Y., Woodruff, P. W., Brammer, M. (1998). The functional anatomy of imagining and perceiving colour. *Neuroreport*, 9(6), 1019-1023.
- Hsu, N. S., Frankland, S. M., & Thompson-Schill, S. L. (2012). Chromaticity of color perception and object color knowledge. *Neuropsychologia*, 50(2), 327-333. doi: DOI 10.1016/j.neuropsychologia.2011.12.003
- Hsu, N. S., Kraemer, D. J. M., Oliver, R. T., Schlichting, M. L., & Thompson-Schill, S. L. (2011). Color, context, and cognitive style: Variations in color knowledge retrieval as a function of task and subject variables. *Journal of Cognitive Neuroscience*, 23(9), 2544-2557. doi: 10.1162/jocn.2011.21619
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive Fields and Functional Architecture of Monkey Striate Cortex. *Journal of Physiology-London*, 195(1), 215-243.
- Ishai, A., & Sagi, D. (1995). Common Mechanisms of Visual-Imagery and Perception. *Science*, 268(5218), 1772-1774. doi: DOI 10.1126/science.7792605
- Jakobson, L. S., Pearson, P. M., & Robertson, B. (2008). Hue-specific colour memory impairment in an individual with intact colour perception and colour naming. *Neuropsychologia*, 46(1), 22-36. doi: DOI 10.1016/j.neuropsychologia.2007.08.023
- Keogh, R., & Pearson, J. (2011). Mental imagery and visual working memory. *PLoS One*, 6(12), e29221. doi: 10.1371/journal.pone.0029221
- Kosslyn, S. M., & Thompson, W. L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin*, 129(5), 723-746. doi: Doi 10.1037/0033-2909.129.5.723
- Kosslyn, S. M., Ganis, G., & Thompson, W. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, 2, 635-642.
- Kosslyn, S. M., Pascual-Leone, A., Felician, O., Camposano, S., Keenan, J. P., Thompson, W. L., . . . Alpert, N. M. (1999). The role of Area 17 in visual imagery: Convergent evidence from PET and rTMS. *Science*, 284(5411), 167-170. doi: DOI 10.1126/science.284.5411.167
- Kosslyn, S. M., Thompson, W. L., Kim, I. J., & Alpert, N. M. (1995). Topographical representations of mental

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- images in primary visual cortex. *Nature*, 378(6556), 496-498. doi: 10.1038/378496a0
- Koutstaal, W., Wagner, A. D., Rotte, M., Maril, A., Buckner, R. L., & Schacter, D. L. (2001). Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia*, 39(2), 184-199. doi: 10.1016/S0028-3932(00)00087-7
- Lewis, D. E., O'Reilly, M. J., Khuu, S. K., & Pearson, J. (2013). Conditioning the Mind's Eye: Associative Learning With Voluntary Mental Imagery. *Clinical Psychological Science*. doi: 10.1177/2167702613484716
- Lu, A., Xu, G., Jin, H., Mo, L., Zhang, J., & Zhang, J. X. (2010). Electrophysiological evidence for effects of color knowledge in object recognition. *Neuroscience Letters*, 469(3), 405-410. doi: 10.1016/j.neulet.2009.12.039
- McClain, L. (1983). Color Priming Affects Stroop Interference. *Perceptual and Motor Skills*, 56(2), 643-651.
- McNorgan, C. (2012). A meta-analytic review of multisensory imagery identifies the neural correlates of modality-specific and modality-general imagery. *Frontiers in Human Neuroscience*, 6. doi: 10.3389/fnhum.2012.00285
- Miceli, G., Fouch, E., Capasso, R., Shelton, J. R., Tomauiolo, F., & Caramazza, A. (2001). The dissociation of color from form and function knowledge. *Nature Neuroscience*, 4(6), 662-667. doi: 10.1038/88497
- Pearson, J., & Brascamp, J. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences*, 12(9), 334-341. doi: DOI 10.1016/j.tics.2008.05.006
- Pearson, J., Clifford, C. W. G., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Current Biology*, 18(13), 982-986. doi: 10.1016/j.cub.2008.05.048
- Pearson, J., Rademaker, R. L., & Tong, F. (2011). Evaluating the mind's eye. *Psychological Science*, 22(12), 1535-1542. doi: 10.1177/0956797611417134
- Pelli, D. G. (1997) The VideoToolbox software for visual psychophysics: Transforming numbers into movies, *Spatial Vision* 10:437-442.
- Pérez-Carpinell, J., de Fez, M. D., Baldoví, R., & Soriano, J. C. (1998). Familiar objects and memory color. *Color Research & Application*, 23(6), 416-427. doi: 10.1002/(sici)1520-6378(199812)23:6<416::aid-col10>3.0.co;2-n
- Rademaker, R. L., & Pearson, J. (2012). Training visual imagery: Improvements of metacognition, but not imagery strength. *Frontiers in Psychology*, 3, 224. doi: 10.3389/fpsyg.2012.00224
- Schacter, D. L., Dobbins, I. G., & Schnyer, D. M. (2004). Specificity of priming: a cognitive neuroscience perspective. *Nat Rev Neurosci*, 5(11), 853-862. doi: 10.1038/nrn1534
- Sherwood, R., & Pearson, J. (2010). Closing the mind's eye: Incoming luminance signals disrupt visual imagery. *PLoS One*, 5(12), e15217. doi: 10.1371/journal.pone.0015217
- Shuren, J. E., Brott, T. G., Schefft, B. K., & Houston, W. (1996). Preserved color imagery in an achromatopsic. *Neuropsychologia*, 34(6), 485-489. doi: 10.1016/0028-3932(95)00153-0
- Simmons, W. K., Ramjee, V., Beauchamp, M. S., McRae, K., Martin, A., & Barsalou, L. W. (2007). A common neural substrate for perceiving and knowing about color. *Neuropsychologia*, 45(12), 2802-2810. doi: DOI 10.1016/j.neuropsychologia.2007.05.002
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. *Cerebral Cortex*, 15(10), 1570-1583. doi: 10.1093/cercor/bhi035
- Tootell, R. B. H., Hadjikhani, N. K., Mendola, J. D., Marrett, S., & Dale, A. M. (1998). From retinotopy to recognition: fMRI in human visual cortex. *Trends in Cognitive Sciences*, 2(5), 174-183. doi: http://dx.doi.org/10.1016/S1364-6613(98)01171-1
- Tootell, R. B. H., Hadjikhani, N. K., Vanduffel, W., Liu, A. K., Mendola, J. D., Sereno, M. I., & Dale, A. M. (1998). Functional analysis of primary visual cortex (V1) in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 95(3), 811-817. doi: DOI 10.1073/pnas.95.3.811
- Xiao, Y. P., Wang, Y., & Felleman, D. J. (2003). A spatially organized representation of colour in macaque cortical area V2. *Nature*, 421(6922), 535-539. doi: Doi 10.1038/Nature01372

APPENDIX C

Published version of Study 3: Object Memories Defined by Color

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The Color "Fruit": Object Memories Defined by Color

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Abstract

Most fruits and other highly color-diagnostic objects have color as a central aspect of their identity, which can facilitate detection and visual recognition. It has been theorized that there may be a large amount of overlap between the neural representations of these objects and processing involved in color perception. In accordance with this theory we sought to determine if the recognition of highly color diagnostic fruit objects could be facilitated by the visual presentation of their known color associates. In two experiments we show that color associate priming is possible, but contingent upon multiple factors. Color priming was found to be maximally effective for the most highly color diagnostic fruits, when low spatial-frequency information was present in the image, and when determination of the object's specific identity, not merely its category, was required. These data illustrate the importance of color for determining the identity of certain objects, and support the theory that object knowledge involves sensory specific systems.

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Introduction

Color can be highly informative of an object's identity. Accordingly, most animals have some ability to perceive color, including mammals which typically have dichromatic color vision [1,2]. The trichromatic color vision of humans and other primates is a relatively new genetic development, allowing for improved discrimination between various shades of red and green [3]. This evolution is theorized to have been driven by the color of tropical fruits [4–6], resulting in the development of a visual system especially well tuned to long wavelength colors (red, orange and yellow), which often signal the most nutritious fruit [7]. These evolutionary theories of color vision have gained popularity and support in recent years, but typically make no attempt to explain contributions of higher-level cognitive processes, such as how an object's color information is encoded, organized and recalled from memory.

Many objects, such as ripened fruit, tend to have specific colors. For example, ripe bananas and lemons are always colored yellow. Such objects are commonly referred to as being highly color diagnostic, as their colors will provide additional information about their identity [8]. As a result when the shape of an object is made ambiguous through image blur, its colors can have a strong facilitatory effect on its recognition [9]. This improved ability to identify an object may simply involve using color channels to help define its contours, as suggested by numerous studies [10–12]. However, studies using highly color-diagnostic objects have found that the addition of color information leads to greater facilitation for these objects when compared to those less linked to color [13–16]. This color based facilitation appears to result in the activation of a more extensive neural network than colorless images, which makes object recognition faster [17]. These findings illustrate how

object recognition can be facilitated by the color specific information stored within memory.

Memory of these object-color associations can also greatly influence the apparent coloration of a visually presented object. A seminal study on such memory color effects [18] has demonstrated that an object's perceived color is skewed towards what the observer expects it to be, based on knowledge gained from previous experience. These memory colors are independent of the influence of color constancy in that they are observable even when all objects in a scene are uniformly colored or when an object is presented in isolation. Therefore, while color constancy attempts to determine the "true" color of an object by estimating and then discounting the color of the illumination [19], the memory color effect adjusts the perceived colors of an object to match the association held within memory. This effect occurs involuntarily and has been demonstrated for both natural objects [20–23] and man-made objects [24]. Along with the previously discussed literature, this memory color effect shows that an object's identity and its coloration can be highly interactive. However, the mechanisms underlying these interactions remain largely unknown.

There appears to be an overlap of the neural areas involved in the processing of color perception and stored color knowledge [25–27]. Such an overlap would identify the mechanisms of object identity-color interactions and support the theory that conceptualized knowledge is grounded within modality specific systems [28]. According to this theory the storage and retrieval of knowledge about an object, such as its color, involves processing within the same neural areas involved during the perception of that object.

However, the functional independence of color perception and color knowledge has been demonstrated in multiple case studies

[29–31], and implicated in many neuroimaging studies [17,32–34]. These findings indicate it is possible to recall color knowledge from memory without being able to process perceptual colors, and vice-versa. If these two processes can truly operate independently of one another it would be indicative of a double dissociation of color perception and color knowledge. These results conflict with the theory of modality grounded knowledge, leading to a great deal of debate [28]. If perceptual color processing were clearly shown to have an effect on the retrieval of object color knowledge this would support the theory of modality grounded knowledge as applied to color perception, which would in turn facilitate a resolution to this ongoing debate.

Many behavioral studies have already made important contributions to this resolution. It has been shown that object recognition can be interfered with through the prior presentation of the name or picture of an object known to be the same color [35,36]. This appears to be a kind of color-knowledge-based negative priming that will only occur if the observer knows that the two objects are typically the same color. However, this interference has been shown to only occur when the object to be recognized is shown in its appropriate color [37]; no recognition interference was observed for colorless or inappropriately colored objects. This indicates that color knowledge can play a role in object recognition processing, but it appears as though this knowledge may require activation by the visual coloration of the object to be recognized [38].

In contrast, a type of knowledge-based positive color priming has recently been demonstrated in a study showing that the names of objects known to share similar colors can prime each other in a word recognition task [39]. As these object names were merely colorless words, this priming did not require the presentation of any visual colors. This form of priming is based on the object's known color associates, indicating that the stored knowledge of similarly colored objects appear to have overlapping neural representations. However, this priming was entirely semantic and did not involve the processing of any perceptual colors, therefore it does not demonstrate that object knowledge requires perceptual color processing. It may simply be that there is an overlap between the neural representations of these objects that does not involve any perceptual processing.

The previously mentioned studies have shown that color knowledge can play an important role in visual object recognition. However, whether sensory colors can have an influence on stored color knowledge has not yet been clearly demonstrated. The demonstration of this kind of influence would suggest that processing for color perception and color knowledge involve the same neural mechanisms, as predicted by the theory of modality grounded cognition. The aim of the present study is to build upon these previous findings by showing that such an interaction is possible.

In the current study we sought to determine if perceptual colors can interact with the stored knowledge of highly color diagnostic objects. Specifically, we tested whether the recognition of achromatically presented fruit objects can be facilitated using visual color primes. Achromatic presentation of the fruit objects ensures that the only possible links between them and the perceptual color primes are those stored within memory. If significant facilitation is found using such a priming task it would suggest that memory for highly color diagnostic objects at least partially involves similar neural processing as their perceptual colors. Such a result would provide compelling support for the theory that object color knowledge is grounded in perceptual processing areas [28].

We assessed the effectiveness of our color primes using two separate experimental tasks, object naming (Experiment 1) and object categorization (Experiment 2). As the presence of an object's surface details are known to have different effects on its categorization and naming [40], it seems possible that our color primes would also have different effects in these two tasks. In the categorization task observers were merely required to categorize the objects as either a "Fruit" or "Car", they were not required to determine the objects' specific identities. As a result, our color primes may be ineffective in this task, as it is the specific identities of the fruit that are known to be associated with different colors. This result seems especially likely as visual objects are known to be categorized before their specific identities can be determined [41–43].

In both experiments we tested this priming under different visibility conditions. Previous object recognition studies have shown that visual colors can produce greater facilitation for blurred or degraded object images [16,40,44], suggesting that our color priming may also be maximally effective under these conditions. Therefore, in addition to normal achromatic photographs, we tested highly blurred images that preserved the low spatial-frequency luminance information while removing most of the objects' shape and texture. In Experiment 1 we also tested an edges-only version of the photographs that preserved the objects' high spatial-frequency shape and texture while removing most of the luminance information. To reiterate, there were no shared visual features between our color primes and the achromatic object targets used in any of these experiments. Therefore, any observed priming must be based upon on object specific color knowledge stored in memory [26].

Materials and Methods

Ethics Statement

This study received ethical approval from the University of New South Wales Human Research Ethics Advisory (HREA) panel. All participants gave written, informed consent before the start of the experiment. Upon completion the participants were debriefed in a follow-up interview.

Participants

A total of 21 students (9 males) were recruited from the University of New South Wales for this study ($n_{\text{naming}} = 11$; $n_{\text{categorization}} = 15$). All participants had normal, or corrected to visual acuity and color vision. Five individuals participated in both the naming and categorization experiments in separate sessions.

Stimuli

All stimuli were presented using MATLAB (version 7.10.0 R2010a). Experiment 1 used a 32 cm × 51 cm iMac monitor with a Nvidia GeForce GT 120 chipset at a resolution of 1920 × 1200. Experiment 2 used a 27 cm × 35.5 cm Philips 109P4 monitor at a resolution of 1152 × 870 @ 75 Hz. Both experiments involved the presentation of colored Gaussian blobs and achromatic photographs on a black background (luminance < 0.01 cd/m²). Stimuli were presented in the center of the screen with a circular fixation mark overlaid (diameter = 0.3°).

The Gaussian blobs were created using Psychtoolbox [45] for MATLAB. Six differently colored Gaussians ($\sigma_{\text{width}} = 2.7^\circ$; $\sigma_{\text{height}} = 1.8^\circ$) were used in this study: red (CIE $x = 0.628$ $y = 0.338$ lum = 61.7 cd/m²), orange (CIE $x = 0.506$ $y = 0.431$ lum = 110 cd/m²), yellow (CIE $x = 0.392$ $y = 0.515$ lum = 234 cd/m²), yellow-green (CIE $x = 0.344$ $y = 0.553$ lum = 134 cd/m²), green (CIE $x = 0.279$ $y = 0.600$ lum = 200 cd/m²) and blue (CIE

$x = 0.142$ $y = 0.071$ $\text{lum} = 24 \text{ cd/m}^2$). These colors were chosen due to their relevance to fruit perception, except blue which acted as a control. These colors were not isoluminant.

The photographs chosen for this study consisted of various kinds of fruit and cars. Fruit photographs were taken in the lab using a Nikon D50 camera and store-bought fruits. All fruits were photographed from a canonical angle; as though the viewer is looking down at them upon a table. Any photographs containing extraneous or distracting visual features such as blemishes, discolorations, and lighting effects were discarded. The chosen fruit types were apples, bananas, grapes, lemons, oranges, pears, persimmons and strawberries. Fruit types were selected based upon their familiarity and color diagnosticity as determined in previous color diagnosticity studies using fruit stimuli [15,16,46]. The fruit rated high in color diagnosticity were bananas (yellow), lemons (yellow), oranges (orange), and strawberries (red), while those rated moderate to low in color diagnosticity were apples, grapes, and pears. Persimmons were included as an experiential control, as it is our understanding that they have not been used in any prior color diagnosticity experiments. This is likely because most people have no knowledge of persimmons, and knowledge is required for an object's color to be diagnostic of its identity. Consequently, though persimmons always appear in a particular shade of reddish-orange, none of the participants had this knowledge, making it a non-color diagnostic object. Car photographs were found using various internet sources. The car photographs were included as a non-fruit control condition, as cars have been consistently rated very low in color diagnosticity in previous research. The chosen car types are classic cars, convertibles, luxury cars, sedans, smart cars, sport-utility vehicles, pickup-trucks and vans. All objects were displayed in achromatic grayscale with their backgrounds removed. These objects were centered and resized to fit on top of a gray rectangle (width = 16.2"; height = 10.9"). See the left side of Figure 1 for example stimuli.

In Experiment 1, the naming experiment, a total of 54 photographs were used: six photographs of each kind of fruit, except persimmons, and only one photograph of each kind of car, except sports-cars, pickup-trucks and vans. This resulted in a total

of 8 different kinds of objects used in this experiment. Depending on the experimental condition, the photographs were filtered to remove either the low or high spatial-frequency information. The low spatial-frequency versions were created by convolving each photograph with a 2-D Gaussian filter of the same size as the photographs and a standard deviation of 5 pixels ($\sigma \approx 0.3^\circ$). The high spatial-frequency versions were created by subtracting the low spatial-frequency versions from the original photographs.

In Experiment 2, the categorization experiment, a total of 96 photographs were used: six photographs of each kind of fruit and car. Only the normal photographs and low spatial-frequency versions were used in this experiment.

Design

The two experiments in this study utilized a 6×8 within subjects design. The two independent variables were prime color and object type. In each experiment the potential interactions between the levels of prime color and object type were tested independently for each spatial-frequency condition. In Experiment 1 there were three spatial-frequency conditions (normal, low spatial-frequencies only, high spatial-frequencies only) while in Experiment 2 there were only two spatial-frequency conditions (normal, low spatial-frequencies only).

In Experiment 1 the different object types were apples, bananas, grapes, lemons, oranges, pears, strawberries and cars. In Experiment 2 the potential interactions between prime color and object type were independently tested for each of the two object categories (fruit, car). This independent analysis was conducted to more directly compare the effects of the six differently colored primes across the eight object types within each category. The fruit types were apples, bananas, grapes, lemons, oranges, pears, persimmons and strawberries. The car types were classic cars, convertibles, luxury cars, sedans, smart cars, sport-utility vehicles, pickup-trucks and vans. No cross-category comparisons were made in this categorization experiment.

Procedure

All participants were seated in a dark room approximately 57 cm from the monitor. A chinrest was not used in Experiment 1

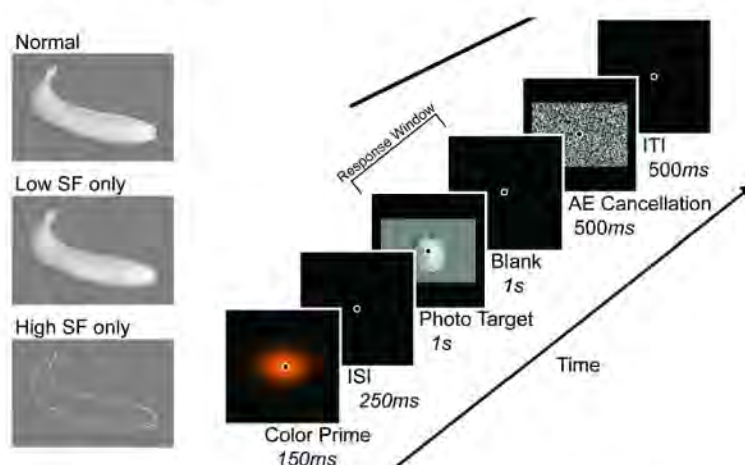


Figure 1. Example photographic stimuli and experimental timeline. (Left) Example photograph targets as shown in each of the three conditions. All photographs were presented on a black screen, in grayscale, with their backgrounds removed. (Right) Experimental timeline. In Experiment 2 the blank screen immediately following the photograph target was removed, thus shortening the response window to only 1 s. doi:10.1371/journal.pone.0064960.g001

as it would interfere with the participants' ability to vocalize their responses. The basic experimental timeline shown on the right side of Figure 1 was used in both experiments. At the start of each trial the Gaussian color prime was shown for 150 ms, followed by a 250 ms blank screen. Then the target photograph was shown for 1 s, followed by a 1 s blank screen. Participants were only allowed to vocalize their responses during this 2 s response window. Then a randomized white noise pattern was displayed for 500 ms to remove any luminance after-effects produced by the photographs, which was followed by a 500 ms inter-trial interval wherein the screen would remain blank.

In Experiment 2 the blank screen immediately following the target photograph was removed, thus shortening the response window to only 1 s. This shortening of the response window was due to the observation that the button-press reaction times were generally much quicker than the vocalized response reaction times. Failure to react within the response window for either experiment resulted in the trial being repeated at a randomly determined point later in the session.

In Experiment 1 the participants were instructed to speak aloud the name of the object being displayed in the target photograph as quickly and accurately as possible. Participants were urged to vocalize whichever term they best associated with the object's specific identity (i.e., "apple"). The only exception to this was the car photographs, which were responded to simply as "car".

In Experiment 2 the participants were instructed to categorize the objects in the target photographs as a fruit or car by pressing the "F" or "C" keys on the keyboard as quickly and accurately as possible. Incorrect responses resulted in the trial being repeated at a randomly determined point later on in the experimental session and a buzzer noise was played to notify the participants of their error.

Data preparation

In Experiment 1 the naming accuracy and vocalization reaction time for each trial were manually determined after the experimental session was completed. The visual waveform and auditory playback were reviewed for each trial using a MATLAB program written specifically to analyze the sound-waves of this study. Reaction times were determined by marking the point of vocalization onset, as indicated by systematic changes in the waveforms' amplitudes while ignoring ambient noises and non-verbal utterances. Variations in the waveform shapes due to individual participant differences were also taken into consideration when marking this onset of vocalization. Accuracy was determined by comparing the auditory playback to the correct answer being textually displayed in the program window. The raters were blind as to the color prime of each trial; only the participant's vocalization and the correct answer were shown.

In Experiment 2 the program automatically determined the accuracy and reaction time of each participant's button-press responses. All incorrect responses were recorded and the trial was repeated at a randomly determined point later in the block. Incorrect responses were excluded from analysis in both experiments due to the participants having made very few errors. In the normal-image condition of Experiment 2 a single participant was excluded from analysis due to consistently producing outlying reaction times.

Results

Experiment 1 - Naming

In this experiment we sought to determine if naming speeds for the achromatic fruit images could be facilitated through the

presentation of color primes. The priming was tested using photographs that contained different kinds of spatial-frequency information (normal photographs, low spatial-frequencies only, high spatial-frequencies only). Our hypothesis predicted an interaction between the color primes and the object types, with diagnostic colors resulting in the fastest reaction times. It was also predicted that the priming effects would be strongest in the low spatial-frequency condition, as it has been shown that an object's color will maximally facilitate its recognition when the shape is hard to determine [16,40,44].

A preliminary 3-way within-subjects ANOVA across the 3 spatial-frequencies, 6 prime colors, and 8 object types was conducted. A significant interaction was found between these three factors $F(70, 700) = 1.51$, $p = 0.006$, observed $1 - \beta = 1.00$. This indicates that the removal of certain kinds of spatial-frequency information had a significant effect on the color primes' ability to facilitate the recognition for the target objects. However, this result does not indicate whether a statistically significant amount of color-associate priming was found in any or all of the spatial-frequency conditions. Additional tests were conducted to more directly address the main hypothesis.

For the normal, unfiltered photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 object types was conducted. A significant interaction was found between object type and prime color $F(35, 350) = 1.50$, $p = 0.039$, observed $1 - \beta = .991$. As can be seen in Figure 2, the color orange was the most effective color prime for oranges, but the diagnostic colors of the other fruits do not seem to be any more effective than the non-diagnostic colors. A total of 20 Bonferroni corrected analyses were conducted for the highly color-diagnostic objects to determine if their diagnostic colors resulted in significantly faster naming speeds than their non-diagnostic colors. For the bananas, yellow was found to produce significantly faster naming speeds than yellow-green ($t = 3.61$, $p < 0.001$). For the oranges, the color orange was found to produce significantly faster naming speeds than red ($t = 3.82$, $p < 0.001$), yellow-green ($t = 4.61$, $p < 0.001$), and blue ($t = 3.49$, $p < 0.001$). For the lemons and strawberries no significant differences in naming speed were found. Though only two of the four highly color-diagnostic fruits showed significant differences between their diagnostic and non-diagnostic colors, these findings support our hypothesis by showing significant priming effects driven by the known color associates of the achromatically presented fruits.

A significant main effect of color prime was also found $F(5, 50) = 3.54$, $p = 0.008$, observed $1 - \beta = .887$, indicating that one or more of the color primes produced significantly faster reaction times than the others across all object types. Additionally, a highly significant main effect of object type was found $F(7, 70) = 27.14$, $p < 0.001$, observed $1 - \beta = 1.00$, indicating that some of the objects could be named faster than the others regardless of prime color. This effect can be clearly seen in Figure 2, wherein reaction times for the bananas and strawberries were much faster than lemons and oranges. This illustrates that the distinctiveness of the objects' shapes had a large influence on their recognition speeds.

For the high spatial-frequency photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 object types was conducted. No significant interaction was found between object type and prime color $F(35, 350) = 0.88$, $p = 0.664$, observed $1 - \beta = .851$. This indicates that the priming was ineffective when the low spatial-frequencies were removed from the object photographs. Only a marginally significant main effect of prime color was found $F(5, 50) = 2.32$, $p = 0.057$, observed $1 - \beta = .697$. However, a highly significant main effect of object type was found $F(7, 70) = 24.41$, $p < 0.001$, observed $1 - \beta = 1.00$, once again

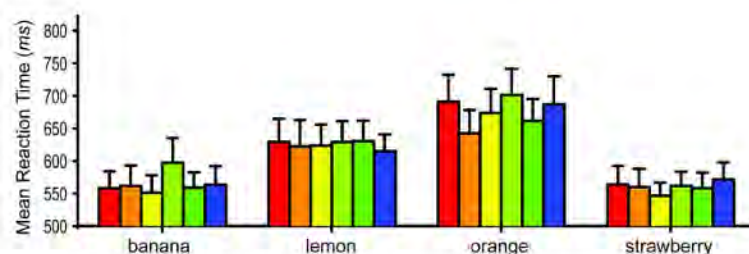


Figure 2. Naming reaction times for highly color-diagnostic objects. Bar color indicates prime color. Error bars show ± 1 SEM. $n = 11$. doi:10.1371/journal.pone.0064960.g002

indicating that some of the objects could be named faster than others regardless of the color of the prime.

For the low spatial-frequency photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 object types was conducted. A significant interaction was found between object type and prime color $F(35, 350) = 1.55$, $p = 0.027$, observed $1 - \beta = .993$. As can be seen in Figure 3, the most effective color prime was *yellow* for the bananas and lemons, but *orange* was not the most effective for oranges, and *red* was not the most effective for strawberries. A total of 20 Bonferroni corrected analyses were conducted to determine if there were any differences in the naming speeds for each highly color-diagnostic object's diagnostic color and its non-diagnostic colors. For the lemons, yellow was found to produce significantly faster naming speeds than red ($t = 3.62$, $p < 0.01$). For the bananas, oranges, and strawberries no significant differences in naming speed were found. Though only one of the four highly color-diagnostic fruits showed significant differences between their diagnostic and non-diagnostic colors, this finding supports our hypothesis by showing significant priming effects driven by the known color associates of the achromatically presented fruits.

Additionally, for the low spatial-frequency photographs a significant main effect of prime color was found $F(5, 50) = 4.26$, $p = 0.003$, observed $1 - \beta = .942$, indicating that the color primes produced significantly different reaction times across all object types. A highly significant main effect of object type was also found $F(7, 70) = 42.54$, $p < 0.0001$, observed $1 - \beta = 1.00$, indicating that the participants were able to name some of the objects quicker than others regardless of prime color.

Experiment 2 - Categorization

In Experiment 2 we sought to determine if similar results could be produced using a categorization task in place of the naming task. Though we made the same predictions as Experiment 1, it

seemed likely that our color primes would have different effects in this categorization task, as an object's color is known to have different effects on its categorization and naming [40]. However, as cars are generally not color diagnostic, we predicted no interaction between the color primes and car types. For various reasons 10 of the 15 individuals who participated in this experiment only completed one of the two conditions ($n_{\text{both}} = 5$, $n_{\text{normal_only}} = 7$, $n_{\text{LSF_only}} = 3$). Though it would have been preferable to have all participants complete both conditions, this is not problematic to the following analyses as they compare differences within the two spatial-frequency conditions, not across them. Note also that while the labels "fruit" and "car" might not be at the same categorical level [47], the car stimuli were merely used as a control condition and no statistical analyses compared these two categories of objects; the data were split by category ("fruit" vs "car") to facilitate the comparison of the objects within each. Preliminary 3-way within-subjects ANOVAs similar to that of Experiment 1 were not conducted for this experiment as many participants were unable to complete both of the spatial-frequency conditions.

For the normal fruit photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 fruit types was conducted. No significant interaction between fruit type and prime color was found $F(35, 385) = 1.32$, $p = 0.108$, observed $1 - \beta = .979$. Like Experiment 1, a significant difference in the mean reaction times was found between the 8 fruit types $F(7, 77) = 3.74$, $p = 0.002$, observed $1 - \beta = .968$. This seems to indicate that some of the fruit objects were easier to recognize as belonging to the "fruit" category. Also, a highly significant difference was found between the 6 prime colors $F(5, 55) = 4.21$, $p = 0.003$, observed $1 - \beta = .941$, suggesting that some colors were better than others at priming objects within the "fruit" category. As can be seen on the top-left side of Figure 4 the color orange appeared to produce the fastest reaction times regardless of fruit type. A total of

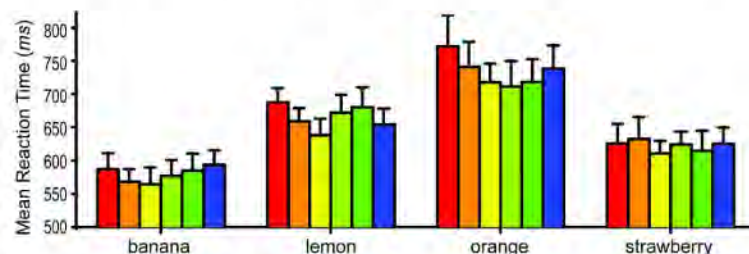


Figure 3. Naming reaction times for the highly color-diagnostic low spatial-frequency objects. Bar color indicates prime color. Error bars show ± 1 SEM. $n = 11$. doi:10.1371/journal.pone.0064960.g003

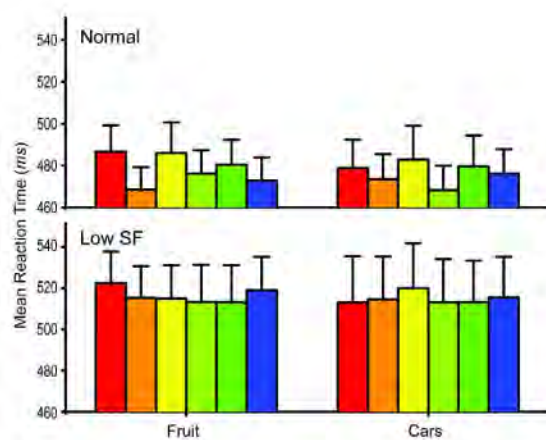


Figure 4. Mean categorization reaction times across all objects separated by category and spatial-frequency condition. (Top) Normal: Unfiltered target photographs $n=12$. (Bottom) Low SF: Low spatial-frequency target photographs $n=8$. Bar color indicates prime color. Error bars show +1 SEM. doi:10.1371/journal.pone.0064960.g004

5 Bonferroni corrected analyses were conducted to determine if the reaction times for orange were significantly faster than the other 5 colors across the 8 different fruit types. The color orange produced faster reaction times than red ($t=3.62$, $p=0.003$), and yellow ($t=3.50$, $p=0.0045$).

For the normal car photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 car types was conducted. No significant interaction between car type and prime color was found $F(35, 385)=1.17$, $p=0.108$, observed $1-\beta=.955$. No significant difference in the mean reaction times was found between the 8 car types $F(7, 77)=0.87$, $p=0.534$, observed $1-\beta=.362$. This seems to indicate that all of the car objects were equally easy to recognize as belonging to the "car" category. No significant difference was found between the 6 prime colors $F(5, 55)=1.66$, $p=0.160$, observed $1-\beta=.534$. However, as can be seen on the top-right side of Figure 4 the color yellow-green appeared to produce the fastest reaction times regardless of car type.

For the low spatial-frequency fruit photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 fruit types was conducted. Unlike the normal spatial-frequency condition a significant interaction between fruit type and prime color was found $F(35, 245)=1.56$, $p=0.028$, observed $1-\beta=.992$. A total of 20 Bonferroni corrected analyses were conducted to determine if there were any differences in the categorization speeds for each highly color-diagnostic object's diagnostic color and its non-diagnostic colors, but no significant differences were found.

Unlike the normal spatial-frequency condition, no significant difference in the mean reaction times was found between the 8 fruit types $F(7,49)=1.24$, $p=0.302$, observed $1-\beta=.473$. This indicates that when high spatial-frequency information is removed from the images, the fruit objects are equally easy to recognize as belonging to the "fruit" category. No significant difference in the mean reaction times was found between the 6 prime colors $F(5, 35)=1.79$, $p=0.14$, observed $1-\beta=.545$.

For the low spatial-frequency car photographs a 2-way within-subjects ANOVA across the 6 prime colors and the 8 car types was conducted. No significant interaction between car type and prime color was found $F(35, 245)=0.68$, $p=0.912$, observed

$1-\beta=.693$. However, a highly significant difference in the mean reaction times was found between the 8 car types $F(7, 49)=5.31$, $p<0.001$, observed $1-\beta=.995$. No significant difference was found in the mean reaction times between the 6 prime colors $F(5, 35)=0.59$, $p=0.710$, observed $1-\beta=.191$.

Discussion

This study demonstrates the priming of object recognition using known color associates. Facilitating the recognition of achromatic objects through prior exposure to a known color associate provides evidence of a functional relationship between the processing of color perception and color knowledge (eg. memory). This novel finding was observed using fruit stimuli and appears to have been driven by the color diagnosticity of the fruit objects, the low spatial-frequency information of their images, and the level of identity specificity required for the recognition task. To aid in the demonstration of these color priming effects the current study specifically utilized a within-subjects design, small sample-size, and selective range of stimuli. Unfortunately these design choices limit the generality of the current findings. While future studies are required to fully explain the driving forces of color associate priming—color diagnosticity, spatial-frequency, and identity specificity have been positively identified as contributing factors and are discussed in detail below.

Identity Specificity

The color primes appear to have different effects on the object naming and categorization tasks. Though significant interactions between prime color and fruit type were found in the low spatial-frequency conditions of both tasks these two results are highly dissimilar. The follow-up tests in the naming task yielded significant results, but those of the categorization task did not. None of the highly color-diagnostic objects were primed by their diagnostic colors when the participants were required to categorize the fruit objects, which does not provide evidence of color associate priming. This difference between the two tasks appears to be due to the differences in how the participants were required to respond.

In Experiment 2 the participants categorized the objects as being either "fruit" or "car", but were not required to identify what kind of fruit or car it was. In other research, the ability of an object's color to facilitate its recognition has been shown to be modulated by the level of identity the observer is attempting to determine [40]. Additionally, in the normal time course of object recognition processing the general categories to which an object belongs are determined before its specific identity is achieved [41–43]. Therefore, though object recognition normally requires only a fraction of a second, it is highly likely that the participants were responding well before they were able to determine the object's specific identity. In fact, many participants claimed to have used this kind of strategy in the follow-up interviews. Simply put, it seems that the fruit objects were not primed by their color associates in the categorization task simply because the participants were not required to recognize them at such a specific level.

However, the time course of object recognition suggests an alternative interpretation of these results. It may be the case that priming did indeed occur, but it facilitated recognition for objects within the "fruit" category instead of specific fruit types. This would explain the lack of a significant interaction between prime color and fruit type and the highly significant main effect of prime color found for the normal, unfiltered object photographs. As Figure 4 shows, the orange prime produced the fastest reactions across all types of fruit, and the follow-up statistical analyses

confirmed that these reaction times were significantly different from most of the other prime colors, which seems to suggest that orange is the color most closely associated with the category "fruit". This interpretation is particularly intriguing as it could have been predicted based on the evolutionary theories of color vision in primates. In tropical rainforests primates are known to predominantly seek out and consume yellow/orange fruits [3,5], as these colors are typically indicative of ripeness [7]. Therefore it may be that evolutionary processes have strengthened the link between yellow/orange colors and the recognition of fruits. Alternatively, it may instead be the case that viewing the orange Gaussian color activated the word "orange" which then worked as a semantic prime for the other fruit objects, or it may simply be that the participants had formed strong prior associations between this particular range of fruit types and the color orange. Regardless, the orange prime produced the greatest facilitation for categorizing the fruit objects used in this study, even for types of fruit that do not normally appear orange.

Spatial-frequency Information

Object recognition is greatly facilitated by the presence of an object's many visual features, including shape, texture and luminance. The facilitatory effects of these features can be so great that the contributions of color information may be diminished to the point of being inconsequential for object recognition purposes [16,40,44]. Therefore, in both experiments we attempted to amplify the color priming effects by removing one or more of these visual features from the target photographs.

In Experiment 1 the naming reaction times were measured for the original photographs, photographs that contained only the low spatial-frequency luminance information, and photographs that contained only the high spatial-frequency shape and texture information. All three conditions produced the same general trends, which suggests that the presence or absence of the other visual features did not greatly influence the effectiveness of the color primes. The only obvious difference between the three conditions was in their overall reaction time speeds. The low and high spatial-frequency conditions had much slower reaction times than the normal condition, likely reflecting an increase of task difficulty. Despite this overall similarity, significant color priming effects were only found for the normal and low spatial-frequency conditions; no color priming was found for the high spatial-frequency condition. Interestingly this suggests the color associate priming was driven by the low spatial-frequency luminance information of the target objects. Despite our predictions it does not appear to simply be the case that color will become more informative of object identity when shape information has been degraded. Instead, this result appears to indicate that color information has its greatest influence on the early stages of object recognition, as low spatial-frequencies are known to typically be processed before high spatial-frequencies [48–50].

References

- Jacobs GH (1993) The distribution and nature of colour vision among the mammals. *Biological Reviews* 68: 413–471.
- Surridge AK, Osorio D, Mundy NI (2003) Evolution and selection of trichromatic vision in primates. *Trends in Ecology & Evolution* 18: 198–205.
- Bowmaker JK (1998) Evolution of colour vision in vertebrates. *Eye* 12: 541–547.
- Allen G (1879) *The colour-sense: Its origin and development*. London: Trübner & Co.
- Regan BC, Julliot C, Simmen B, Vienot F, Charles-Dominique P, et al. (2001) Fruits, foliage and the evolution of primate colour vision. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 356: 229–283.

Color Diagnosticity

Color information is a feature of almost all visual objects. The inclusion of color within an image has been shown to facilitate the recognition of a wide range of objects [10–12]. However, studies have shown that the recognition of color-diagnostic objects, objects that are well known to have a specific color [14], generally show the greatest benefit from the inclusion of color information [13,15,16]. Therefore, the current study compared the effectiveness of various color primes across a range of objects varying in their color diagnosticity. It was predicted that the most color diagnostic objects (bananas, lemons, oranges, and strawberries) would show the strongest priming effects. It is important to note that the color primes used in this study were not isoluminant, but their luminance differences did not appear to have a measurable influence on the priming effects.

Across the normal and low spatial-frequency conditions of Experiment 1 the bananas, lemons and oranges were found to be differentially influenced by the color primes at a statistically significant level. These objects were most primed by their diagnostic colors (*yellow-banana*, *yellow-lemon*, *orange-orange*), which supports our hypothesis. Though these data may appear somewhat understated, the finding of any such priming is indicative of an interaction between color perception and color knowledge processing. This interaction is likely due to an overlap between the processing of visually presented colors and the color knowledge associated with these highly color-diagnostic fruit objects. This is a novel finding that provides support for the theory of modality grounded object knowledge, which for highly color-diagnostic objects appears to include color processing areas.

Conclusions

Colorless object images can be primed by the prior presentation of their known color associates. This color associate priming is based entirely on the color information stored within object knowledge. Three factors that have an influence on this color priming have been identified: the color-diagnosticity of the objects, their spatial-frequency information, and the required level of identification specificity. These findings are in line with the previous behavioral research, and provide support for the theory that object knowledge is grounded within modality specific systems [28,51] by demonstrating an interaction between the processing of color perception and object knowledge.

Author Contributions

Conceived and designed the experiments: DL SK. Performed the experiments: DL. Analyzed the data: DL. Wrote the paper: DL JP SK.

11. Uttl B, Graf P, Santacruz P (2006) Object color affects identification and repetition priming. *Scandinavian Journal of Psychology* 47: 313–325.
12. Wurm LH, Legge GE, Isenberg LM, Luebker A (1993) Color improves object recognition in normal and low vision. *Journal of Experimental Psychology: Human Perception and Performance* 19: 899–911.
13. Rossion B, Pourtois G (2004) Revisiting Snodgrass and Vanderwart's object pictorial set: The role of surface detail in basic-level object recognition. *Perception* 33: 217–236.
14. Bramão I, Inácio F, Faisca L, Reis A, Petersson KM (2011) The influence of color information on the recognition of color diagnostic and noncolor diagnostic objects. *The Journal of General Psychology* 138: 49–65.
15. Tanaka JW, Presnell LM (1999) Color diagnosticity in object recognition. *Perception & Psychophysics* 61: 1140–1153.
16. Theriault D, Yaxley R, Zwaan R (2009) The role of color diagnosticity in object recognition and representation. *Cognitive Processing* 10: 335–342.
17. Bramão I, Faisca L, Forkstam C, Reis A, Petersson KM (2010) Cortical brain regions associated with color processing: An fMRI study. *Open Neuroimaging Journal* 4: 164–173.
18. Hering E (1920) *Grundzüge der Lehre vom Lichtsinn*. Berlin: Springer-Verlag.
19. D'Zmura M, Lennie P (1986) Mechanisms of color constancy. *Journal of the Optical Society of America A* 3: 1662–1672.
20. Hansen T, Olkkonen M, Walter S, Gegenfurtner KR (2006) Memory modulates color appearance. *Nature Neuroscience* 9: 1367–1368.
21. Hurlbert AC, Ling Y (2005) If it's a banana, it must be yellow: The role of memory colors in color constancy. *Journal of Vision* 5: 787.
22. Pérez-Carpinell J, de Fez MD, Baldoví R, Soriano JC (1998) Familiar objects and memory color. *Color Research & Application* 23: 416–427.
23. Olkkonen M, Hansen T, Gegenfurtner K (2008) Color appearance of familiar objects: Effects of object shape, texture, and illumination changes. *Journal of Vision* 8: 1–16.
24. Witzel C, Valkova H, Hansen T, Gegenfurtner K (2011) Object knowledge modulates colour appearance. *i-Perception* 2: 13–49.
25. Simmons WK, Ramjee V, Beauchamp MS, McRae K, Martin A, et al. (2007) A common neural substrate for perceiving and knowing about color. *Neuropsychologia* 45: 2802–2810.
26. Hsu NS, Frankland SM, Thompson-Schill SL (2012) Chromaticity of color perception and object color knowledge. *Neuropsychologia* 50: 327–333.
27. Hsu NS, Kraemer DJM, Oliver RT, Schlichting ML, Thompson-Schill SL (2011) Color, context, and cognitive style: Variations in color knowledge retrieval as a function of task and subject variables. *Journal of Cognitive Neuroscience* 23: 2544–2557.
28. Barsalou LW, Simmons WK, Barbey AK, Wilson CD (2003) Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences* 7: 84–91.
29. Shuren JB, Brott TG, Scheffl BK, Houston W (1996) Preserved color imagery in an achromatopsic. *Neuropsychologia* 34: 485–489.
30. De Vreese LP (1991) Two systems for colour-naming defects: Verbal disconnection vs colour imagery disorder. *Neuropsychologia* 29: 1–18.
31. Luzzatti C, Davidoff J (1994) Impaired retrieval of object-colour knowledge with preserved colour naming. *Neuropsychologia* 32: 933–950.
32. Chao LL, Martin A (1999) Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience* 11: 25–35.
33. Miceli G, Fouch E, Capasso R, Shelton JR, Tomaiuolo F, et al. (2001) The dissociation of color from form and function knowledge. *Nature Neuroscience* 4: 662–667.
34. Lu A, Xu G, Jin H, Mo L, Zhang J, et al. (2010) Electrophysiological evidence for effects of color knowledge in object recognition. *Neuroscience Letters* 469: 405–410.
35. Joseph JE, Proffitt DR (1996) Semantic versus perceptual influences of color in object recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*; *Journal of Experimental Psychology: Learning, Memory, and Cognition* 22: 407.
36. Joseph JE (1997) Color processing in object verification. *Acta Psychologica* 97: 95–127.
37. Bramão I, Faisca L, Petersson KM, Reis A (2010) The influence of surface color information and color knowledge information in object recognition. *The American Journal of Psychology* 123: 437–446.
38. Bramão I, Faisca L, Forkstam C, Inácio F, Araújo S, et al. (2012) The interaction between surface color and color knowledge: Behavioral and electrophysiological evidence. *Brain and Cognition* 78: 28–37.
39. Yee E, Ahmed SZ, Thompson-Schill SL (2012) Colorless green ideas (can) prime furiously. *Psychological Science* 23: 364–369.
40. Price CJ, Humphreys GW (1989) The effects of surface detail on object categorization and naming. *The Quarterly Journal of Experimental Psychology Section A* 41: 797–828.
41. Hamm JP, Johnson BW, Kirk IJ (2002) Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology* 113: 1339–1350.
42. Large ME, Kiss I, McMullen PA (2004) Electrophysiological correlates of object categorization: Back to basics. *Cognitive Brain Research* 20: 415–426.
43. Rogers TT, Patterson K (2007) Object categorization: Reversals and explanations of the basic-level advantage. *Journal of Experimental Psychology: General* 136: 451–469.
44. Mapelli D, Behrmann M (1997) The role of color in object recognition: Evidence from visual agnosia. *Neurocase* 3: 237–247.
45. Brainard DH (1997) The Psychophysics Toolbox. *Spatial Vision* 10: 433–436.
46. Naor-Raz G, Tarr MJ, Kersten D (2003) Is color an intrinsic property of object representation? *Perception* 32: 667–680.
47. Rosch E, Mervis CB, Gray WD, Johnson DM, Boyes-Braem P (1976) Basic objects in natural categories. *Cognitive Psychology* 8: 382–439.
48. Navon D (1977) Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology* 9: 353–383.
49. Parker DM, Lishman JR, Hughes J (1992) Temporal integration of spatially filtered visual images. *Perception* 21: 147–160.
50. Schyns PG, Oliva A (1994) From blobs to boundary edges: Evidence for time- and spatial-scale-dependent scene recognition. *Psychological Science* 5: 195–200.
51. Wilson M (2002) Six views of embodied cognition. *Psychonomic Bulletin & Review* 9: 625–636.

