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RESPONSE TIME STUDIES OF SPATIAL LOCATION AND OBJECT IDENTITY: EXAMINATION OF THE DUAL PATHWAY MODEL OF HIGHER ORDER VISION

by

ANDREW STEFAN HERMANN

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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ABSTRACT

RT STUDIES OF SPATIAL LOCATION AND OBJECT IDENTITY: EXAMINATION OF THE DUAL PATHWAY MODEL OF HIGHER ORDER VISION

by

ANDREW STEFAN HERMANN

Advisor: Professor John Antrobus

Relating location and identity in visual object recognition to structure and function within higher order vision have produced diverse cognitive models. The dual pathway model proposes that magnocellular "transient" and parvocellular "sustained" cell sites in occipital cortex project forward in parallel dynamic synchrony through extra-striate regions upward to posterior parietal cortex (PPx) as dorsal ("where") pathway for processing spatial location, and downward to inferior temporal cortex (IT) as ventral ("what") pathway to process color and form for identity, then continue onward to hippocampus/rhinal cortex, binding information in memory.

Fifty-seven university students participated in response time (RT) and accuracy studies judging location, identity, and location+identity of digitized Snodgrass and Vanderwort (1980) drawings of common objects, assessing location and identity to determine effects of: (1) respective rate of processing; (2) hue; (3) spatial frequency filtering (SFF) using Butterworth digital highpass (9.50 - 11.00 cpd) and lowpass (0.01 - 1.50 cpd) filters; and (4) speed-accuracy tradeoff (SAT) methodology to reveal ongoing processing.

Owing to the inadvertent use of "only" in my instructions, rather than "Location" and "Identity," I am unable to clearly identify the processes that produced my data. Therefore, I can make no unequivocal claims regarding location versus identity processing, and any statements regarding this data must be viewed as speculative. Future research, however, offers the possibility of clarifying these ambiguities.

Nevertheless, results support and extend the dual pathway model. Location was processed faster than identity. Bw stimuli rt's were faster than rgb stimuli, indicating rgb doesn't aid identity processing. SAT method revealed steep improvement in location during 351 - 700 ms with sharp fall-off from 701 - 1050 ms. Identity improved gradually during 701 - 1050 ms, maintaining during 1051 - 1400 ms. Conjoint location+identity judgments revealed effects of location, followed afterwards by identity. Finally, a double dissociation occurred: identity was more accurate for unfiltered and highpass objects and location more accurate for unfiltered and lowpass-filtered objects.

Highpass filter inhibited location, while lowpass filter inhibited identity, emulating dorsal and ventral agnosias. SAT illuminated cognitive processing otherwise obscured. SFF/SAT paradigms may help characterize clinical disorders (e.g., Multiple Sclerosis, Alzheimer's Dementia, and Dyslexia).

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Allison, my wife, whose creativity, intelligence, beauty, patience, and love has sustained me throughout this ordeal, and who has joined me in my voyage, loyally at my side, to and from the lands of Ithaca. And with Allison, I thank my three year-old twin sons, Jonas and Lukas (cited alphabetically), my editors extraordinaire, who have inked or penned many a page for me- all of whom I love greater than the sun and the moon and the stars up above. Next, my parents and siblings and relatives: my parents, Deborah and Howard, who have loved and supported me in every way imaginable and have stood as beacons and role models for a rewarding, satisfying, emotionally and intellectually fulfilling life. And my siblings and their families, without whose support, guidance, perspective, and love I would not have had the courage to overcome all obstacles; Kate, whose her caring, concern, faith, and assistance helped me carry on; Rachel, her husband, Anthony, and my niece, Stephanie, and nephew, Alex, who have provided guidance and perspective in the world of academia and parenthood and who reminded me that distance and time mean nothing when you really care for other people; Peter, his wife Tammy, and my nieces Camilla, Julia, and Oliver (by age), whose support, understanding, love, and reminding me of what really matters, kept my eye always upon the future; And to my Uncle John and Aunt Dorothy who have maintained constant faith in me over this marathon, sharing the moments that mattered most with us, for which I will always be grateful. And then there are so many other relatives and friends who have shown such great caring and support over this journey, I have no hope in naming them all. Finally, I must thank those who have come before, and are no longer here to share this wonderful day with us: my grandparents, Amalie and Shakman, my aunt and uncle Goldie and Norman, and others who would know how much this day means.

For training in Neuropsychology and Cognitive Remediation:

I must thank many people, a great number of whom I am lucky enough to call friends, also. First, I must thank the late, and so very wonderful, Nelson Butters, for his guidance, judgment, humor, and training, and without whom I would not have taken this path in the first place; Jim Becker, who, taught me that one can always learn more; to Edith Kaplan who showed me that CT scans are far easier to read when you hold them right side up; also, the late Lou Gerstman, a kind and caring advisor, who was active in far more than 100 dissertations, ensuring their statistical accuracy; Jason Brown, who opened my eyes to the true A. R. Luria, and who made me see that neuropsychology spans multilingual domains, and who taught me that for every idea I had, there are ten more that can be spun out -- Jason, you may now retire, content; my deepest thanks also to Floyd Turner, whose clinical acumen, compassion, caring, friendship, and fundamental humanism has meant more to me and my family than he will ever know; and too, Charles Turner, who made himself available as acted as a kindhearted, statistically unbiased, mathematical arbiter, and scientific advisor to prevent skew from entering where it could not; David Kassoff, who has helped bring comfort and courage in my hearth and home; Additionally, I must thank Judith Baumrin for teaching me the initial steps to follow the road of remediation, and for making me see the importance and beauty of Sylvia Ashton Warner's perspective on learning. To Antoinette Lynn, whose love, caring, friendship, understanding, insight, and guidance helped me through; To Rita Rudel, Minna Broman, and Rita Haggerty, who taught me diagnostic and testing skills; Further, to Lissa Weinstein and Jane Healy who working together taught me the incredible power and importance of integrating clinical and neuropsychological understanding, and made the experience edifying, enchanting, continually rewarding, and fun. I am grateful also to Elkhonon (Nick) Goldberg for enlightening me further upon subcortical processing, frontal lobe function, and the effects of tearing and shearing of the long white fibers on cognitive function. I must also thank Oliver Sacks, Harold Klawans, and so very many other authors who transformed the educational process into neurological and neuropsychological tales which have kept me enthralled and have taught me to value the importance of clinical observation. Further, I must thank Melissa and Giri Chepuru and family for their friendship and support, and for being truly instrumental in showing me what is necessary to create a signature document. In addition, to Marisa Levine, a true "go-getter." She took on far more responsibility and independence than I would have thought possible of someone her age, even when it meant that one could not always be there to oversee every step, and for that I am grateful. Finally, but not least, I must thank Bill Dince for ensuring my professionalism, and for the knowledge that nothing would make him happier than witnessing the completion of my doctoral degree. And with Bill, his wife Dana, and children Aaron and Leah; all of whom have made me see what it means to be truly a friend.

For intellectual training and guidance surrounding my dissertation,

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Clearly, this has been a profound educational experience, but as with all experiences one learns that those who fail to learn the lessons of history are doomed to repeat them. And with that I cite the words of G. Grouigneau, in his preface to his 1884 work, Etude Clinique et Experimentale Sur la Vision Mentale, "Nous n'avons pas la témérité de croire que nous avons résolu dans tous ses termes le problème qui fait le sujet de cette thèse, nous voulons seulement essayer de contribuer pour notre part à sa solution, trop heureux si nous réussissons dans notre entreprise." Finally, there are many others who extended themselves far beyond the call of duty, and for which I will always feel regret that in my hurry to complete these acknowledgments that I have failed to mention. That oversight is solely my own for which I take full responsibility, and beg their pardon, as it was unintentional. But, I have learned that is often the case in research, in which one is left to ponder, "if only?

Educators from the Program in Experimental Cognition:

An instance of this which I have the good fortune to correct is those below: I am deeply and fully thankful to those members of my program for providing me with the valuable educational experience and training in cognition, neuropsychology, politics, and life: Of first note must be my advisor, John Antrobus who taught me what it really means to be a good advisor and of the fulfillment of the academic quest, and who further made me see that it can truly take a lifetime to answer a research question in full. Also, to Jeff Rosen, who made me see that an unexamined life is a life not worth leading, and who rose to the occasion to participate in my doctoral defense when MSG could not attend due to other commitments. Yaakov Stern and Richard Mayeux, who gave me a true glimpse into the life of clinical research and the importance of ethical treatment of others. Finally, I thank Jeff Halperin who taught me the importance of the statement that, "One's word is One's bond."

A Final Note:

Finally, I am in the embarrassing position of having to thank myself for working so very hard to earn every single penny that I spent on this project: from the purchase of a specialized computer flown over from Japan, payment to programmers and purchase of software, reimbursement to volunteer participants, and so many other costs, down to the smallest items including phone calls, xeroxing of forms, pencils, and even paper. Thus, I can truly say that all of this research with costs in five figures, was solely and completely earned and funded by myself. And with that I return - just like Candide to "cultivate (my) garden" albeit in Scarsdale, (to which my in-laws have offered to get me wholesale prices), with time now to build my photography darkroom, relearn the flute, study languages, art, philosophy, literature, and antiquarian neuroscience, and perhaps even architecture, and to hone my professional craft - full circle like Odysseus home from his travels back to my family where I belong, who have waited so patiently and so faithfully for my return and who share the joy I feel forever more, "...and yes I said yes I will Yes." I have much to make up to my family for time spent on educational pursuits - I hope this is a start....

--Andrew S. Hermann (no longer A.B.D.)

LIST OF TABLES

LIST OF FIGURES

TABLE OF CONTENTS

INTRODUCTION

Researchers in the field of visual object processing often elaborate upon existing models of visual system function in an effort to relate experimental findings to new insights in visual system organization.[1] These attempts to link visual system structure with cognitive processing reflect a wide range of theoretical perspectives from perceptual (Biederman & Cooper, 1991a, 1991b, 1992; Biederman, Hummel, Cooper, & Gerhardstein, 1993; Gerhardstein & Biederman, 1991, May) to semantic (Boucart & Humphreys, 1992; Humphreys & Riddoch, 1987a, 1987b; Riddoch & Humphreys, 1987b). Recent advances in the understanding of the organization of the higher order visual system based on neuroanatomical, clinical, and experimental research and neural net simulations, now offer the opportunity to clarify these information processing models.

Investigation of the higher order visual system has culminated in a dual pathway model of visual system function which provides for the analysis, integration, and storage of spatial and patterned aspects of visual information for the perception and the re-perception of the location and the identification of visual objects (Andersen, Essick, & Siegel, 1985; Felleman & Van Essen, 1991; Friedman-Hill, Robertson, & Treisman, 1995; Gross, 1973, 1992, 1998; Gross, Desimone, Albright, & Schwartz, 1984; Gross, Schiller, Wells, & Gerstein, 1967; Livingstone & Hubel, 1987; Maunsell, 1987; Mishkin, Ungerleider, & Macko, 1983; Pohl, 1973; Rocha-Miranda, Bender, Gross, & Mishkin, 1975; Rolls, 1990; Schiller, 1993; Schiller & Lee, 1991; Treisman, 1992; Ungerleider & Mishkin, 1982; Van Essen, Felleman, DeYoe, & Knierim, 1993; Van Essen & Maunsell, 1983).

The dorsal pathway projects forward from occipital cortex through extrastriate regions upward to the posterior parietal cortex (PPx) for processing spatial location of visual objects (Andersen, 1989; Flechsig, 1896, 1920; Mishkin, 1972; Mishkin, Lewis, & Ungerleider, 1982; Mishkin & Ungerleider, 1982; Zipser & Andersen, 1988); in contrast, the ventral pathway projects forward from occipital cortex through extrastriate regions downward to the inferior temporal cortex (IT) for processing color and form for the identity of visual objects. (Flechsig, 1896, 1920; Gross, 1973, 1992, 1998; Macko, Jarvis, Kennedy, Miyaoka, Shinohara, Sokoloff, & Mishkin, 1982; Macko, Kennedy, Sokoloff, & Mishkin, 1981; Mishkin, 1972; Rocha-Miranda, Bender, Gross, & Mishkin, 1975; Rockland & Pandya, 1981).

This organization of the dual-pathway system indicates that location information is processed at PPx independently from identity information at IT, before projecting separately through limbic structures to the hippocampus where this information is apparently combined and stored as either fused, or multipart, representations in associated neural network ensembles (Desimone & Schein, 1987; Felleman & Van Essen, 1991; Goodale, Milner, Jakobson, & Carey, 1991; Gross, 1992, 1994; Gross et al., 1984; Johnson & Chalfonte, 1994; Kesner, 1989; Kosslyn, 1987, 1991; Kosslyn & Koenig, 1992; Livingstone & Hubel, 1988; Martin-Elkins & Horel, 1992; Maunsell & Newsome, 1987; McNaughton, Barnes, Meltzer, & Sutherland, 1989; Mishkin & Appenzeller, 1987; Mishkin et al., 1983; Mishkin & Murray, 1994; Rueckl, Cave, & Kosslyn, 1989; Rocha-Miranda et al., 1975; Rolls, 1989; Rolls et al., 1989; Schiller, Logothetis, & Charles, 1990a, 1900b; Zeki, 1992; Zipser, 1991; Zola-Morgan, Squire, & Amaral, 1986).

While the contributions of a wide array of researchers, clinicians, and theoreticians over the last two centuries have laid the foundation for current insights into this parallel hierarchical system, the proposed organization of this system has yet to be assessed directly through controlled experimentation with human participants using response time (RT) paradigms.

REVIEW OF LITERATURE

History of Localization in the Dual Pathway System

In 1873, David Ferrier advanced the view that, rather than the occipital cortex, the angular gyrus of the parietal lobe was the true locus of visual impressions in the brain (Finger, 1994; Glickstein, 1985; Gross, 1998).[2] Ferrier reported that electrical stimulation of the angular gyrus of monkeys caused conjugate eye movements, whereas stimulation of the occipital cortex did not. Moreover, he found bilateral lesions of the angular gyrus resulted in blindness while large bilateral occipital lobe lesions did not. Ferrier, however, was not familiar with Lister's antiseptic preparations. As a consequence, the animals lived less than four days post-operatively preventing assessment of longer term post-surgical recovery of function. Also, Ferrier removed only two-thirds of the visual cortex when oblating the occipital lobes which, unbeknown to him, spared approximately the peripheral 30° of the visual field and "a few degrees of the entire representation of the lower half of the vertical meridian..." (Gross, 1998, pp. 72-73) accounting for findings of preserved vision (Glickstein, 1985; Gross, 1994).

Ferrier's claim that the parietal lobe was the cortical locus for vision was challenged by Hermann Munk (1881/1960) who asserted, instead, that the occipital lobe was the sole cortical site for visual processing. In support of his view, Munk reported that total occipital lobe removal produced complete absence of vision. In contrast, limited occipital lobe lesions caused failures only of visual recognition. It is also notable that Munk was acquainted with Lister's antiseptic preparations. Thus, he was able to study the dogs' recovery of function for up to 5 years post-operatively. Munk concluded that the occipital cortex was the sole cortical locus for vision, while the function of the angular gyrus was only for eye movements and blinking (Finger, 1994; Gross, 1994).

To support Ferrier's earlier research finding, Ferrier and Yeo (1886) conducted follow-up studies. This time when they performed bilateral lesions of the angular gyrus of the parietal lobe, their surgery produced only temporary blindness. In contrast, their bilateral lesions of both the angular gyrus and occipital lobes produced complete and permanent blindness. Ferrier and Yeo concluded that the combination of both the angular gyrus and occipital lobe lesions were required to produce total and permanent blindness. In the course of their ablation studies, however, Ferrier and Yeo, in 1884, noted an unexpected consequence of surgical removal of the angular gyrus in one of the animals. Ferrier and Yeo noted that, following recovery from surgery, this animal, "case 8," evidenced significant difficulties in its ability to localize and reach for stimuli;

> . . . A piece of orange was held before it, whereupon it came forward in a groping manner and tried to lay hold at first, but missed repeatedly. . . . it was evidently able to see its food, but constantly missed laying hold of it, putting its hand beyond it or short of it . . . When it was walking on a table it tumbled off, having come too

> near the edge without seeming to be aware of the fact (Gross, 1994, pp. 460-461).

Thus, while Ferrier and Yeo's "case 8," was able to correctly determine the identity of visual objects, it failed to accurately localize them in space.

In 1888, Brown and Schäfer, however, challenged Ferrier and Yeo's belief that cortically-based vision depended exclusively on the combined contributions of the parietal and occipital lobes.[3] According to Brown and Schäfer, their research indicated an important occipito-temporal role in vision as, "...total removal of the occipital lobe produced permanently blind animals, but only if the lesion extended on the ventral surface into the temporal lobe." (Gross, 1998; p. 72). Further, they described the consequence of temporal lobe lesions. They discovered that bilateral temporal lobe lesions led to a significant reduction in the aggressive behavior in one of the monkeys, "animal 6," which they referred to as "the tame one." An additional, and striking, feature they recorded was that this animal evidenced a severe deficit as well in visual recognition.[4] Brown and Schäfer observed that, "He gives evidence of hearing, seeing and of his senses generally, but it is clear that he no longer clearly understands the meaning of the sights, sounds, and other impressions that reach him" (Gross, 1994, p. 460). While Brown and Schäfer's "animal 6," could accurately localize objects in space, it failed to correctly determine the identity of the visual objects. Brown and Schäfer's characterization of "animal 6," is reminiscent of John Hughlings Jackson's (1876/1932) description of a patient who was impaired in the recognition of objects, people, and other visually presented stimuli. Jackson's patient was able to see, yet failed to recognize presented stimuli. At autopsy it was discovered that the patient had suffered damage to the temporal lobe. Thus, while Brown and Schäfer's "animal 6," was able to correctly localize objects in space, it failed to recognize their identity.

Visual Agnosia and the Dorsal and Ventral Pathways

In Munk's (1881/1960) characterization of object recognition deficits, he distinguished between "cortical blindness" (rindenblindheit), which was caused by complete removal of the occipital lobes, and "psychic blindness" (seelenblindheit), which resulted from limited lesions of the occipital lobe, in which there was a failure only in visual recognition. Dogs with psychic blindness failed to recognize objects, food, or flaming matches despite the fact that the animals could identify objects by touch or smell, and could ambulate over, under, and around the objects they failed to recognize. Munk believed that the dogs had lost their store of visual memories and would have to relearn this knowledge. Munk's description of visual impairments suggests that these more limited lesions may have affected the occipito-temporal pathway, but others failed to replicate and criticized his results. As a result, the controversy continued even though others, such as William James and later Klüver and Bucy adopted Munk's term, "Psychic Blindness." Nevertheless, based on Munk's description, it is apparent that animals with psychic blindness were able to see, but failed to recognize the objects they viewed.

The first detailed theory of disturbances in visual recognition in humans was postulated by Lissauer in 1889. He proposed a stage model in which object recognition depended both on early perceptual processes as well as later stages in which visual impressions were combined to permit access to internal representations. The early stage, termed "apperception," was the stage at which conscious perception of sensory impressions of separate visual attributes were combined together into a whole. Patients with apperceptive deficits would be expected to be unable to match, copy, or correctly identify objects. The latter stage, which he termed "association," referred to the impartment of meaning to the content of perception by matching and linking it to previous experience. Patients with associative deficits should be able to copy normally, because they perceive normally, however, they would be expected to fail to show recognition of an object's meaning. Lissauer's nomenclature was supplanted shortly afterward by the term "visual agnosia" by Sigmund Freud (1891/1953) to characterize deficits in the recognition of visual objects.

Over the last century, Lissauer's and Freud's conceptions of visual recognition deficits have advanced such that visual agnosia is now conceptualized as a modality specific failure in recognition which is <u>not</u> attributable to elementary sensory deficits, mental deterioration, aphasic naming, unfamiliarity with material, or attentional disturbances (Bauer, 1993). Bauer (1993) states that, "Complex visual abilities are made up of dissociable ('modular') information processing streams, including form discrimination, color perception, luminance, size, movement, and spatial localization and integration." Bauer concludes that, "variability among apperceptive agnosics reflects the fact that in individual cases these streams can be impaired singly or in combination" (p. 227).

Lesions to IT have been associated with "narrow apperceptive agnosia" (Farah, 1990). Despite preservation of such elementary visual functions as acuity, visual fields, luminance detection, color vision, depth, and movement perception, these patients are unable to recognize, match, copy, or discriminate simple visual forms. Their impairment in the identification of visual stimuli is consistent with Brown and Schäfer's (1888) bilateral temporal lobe-lesioned "animal 6," as well as of that of temporal lobe damaged patients described by Hughlings Jackson (1876/1932), Goldstein and Gelb (1918), and Benson and Greenberg (1969). This deficit in visual recognition is also consistent with deficits in visual object recognition described by Klüver and Bucy (1938), who later rediscovered Brown and Schäfer's (1888) observation of impairment in visual form identification, despite intact spatial and elementary visual perception (also termed a ventral agnosia).

The means by which patients with temporal lobe lesions compensate for their impairment in identification of visual forms is consistent with separate pathways for transmission of form versus spatial information. For example, while the patients described by Benson and Greenberg (1969), and Goldstein and Gelb (1918) were unable to identify stationary visual forms, both patients could compensate for deficits in visual form identification if permitted to trace the outline of stimuli kinesthetically, or by making many small head movements thereby using movement cues to aid in form detection. Goldstein and Gelb (1918) reported that their patient "Schn.," successfully traced stimuli using his hand and head movements, but his recognition ability deteriorated when he was prevented from using kinesthetic and proprioceptive feedback. Preservation of these patients' ability to use kinesthetic and movement cues to help detect and copy figures suggests that when the PPx remains intact, it can be used to help compensate for deficits in the processing of visual forms caused by temporal lobe lesions.[5]

Lesions to the parietal lobe have been reported to produce a "spatial agnosia." Patients with spatial agnosia are impaired in their ability to compare stimuli from the external spatial environment with an internal spatial representation (Bisiach & Luzzatti, 1978; Bisiach, Luzzatti, & Perani, 1979; Brain, 1941b). This impairment in the representation of spatial location is consonant with deficits described by Holmes (1918) in six soldiers who, due to parieto-occipital injuries, exhibited gross spatial directional errors when reaching for objects in space regardless of visual field as well as deficits in route learning, spatial navigation, and determination of spatial relations. These deficits also are consistent with the description by McCarthy and Warrington (1990) of a visuospatial agnosic patient with parietal lobe damage, and by Luria's (1972) description of a spatial apractic patient, Zazetsky, who suffered parieto-occipital damage. Moreover, these findings are consonant also with Ferrier and Yeo's (1884) description of "case 8" in which angular gyrus lesions impaired the animal's ability to correctly localize and reach toward stimuli.

As described by Luria (1973), individuals with lesions to the inferior parietal and parieto-occipital region were impaired in the ability to find their bearings within a system of spatial coordinates and easily lost their sense of direction. Similarly, they had difficulty determining the orientation of external objects in space. Luria described the difficulty they experienced performing such daily tasks as making the bed; they were unable to determine how to orient the blanket in space. Mentally reversing spatial relations was a problem as well, making dressing problematic, because they often placed their arm into the wrong sleeve. Telling time also was difficult if clocks did not have numbers as these individuals could not distinguish between symmetrical positions on the clock face.

Luria's report of Zazetsky's behavioral impairments from parietal lobe lesions is consistent with this view. Zazetsky could not figure out which direction to walk home even if only a block away from his house. Moreover, he could no longer determine how to follow spatial commands, and could not gauge the distance and spatial relations between objects. Similarly, he experienced difficulty guiding his body or limbs in space to communicate through physical gestures and, when he attempted to sit down, he worried he would miss the seat and fall over. Additionally, Luria described that Zazetsky was unable to interpret diagrams, maps, or spatial directions. As Zazetsky, himself, reported in his diary,

> Suddenly the words right, left, back, forward, up, and down occurred to me, but they weren't any help, since I didn't really understand what they meant. A minute later, I remembered the words south, north, east, and west. But when I tried to figure out what the relationship was between any two of these words, I was lost (Luria, 1972, p. 53).

Thus, the consequence of parietal damage on spatial function and representation is profound and clearly separable from temporal lobe damage.

Location and Identification of Visual Objects in the Dorsal and Ventral Pathways

It is only within the last twenty-five years that researchers have come to understand how the higher order dual pathway visual system serves as an extension of the geniculo-striate visual system (Mishkin, 1972;

Pohl, 1973).[6] Originating at the level of the retina, axons from two separate classes of retinal ganglion cells leave the eye and project in parallel along the optic nerve to separate magnocellular (M-cell) and parvocellular (P-cell) layers of the lateral geniculate nucleus (LGN). These two cell types then project onward to convey fundamentally different characteristics of visual information to separate sites within the primary visual cortex, which is where the dual pathway higher order visual system begins (DeMonasterio & Schein, 1982; Kosslyn, Flynn, Amsterdam, & Wang, 1990; Livingstone & Hubel, 1988; Lund, 1988; Mignard & Malpeli, 1991; Ungerleider & Desimone, 1986; Campbell, 1974; Graham, 1980; Schneider, 1969).[7]

The cells of the M-cell pathway are large, rapid responding, fast conducting, transient response cells with high contrast sensitivity, low spatial frequency, low spatial resolution and low acuity, and little or no color sensitivity, except for a slight response to diffuse red wavelength light in area MT (Cohen, 1993; Derrington, Krauskopf, & Lennie, 1984; Derrington & Lennie, 1984; Dreher, Fukada, & Rodieck, 1976; Hubel & Livingstone, 1990; Kaplan & Shapley, 1982; Schiller & Stryker, 1972; Shapley, Kaplan, & Soodak, 1981; Weisel & Hubel, 1966. Perceptual studies indicate that the M pathway conveys information about spatial location, contrast, depth and motion perception (Galaburda & Livingstone, 1993; Livingstone & Hubel, 1987). Gross (1998), notes that the dorsal pathway is subdivided into a stream for spatial vision culminating in the PPx, and one sensitive to stimulus movement proceeding to area STP. Finally, Gross concludes, ". . . the dorsal stream is crucial for visuomotor function, as well as spatial vision, as Ferrier noticed."

Beginning from the primary visual cortex, these M-cells comprise the dorsal pathway of the dual pathway system, projecting forwards through extra-striate cortical regions via the superior longitudinal fasciculus upward to the PPx for processing the spatial location of visual objects (Anderson, 1989; Flechsig, 1896, 1920; Goldberg & Robinson, 1977, 1980; Goldberg & Seagraves, 1987; Lynch, 1980; Mishkin, 1972; Mishkin et al., 1983; Wurtz, Goldberg, & Robinson, 1980, 1982).[8] According to Cohen (1993), the PPx represents the pinnacle of the M-cell (dorsal) pathway, it consists of cells tuned to detect and convey broad, low spatial frequency, spatial characteristics of visual stimuli for detection of spatial location of visual objects. As a result, these neurons would not effectively convey information regarding the color and form of visual objects. Moreover, this pathway has been shown to be selectively stained by use of antibody stain CAT-301 (McGuire, Hockfield, & Goldman-Rakic, 1989).

Once visual input is processed at the PPx (the summit of the dorsal pathway), most projections travel to the parahippocampal gyrus (area TF) before continuing onward to the posterior two-thirds of the entorhinal cortex (Sakai, Naya, & Miyashita, 1994; Suzuki & Amaral, 1994), and finally to the hippocampus (Gross, 1994).[9]

In contrast to the M-cells which lead to the dorsal pathway, the cells of the P-cell pathway are small, slow responding, slow conducting, sustained response cells with poor contrast sensitivity, high spatial frequency, and fine spatial selectivity for high resolution color and form perception necessary for object recognition (Campbell, 1974; Graham, 1980; Livingstone & Hubel, 1987; Galaburda & Livingstone, 1993).

Beginning from the primary visual cortex, these P-cells make up the ventral pathway of the dual pathway system, projecting forward through extra-striate cortical regions via the inferior longitudinal fasciculus downward to IT cortex for processing the identity of visual objects (Flechsig, 1896, 1920; Lovegrove, Garzia, & Nicholson, 1990; Macko et al., 1982; Macko, Kennedy, Sokoloff, & Mishkin, 1981; Mishkin, 1972; Rocha-Miranda et al., 1975; Rockland & Pandya, 1981)[10]. Although, it consists primarily of P-cells, the ventral pathway receives M-cell input as well (Desimone, Albright, Gross, & Bruce, 1980; Desimone & Gross, 1979; Gross, 1992, 1994; Gross et al., 1984; Levine, Warach, & Farah, 1985; Mishkin et al., 1983; Rockland & Pandya, 1981; Sagi & Julesz, 1985; Ungerleider, 1985; Ungerleider & Desimone, 1986; Ungerleider & Mishkin, 1982; NB: See Footnote 8, also). Research and clinical findings indicate that color and color and form are processed within the ventral pathway (DeYoe & Van Essen, 1988; Gross, 1994; Iwai & Mishkin, 1968; Livingstone & Hubel, 1988; Martin-Elkins & Horel, 1992; Zeki, 1992). According to Cohen (1993), the ventral pathway, projecting to IT, is dominated by neurons tuned to detect and convey narrow-band, high spatial frequency information for analysis of color and form feature characteristics of visual objects. As a result, these neurons are not tuned to effectively convey information regarding the spatial location of visual objects (Bruce, Desimone, & Gross, 1981; Desimone & Ungerleider, 1986; Ungerleider & Desimone, 1986).

Once visual input has been processed at the IT cortex, the summit of the ventral pathway hierarchy, the majority of IT projections travel to the perirhinal cortex (areas 35 and 36), before continuing onward to the anterior two-thirds of the entorhinal cortex, and finally to the dentate gyrus of the hippocampus (Gross, 1994; Meunier, Bachevalier, Mishkin, & Murray, 1993; Mishkin & Murray, 1994; Sakai & Miyashita, 1993; Sakai, Naya, & Miyashita, 1994; Squire, 1992; Suzuki & Amaral, 1994; Zola-Morgan, Squire, Amaral, & Suzuki, 1989).[11]

Analyzing the evidence for the dual pathway model of visual system function, Cohen (1993) concludes, "The high spatial frequency system reaches its most complex level of representation within the temporal lobe, while the highest level of low spatial frequency system is located in the inferior parietal area (PG)" (p. 208). This output from the PPx and IT cortices project independently through limbic structures to the hippocampus where this visual information is combined and stored as either fused, or multipart, representations in associated neural network ensembles (Squire & Zola-Morgan, 1988). Thus, it is the through the dynamic interconnections of these dual "dorsal[12] and ventral[13]" pathways which serve as the foundation for the formation of a coherent visual-perceptual experience in which stimuli are identified and located in specific positions in space (see Figure 1).

Location of Visual Objects: Posterior Parietal Cortex

The PPx represents the most complex level of representation in the hierarchy of the dorsal pathway underlying the location of visual objects in space (Andersen, 1989; Mishkin, Lewis, & Ungerleider, 1982; Mishkin & Ungerleider, 1982; Zipser & Andersen, 1988). Research and clinical findings indicate that the PPx generates an internal coordinate space in which the locations of objects are represented (Andersen, 1989; Andersen et al., 1985). This representation enables the PPx to direct eye and limb movements to spatial locations necessary for spatial perception and visuomotor processing (Desimone & Ungerleider, 1989; Kolb & Whishaw, 1990), as well as to integrate simple and complex movements in response to the expansion or rotation of visual stimuli (Duffy & Wurtz, 1991;

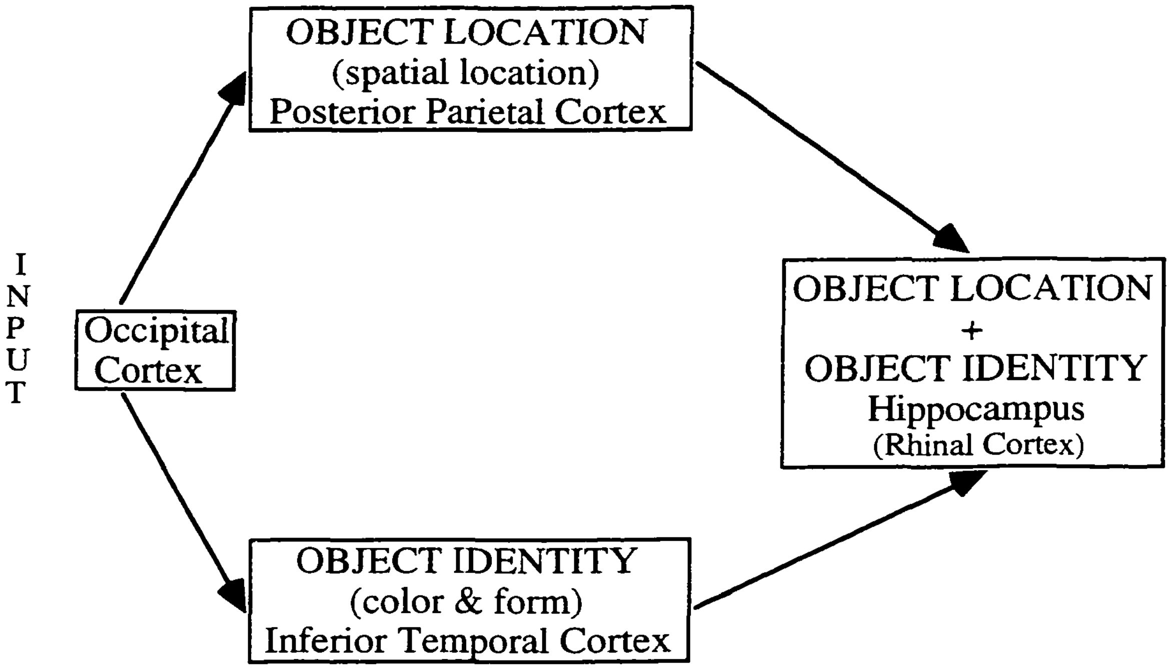


Figure 1. Dual-pathway model showing separate processing of location and object identification.

Motter & Mountcastle, 1981; Saito et al., 1986; Sakata et al., 1985; Snowden et al., 1991; Tanaka et al., 1986).[14]

The PPx comprises the caudal aspect of the parietal lobe and consists of superior and inferior portions. The superior portion contains exclusively somatosensory cortex (Critchley, 1966; Lynch, 1980), whereas, the inferior portion comprises four separate cortical fields (Andersen, Essick, Siegel, 1987; Hyvärinen, 1981; Lynch, 1980; Motter & Mountcastle, 1981; Mountcastle, 1975). These four fields are involved in smooth pursuit eye movements (Andersen & Siegel, 1988; Seltzer & Pandya, 1984); planning saccadic eye movements (Andersen et al., 1985; Newsome, Wurtz, Dürsteler, & Mikami, 1985; Newsome, Wurtz, & Komatsu, 1988; Shubutani, Sakata, & Hyvärinen, 1984); hand manipulation and reaching (Quintana & Fuster, 1993), and the integration of eye position with retinotopic visual information to produce a nonretinotopic, head-centered, representation of space (Andersen, 1989; Andersen et al., 1985; Andersen, Snyder, Li, & Stricanne, 1993; Saito et al., 1986; Sakata, Shibutani, & Kawano, 1980; Zihl, von Cramon, & Mai, 1983; Zipser, 1985; Zipser & Andersen, 1988).

Lesions to PPx cause spatial-perceptual and spatial-behavioral deficits, such as impairments in reaching and navigation, an inability to assess spatial location based on allocentric position or movement of visual and somatosensory information (Benson, 1989; Brown, 1989; Butters, Soeldner, & Fedio, 1972; Damasio & Benton, 1979; Kesner, Farnsworth, & DiMattia, 1989; Luria, 1973; Ratcliff & Davies-Jones, 1972; Warrington & James, 1988); impaired representation of spatial relations in models and drawings (De Renzi, 1985; DiMattia & Kesner, 1988; Holmes & Horrax, 1919; Kesner & DiMattia, 1984; McFie & Zangwill, 1960; see also

Warrington & Taylor, 1973); loss of spatial memories (Kesner & DiMattia, 1984); and disturbance in the spatial distribution of attention (Andersen, 1987; Brain, 1941b; Denny-Brown & Chambers, 1958; Heilman & Watson, 1977; Posner, Walker, Friedrich, & Rafal, 1984, 1987).

Consistent with an impairment in detection of spatial location, Friedman-Hill et al., (1995) tested R.M., a patient with bilateral parieto-occipital lesions. R.M. was relatively accurate when required to report the name and color of one of two simultaneously presented letters. He was at chance, however, when determining whether a target letter was to the left, right, or center, or alternatively up, down, or in the center. In addition, sequential presentation along the horizontal axis produced chance performance. This difference in performance is consistent with the view that damage to the PPx impairs the ability to accurately localize stimuli in space, while preserving the ability to correctly determine the identity of visual objects.

Similar visuospatial impairments have been reported in monkeys with PPx lesions including: determining spatial relations among objects (Milner, Ockleford, & Dewar, 1977; Pohl, 1973; Ungerleider & Brody, 1977); reaching under visual guidance (Critchley, 1966; Holmes, 1918; Holmes & Lister, 1916; LaMotte & Acuna, 1978; Stein, 1978); judging which of two objects are closer to a landmark (Brody & Pribram, 1978; Pohl, 1973); and spatial memory tasks (Levine et al., 1985; Petrides & Iverson, 1979; Quintana & Fuster, 1993; Sugishita, Ettlinger, & Ridley, 1978). Posterior parietal cortex lesions have been shown to cause exclusive impairment to spatial aspects of tasks that are essential for determining object location while leaving identification of visual objects intact (Mishkin & Ungerleider, 1982).

Identification of Visual Objects: Inferior Temporal Cortex

The IT cortex represents the top of the hierarchy for the ventral pathway underlying the perception, identification, and discrimination of visual objects, form, and color (Desimone, 1991; Desimone, Schein, Moran, & Ungerleider, 1985; Desimone & Ungerleider, 1989; DeYoe & Van Essen, 1988; Gross, 1973, 1992, 1994; Gross et al., 1984; Gross, Rocha-Miranda, & Bender, 1972; Maunsell, 1987; Maunsell & Newsome, 1987; Richmond, Wurtz, & Sato, 1983; Tanaka, Saito, Fukada, & Moriya, 1991; Warrington & Taylor, 1973; Ungerleider & Mishkin, 1982; Van Essen & Maunsell, 1983; Wilson & DeBauche, 1981). Although a portion of IT cells respond specifically to patterned stimuli, such as hands and faces (Gross, 1973; Gross, Bender, & Gerstein, 1979; Gross et al., 1972), the majority of IT cells are selective for generalized parameters, such as length, width, size, shape, texture, and color. Responses to more generalized visual parameters suggests that complex stimuli may be coded through the collective response of populations of neurons within this region (Ballard, 1986; Desimone, Albright, Gross, & Bruce, 1984; Desimone & Schein, 1987; Desimone & Ungerleider, 1989; Gross et al., 1972; Gross & Mishkin, 1977; Maunsell & Newsome, 1987; Rolls, Baylis, & Leonard, 1977; Seltzer & Pandya, 1978; Zeki, 1975 1980).[15] Moreover, cells within area IT have been shown to have receptive fields which are more than one hundred times the size of primary visual cortex neurons. These very large receptive fields enable one to respond to stimuli in virtually every part of the visual field (Desimone & Gross, 1979).

Lesions to the IT cortex produce severe deficits in visual recognition and pattern discrimination learning for objects differing in orientation, texture, brightness, color, pattern, shape, or size without impairing visual acuity or detection of target presence (Holmes & Gross, 1984; Humphreys & Riddoch, 1987a, 1987b). Deficits have been reported in recognition of simple objects (Damasio & Damasio, 1983), schematic objects (McCarthy & Warrington, 1986, 1987; Wasserstein, Zappulla, Rosen, Gerstman, & Rock, 1987), complex scenes, geometric figures, incomplete and ambiguous figures (Landsdell, 1970; Warrington, 1982), meaningless forms, abstract drawings as well as absurdities or inconsistencies in drawings, and interpretation of socially relevant visual cues (Delaney, Rosen, Mattson, & Novelly, 1980). Moreover, bilateral lesions have been shown to impair the ability to identify, discriminate, recognize, or assess the significance of objects and faces presented through the visual modality (Damasio, Damasio, & Van Hoesen, 1982; Horel, Keating, & Misantone, 1975; Klüver & Bucy, 1938, 1939; Meadows, 1974; Whiteley & Warrington, 1977).

Thus, lesions to IT impair identification and discrimination of visual object identity without impairing the capacity to determine their spatial location (Farah, 1984, 1985, 1992; Humphreys & Riddoch, 1987a, 1987b; Mishkin et al., 1983; Pohl, 1973).

Integration of Location and Identification of Visual Objects: Hippocampus

Compelling evidence exists that the hippocampus acts as the site for the integration of object location and object recognition into fused, or multipart, representations in memory (Mishkin & Appenzeller, 1987; Zipser, 1985).[16] Output from the dorsal pathway to the PPx for location, and the ventral pathway to IT for identity project to the hippocampus where they are combined into unitary spatial concepts which are combined and stored as either fused, or multipart, representations in associated neural network ensembles (Squire & Zola-Morgan, 1988). O'Keefe and Nadel (1978) suggest that this integration of location and recognition enables the hippocampus to serve as the center for the generation of internal mental representations of the physical layout of the environment (Barnes, 1988; Barnes & McNaughton, 1983; McNaughton, Barnes, Rao, Baldwin, & Rasmussen, 1986; Morris, 1983; Morris, Garrud, Rawlins, & O'Keefe, 1982; Nadel, 1991; O'Keefe, 1983; O'Keefe & Nadel, 1978; Olton, Becker, & Handelmann, 1979; Ono, Nakamura, Fukuda, & Tamura, 1991; Rolls, 1989; Rolls et al., 1989; Rupniak & Gaffan, 1987). Squire and Zola-Morgan (1988) assert that the hippocampus functions in the formation, storage, and retrieval of memories by linking together multiple sensory inputs into a single perceptual event (Kesner, 1989; McNaughton & Morris, 1987; McNaughton et al., 1989; Olton, 1983; Rolls et al., 1989; Weiskrantz, 1987; Wible, Shiben, & Olton, 1991; Zola-Morgan, et al., 1986).

For memory consolidation to take place, information processed by the hippocampus must travel back through the medial temporal lobe to the cortical sites where the perceptions were originally registered (Cohen, 1984). Mishkin and Murray (1994) have speculated that the rhinal (i.e., perirhinal and entorhinal) cortex, which extends hippocampal function as the primary target site of efferent hippocampal projections, may be the final site where this integration occurs. The memory is then encoded permanently as a long-term memory through structural changes which take place at cortical sites where this input was originally processed (Jarrad, 1978, 1983, 1986; Jarrad, Okaichi, Steward, & Goldschmidt, 1984; Mishkin, 1982; Mishkin, Malamut, & Bachevalier, 1984). The hippocampus acts to bind together these distributed storage sites to code specific data for the time, space, and content of an event (Kolb & Wishaw, 1990). The entire memory can be retrieved later as a single event from the various cortical storage sites through their links with the hippocampus (Milner, 1989; Teyler & DiScenna, 1986). As such, hippocampal coordination enables subsequent retrieval of these unified representations from distributed cortical long-term memory (Rolls, 1990).

Lesions to the hippocampus in humans have been shown to cause complete anterograde topographical disorientation. Removal of the hippocampus in the patient, H.M., left him unable to learn to navigate in new environments, while preserving his ability to navigate in environments known prior to surgery (Milner, 1965, 1968, 1972; Rupniak & Gaffan, 1987; Smith, 1988; Smith & Milner, 1981). Further, lesions to the final processing area of the hippocampus (CA1), produced complete anterograde amnesia in the patient, R.B. Moreover, bilateral hippocampal lesions have been shown to impair acquisition of both the location and identity of objects (Jones-Gotman, 1986a, 1986b). In contrast, unilateral right hippocampal lesions have been reported to produce impaired memory for the location of objects and cause deficits in tapping sequences upon blocks which are randomly arranged in space (Corkin, 1984; Jones-Gotman, 1986a, 1986b; Smith & Milner, 1981).

Lesions to the hippocampus in monkeys have been reported to produce deficits similar to those experienced by humans (Mishkin, 1982; Parkinson, Murray, & Mishkin, 1988; Olton & Pappas, 1979; Olton et al., 1979; Fuster, 1995; see also Barnes, 1988). O'Keefe and Nadel (1978) found that monkeys with hippocampal lesions could retain either identity or location of objects if response delays were no longer than several seconds, but were unable to perform tasks which required the integration of both object identity and object location when a delay was imposed (Gaffan & Harrison, 1989). Mishkin and Murray (1994) stated that to successfully perform tasks of new place learning, monkeys must retain memories for both the location and identity of the visual stimulus. When there was no delay imposed, monkeys could successfully perform new place learning tasks since both the PPx and IT cortices were intact to separately process both the location and identity of the stimuli. However, when a delay was imposed, hippocampal-lesioned monkeys could not perform these new place learning tasks since the lesioned monkeys could not integrate, encode, and thus subsequently retrieve the location and identity of the stimulus to perform the task.

Timing Differences for Location and Identification of Visual Objects

The ability of neural pathways to maintain synchronized electrical signals depends on synaptic transmission and conductance properties. Significant differences have been reported in the conduction rates and response latencies of the pathways projecting to PPx and IT in response to visual stimuli (Derrington & Lennie, 1984; Hicks, Lee, & Vidyasagar, 1983; Merigan & Maunsell, 1993; Robinson & Rugg, 1988). The size and diameter of cells and axons of the M-pathway enable them to conduct impulses rapidly and exhibit fine sensitivity to rapid changes in stimulus onset, offset, and movement (Breitmeyer, 1992; Derrington & Lennie, 1984; Gouras, 1969; Hicks et al., 1983; Kaplan & Shapley, 1982; Richmond et al., 1983; Schiller & Logothetis, 1992; Schiller, Logothetis, & Charles, 1991; Schiller & Stryker, 1972; Schwartz & Loop, 1983; Silverman, Trick, & Hart, 1990; Williams, Breitmeyer, & Lovegrove, 1991). Lesions to the M-pathway decrease the sensitivity to rapid changes in low spatial frequency stimuli, and impair the detection of rapidly moving or flickering stimuli (Merigan, Byrne, & Maunsell, 1991; Schiller et al., 1990a, 1990b). Similarly, inactivation of M-cell layers of the LGN significantly reduce, or eliminate, responses in area MT within the dorsal pathway (Desimone et al., 1980; Maunsell, Nealey, & DePriest, 1990; Maunsell & Van Essen, 1983a).

Petersen, Robinson, and Keys (1985) examined the response properties of neurons in area Pdm of the pulvinar and the PPx in conscious monkeys. In their task, as the monkey gazed at a point of light (fixation point) on a screen, spots and bars of light were moved into the monkey's visual field. According to Petersen et al., extensive interconnections between area Pdm (86 ms) of the pulvinar and area 7 (90 ms) of the parietal cortex account for the similarity in the latencies between these areas (Mesulam, Van Hoesen, Pandya, & Geschwind, 1977; Stanton, Cruce, Goldberg, & Robinson, 1977; Trojanowski & Jacobson, 1976; Weber & Yin, 1984).

In a study of response characteristics of neurons in area TE in alert adult monkeys, Richmond et al. (1983) reported mean response onset latencies to either slits of light, sine- or square-wave gratings, shadows of objects, and the objects themselves. They found that 40% percent of the 199 neurons had latencies between 120-220 ms. In a related study, Gross and Rodman (1992) reported that latencies in alert infant monkeys ranged from 110 to 320 ms for responses to slides of monkey faces, scrambled faces, food items, and geometric patterns. In addition, Gross and Rodman reported a mean onset latency of approximately 134 ms for one IT neuron in response to a visual stimulus presented at various locations in the central visual field of a 12-week-old monkey. Additionally, Baylis, Rolls, and Leonard (1987) reported latencies for IT neurons in adult monkeys consistent with those of Gross and Rodman (1992).

Single unit recordings from the fundus of the superior temporal sulcus (STS) supports differential conduction rates between the two pathways. This area of the STS has been shown to receive projections from IT and contains cells which are responsive to facial features (Bruce, Desimone, & Gross, 1977, 1981; Desimone & Gross, 1979; Gross et al., 1972; Rolls et al., 1977; Seltzer & Pandya, 1978; see also Aggleton, Burton, & Passingham, 1980; Jacobson & Trojanowski, 1977; Jones & Powell, 1970; Seltzer & Pandya, 1978). In support of this view, Bruce et al. (1981) found response latencies ranging from 200 - 300 ms in seven face-selective cells of the dorsal (anterior) bank of the STS. Similarly, Perrett, Rolls, and Caan (1982), assessed single unit response properties in 497 cells in adjoining tissue of the fundus of the STS. Using a shutter controlled presentation, they presented simple and complex, neutral and arousing, 2- and 3-dimensional geometrical stimuli and objects as well as real, projected, partial, complete, and jumbled facial features of rhesus monkeys. Perrett et al. found neuronal responses to faces in 48 of the cells. These cell responses were excitatory, sustained, and time-locked to stimulus presentation, with more than 85% of these face-selective cells evidencing latencies between 100 -160 ms. Moreover, a subset of neurons were only responsive to faces presented foveally and evidenced a mean onset latency of 125 ms. It is notable that more than half of these face cells evidenced a constant response magnitude despite rotation or alterations in the color, size, or distance of the facial stimuli.

These relative differences in RT are consistent with prior research that has indicated 100-150 ms RT advantage for low spatial frequency gratings and visual patterns when processed by the dorsal pathway than when processed by the ventral pathway (Breitmeyer, 1992; Petersen, Robinson, & Keys, 1985; Richmond et al., 1983; Robinson & Rugg, 1988; Schiller & Logothetis, 1992; Schiller, Logothetis, & Charles, 1991;

Silverman et al., 1990). These studies have demonstrated a consistent advantage in conduction rates and response latencies which range from 30 ms to 200 ms in the magnocellular system and the dorsal pathway which leads to PPx, relative to the parvocellular system and ventral pathway leading to IT.

Developmental Dyslexia Research and the Dual Pathway Model

The significance of differential conduction rates and response latencies between the pathways projecting to PPx and IT have been shown to influence processing of visual text in dyslexics. Recently, differences have been identified in the magnocellular and parvocellular processing rates in visual dyslexics (Galaburda & Livingstone, 1993; Lovegrove, 1993). Analysis of the LGN of five dyslexics revealed a 27% reduction in the size of M-cell layers relative to the P-cell layers of the LGN (Conley & Fitzpatrick, 1989; Leventhal, Rodieck, & Dreher, 1981; Perry, Oehler, & Cowey, 1984). Smaller cell bodies should produce thinner axons which slow conduction velocities (Coppin & Jack, 1972; Galaburda, 1993; Hursh, 1939). Galaburda and Livingstone (1993) have speculated that this decrement in the M-cells' function may occur at many levels within the visual pathway, and that these cumulative processing abnormalities and delays likely result in "20-50 ms delays in the evoked potential and 100-200 ms delays in tasks that require visual discrimination" (p. 77).

Galaburda and Livingstone (1993) have reported reductions in the visual evoked responses for stimuli processed by the magnocellular pathway in over 75% of the dyslexic children tested (Livingstone, Rosen, Drislane, & Galaburda, 1991; Lovegrove, 1993; Lovegrove et al., 1990; Lovegrove, Martin, & Slaghuis, 1986; Martin & Lovegrove, 1987). Dyslexics have also been shown to be significantly slower than control participants in the maximum rate at which they detect contrast reversal of binocularly presented checkerboard patterns (i.e., flicker fusion rates) at both low spatial frequencies and contrasts. Yet, these participants perform normally if allowed prolonged stimulus presentation (Galaburda & Livingstone, 1993; Livingstone et al., 1991; Lovegrove, 1993; Lovegrove, Billing, & Slaghuis, 1978; Lovegrove et al., 1990; Lovegrove et al., 1986; Martin & Lovegrove, 1987). This dysynchrony in timing between the magnocellular and parvocellular system may account for such dyslexic impairments as letter and word reversals as well as errors in spatial localization when reading text.

Spatial Attention and the Dual Pathway Model

Recent research in the area of visual attention supports the view that the dual pathways process and transmit fundamentally different elements of visual information (Mountcastle, 1978, 1979; Mountcastle, Anderson, & Motter, 1982; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuña, 1975; Mountcastle, Motter, Steinmetz, & Duffy, 1984). While both PPx and IT are active in response to the expectancy of incoming information, they have been shown to do so based on differing stimulus elements (Desimone et al., 1980; Desimone & Gross, 1979; Goldberg & Seagraves, 1987; Wurtz et al., 1980, 1982). This view is strongly endorsed by Cohen (1993), who states, "The activation of neural systems in each of these areas before a target stimulus is presented produces different anticipatory effects."

Investigation of the effects of attention to location, luminance, and movement on the firing rate of neurons in PPx are consistent with dissociation of function between PPx and IT. This finding has been supported by Corbetta, Miezin, Dobmeyer, Shulman, and Petersen (1991) using positron emission tomography, who reported that sites in PPx were activated when participants were instructed to attend to the rate of movement of a set of colored bars, whereas instructing them to attend to the shape, or the color, of the moving bars activated sites in inferior cortical regions.

Attention to spatial aspects of visual stimuli, with or without eye movements, enhances responses in PPx in behaving alert monkeys (Balint, 1909; Bisiach et al., 1979; Bushnell, Goldberg, & Robinson, 1981; Farah, 1990; Hécaen & de Ajuriaguerra, 1954; Hyvärinen, 1982; Hyvärinen, Poranen, & Jokinen, 1980; Merigan & Maunsell, 1993; Mountcastle et al., 1975; Goldman-Rakic, 1992). In contrast, attention to identity, pattern, color, or both pattern and color on delayed matching tasks suppresses the responses of PPx neurons (Fuster & Jervey, 1981; Gross et al., 1979; Mikami & Kubota, 1980; Ridley & Etlinger, 1973).

Conversely, attention to identity, pattern, color, or both pattern and color on delayed matching tasks enhances responses in IT in behaving alert monkeys (Fuster & Jervey, 1981; Gross et al., 1979; Mikami & Kubota, 1980; Ridley & Etlinger, 1973). In contrast, attention to spatial aspects of visual stimuli suppresses the responses of IT neurons (Bushnell et al., 1981; Richmond & Sato, 1982; Richmond, Sato, & Wurtz, 1982; Richmond & Wurtz, 1982; Richmond et al., 1983).

Research by Posner (1992) on processes involved in visual attention have focused on further characterizing the interaction of cognitive and neural systems. Based on his research with normal controls, neurological patients, and Macaque monkeys, Posner (1992) has proposed the existence of a posterior attention network. Through this network, the PPx signals the midbrain to disengage attention from a current focus to prepare for a contralateral shift of attention (Posner & Cohen, 1984; Goldman-Rakic, 1988; Posner, 1992). The superior colliculus then carries out the shift of attention to a new region (see also Sparks & Mays, 1980). Finally, the pulvinar locks attention in place (Petersen et al., 1985; Petersen, Robinson, & Morris, 1987; Posner & Petersen, 1990).

Damage to the sites in the posterior attentional network produce predictable deficits. Individuals with damage to the PPx neglect the side of space contralateral to the lesion, (i.e., hemi-inattention and hemi-neglect; Balint, 1909; Holmes, 1918; Hécaen, Penfield, Bertrand, & Malmo, 1956; Denny-Brown & Chambers, 1958; Heilman, Pandya, Karol, & Geshwind, 1971; Heilman & Valenstein, 1972; Heilman, Watson, & Valenstein, 1985). These individuals are permanently impaired in their ability to disengage from previous ipsilateral foci of attention to locate targets in contralateral space despite intact visual fields (Critchley, 1966; Posner et al., 1984).

Aston-Jones and colleagues (Aston-Jones & Bloom, 1981; Aston-Jones, Foote, & Bloom, 1984; Posner & Petersen, 1990) have reported that in monkeys the parietal lobe, pulvinar, and superior colliculus receive heavy input of norepinephrine fibers from the locus coeruleus, a brainstem nucleus at the level of the fourth ventricle (Foote, Berridge, Adams, & Pineda, 1991). This is in contrast to the ventral visual pathway which receives far less innervation with norepinephrine. Posner and Raichle (1994) posit that norepinephrine modulates levels of arousal. They assert that "norepinephrine can influence a system's speed and efficiency of operation, depending on the level of the neurochemical present. Because the orienting system is under the influence of norepinephrine to a greater extent than the pattern recognition system, we suspect that the orienting system will change in speed or efficiency under circumstances when the "what" (identity) part of the visual system does not" (p. 211). Consistent with this finding they report that presentation of a readiness signal to prepare for a task influences the orienting system involving the dorsal pathway, but has little effect on the actual speed of pattern recognition involving the ventral pathway of the visual system.

The Role of Color for Processing Visual Objects

Recent research and clinical findings have increased our understanding of the cortical role in color vision and its role in object processing (Davidoff, 1991; Sacks, 1995).[17] These findings provide support for the role of the ventral pathway in color processing, and indicate that elements of color and form are processed within separate divisions of the ventral pathway on the way to IT (Gross, 1994; Livingstone & Hubel, 1988; Martin-Elkins & Horel, 1992; Zeki, 1989, 1992). For the most part, however, advances in the understanding of the neuroanatomy underlying color vision have not led to the view that color is essential to object recognition.

The majority of object recognition theories suggest that identification and recognition of visual input is based on edge-detection. Most often, color is viewed as a surface feature, unnecessary for the initial processes of object recognition (Biederman, 1987; Davidoff, 1991; Marr, 1982). Consistent with this viewpoint, a number of investigators have found no difference in the speed of object recognition between photographs and drawings presented in color and black and white (Biederman & Ju, 1988; Davidoff & Ostergaard, 1988). Object recognition speed has also been shown to be independent of color diagnosticity (i.e., whether objects have been seen consistently in the environment as a specific color; for instance, a yellow sun versus a yellow pen; Biederman &

Ju, 1988; Ostergaard & Davidoff, 1985; Wurm, Legge, Isenberg, & Luebker, 1993).

In contrast to Davidoff (1991) and others, Price and Humphreys (1989) suggest that color can be essential to the initial processes of object recognition. Price and Humphreys argue that color can be important for object recognition when objects are of the same category or are structurally similar, such as discriminating between an orange and a grapefruit. Also, Wurm et al., (1993) have reported that color facilitates speed of object recognition when participants view less prototypical, rather than more prototypical, objects. Nevertheless, in each of the color studies referred to above, researchers have used RT to verbal naming as the dependent measure for object recognition. Unfortunately, the generation of verbal labels for visual objects takes place after visual processes underlying object recognition already have occurred and thus obscure any effect of color on RT. This perspective is supported by the work of Warrington and Shallice (1979) and Shallice (1985) who note that object names and objects involve fundamentally different processing systems. In their view, object names are understood by a lexical semantic system, whereas the visual objects themselves are understood by a separate visual conceptual system.

Researchers such as Tsal and Lavie (1993), have sought to explore the relation of color, shape, and location using a key press, rather than a verbal response. By this method, Tsal and Lavie sought to determine if participants automatically attended to one stimulus attribute, such as location, if cued to focus upon another attribute such as color or shape. Tsal and Lavie, argued that prior studies, such as Nissen (1985), confounded processing of targets from nontargets as well as the discrimination of location from color or shape. According to Tsal and

Lavie, this was due to simultaneous presentation of target and nontarget items in a small area of the visual field. Thus, Tsal and Lavie asserted, Nissen's findings could not be considered to have solved either the issue of which attribute preceded another or if one attribute is bound to another. As a result, they argue one must question Nissen's findings that participants were equally accurate when focusing on location and reporting color and shape, or when focusing on color and shape, and reporting location. Additionally, one must therefore question Nissen's conclusion that localization of items is necessary for correct integration of the other features of color and shape.

In their experiments, Tsal and Lavie (1988, 1993) presented participants with individual letter cues of a particular color, shape, or location followed less than 100 ms afterward by a circle of 6 to 8 different target and nontarget letters. The cue letter directed participants to respond, or withhold response, to identify as many letters as possible by either their color, shape, or location, and then afterward report any nontarget letters. According to Tsal and Lavie, presentation of the letter cue would produce an attentional processing advantage for items sharing the cue property, and temporarily suppress or block items which lacked this attribute. Tsal and Lavie reported that the additional letters tended to be those at, or adjacent to, the cue location rather than those which shared the cue property (e.g., other red letters). Tsal and Lavie found that selective processing of targets specified by color or shape is accomplished by attending to their locations, and that the processing of shape or color could not be achieved without attending to location, also. They concluded that localization of items is an automatic, conscious, and necessary precursor to the integration of color and/or shape, and that it acts to bind these features.

Unfortunately, a series of design limitations limit the conclusions which can be drawn from the studies of Tsal and Lavie (1988, 1993). Their cues across the different conditions were inconsistent in duration, and were presented for less than 100 ms. According to Bloch's law, this causes the cues to differ in apparent brightness. Bloch's law states that there is an inverse relation between stimulus duration and apparent brightness for stimuli presented for durations below 100 ms. Moreover, as cues were followed by an interstimulus interval (ISI) which was too brief to saccade to new locations, participants were likely to report more items from that location. In addition, between experiments, cue type, and set size were not preserved. Finally, the stimuli were not equated for letter frequency, and the determination of target sets was based on subjective criteria. Thus, despite their efforts, it is not possible to determine if location, shape, or color are processed individually or together.

Alternatively, Treisman and colleagues have sought to examine the processing of individual and multiple visual feature dimensions through an attentional-spotlight model. In this model, individual features such as orientation, color, and spatial frequency are processed initially in parallel to form an internal map of preconscious feature boundaries (Treisman, 1992; Treisman & Gormican, 1988). While discrimination of the presence of individual feature dimensions can take place at this early stage, consciousness of the locations where features are conjoined in the visual scene can take place only through the subsequent serial mechanism of focal attention.

It is evident, therefore, that researchers differ considerably in their beliefs as to whether location, color, and form are preconscious, spontaneously encoded, apriori substrates for all further stimulus processing or whether they are independent, unitary features, initially available to consciousness and without primacy over other feature dimensions. This ongoing controversy primarily may be due to a failure of these studies to: sufficiently assess the independence of location, form, and color; maintain continuity between the study and the test phase conditions; and, account for the inherent differences in signal propagation speed between the pathway subserving location and the pathway conveying form and color information.

Biederman's Perceptually-Based Model for Processing Visual Objects

In his "recognition by component" theory of object recognition, Biederman (1987) proposes that we parse constituent features of visual input into edges and boundaries based on the gestalt principles of proximity, similarity, continuation, and closure to detect a series of contrasts termed smooth continuation, cotermination, parallelism, and symmetry which remain invariant despite changes in the position of the observer. These properties are conjoined into a set of 24 basic geometric primitives (e.g., cones, spheres, cylinders, blocks, wedges) termed "geons" which may be juxtaposed in over one hundred prepositional relations (e.g., above, below, beside). Once the geons are parsed, they are matched automatically against representations in long-term memory in a parallel process through many simultaneous matches. Thus, objects can be recognized rapidly and accurately by the identification of their constituent geons even when more than one-half of an object's geons are deleted or obscured (Biederman et al., 1993).[18]

Biederman suggests that his research is strongly supportive of a dual system organization for the perception and processing of visual sensory input. He argues that there is an evolutionary basis for independent dorsal and ventral processing streams subserving visual processing. He states that the dorsal pathway represents such metric attributes of spatial location as size, position, orientation, and depth which subserve such spatial and motor interactions as reaching, grasping, navigating toward objects, and circumnavigating around obstacles in one's path, without the determination of an object's identity. In support of his view, Biederman and Cooper (1992) reported a study in which participants were faster and more accurate at naming previously presented items in an old-new shape recognition task when objects remained unchanged versus when they were compared at a different size.

Biederman suggests that the ventral pathway conveys information subserving object identity. He asserts that an essential requirement of this shape pathway is that it must be capable of activating the same mental representations despite wide variations in sensory parameters. He states that the magnitude of perceptual priming of visual objects is determined entirely by the capacity of a stimulus to activate mental representations of the geons and their interrelations, rather than the absolute presence of the specific vertices and edges actually present in the visual input. Moreover, Biederman reports that color facilitates object recognition only if other shape cues are absent or degraded (Biederman & Ju, 1988), and concludes that color, shading, and texture are unnecessary for visual object identification unless one wishes to discriminate among similarly shaped objects. Biederman argues that this strong invariance for shape recognition reflects a fundamental partitioning in the way that the brain handles shape and he reaches the conclusion, "that allowing for response selection, object naming RTs may provide a relatively pure measure of the functioning of the shape system (Biederman et al., 1993, p. 121)." As evidence for this view, Biederman cites studies in which he found an equal magnitude for perceptual priming for the associated response names of nonsense drawings despite alterations in the, "position, size, reflection, orientation, and rotation in depth up to occlusion of parts" of the objects (Biederman et al., 1993; Biederman & Cooper, 1991a, 1991b, 1992; Gerhardstein & Biederman, 1991, May).

The same complications occur, however, as a result of Biederman's choice of "naming" RT as the critical measure of object processing (Biederman & Cooper, 1992; Biederman et al., 1993). In his selection of naming as the critical measure of visual system function, he has chosen a behavioral outcome which appears to occur after component processes of visual object perception, analysis, and identification have taken place. Thus, his failure to find differences in spite of changes in position, size, reflection, and orientation likely results from the selection of a measure which occurs too late in visual object processing to detect any of these differences. Also, his selection of a naming response necessitates involvement of a semantic system which may further influence RT measures. Thus, the selection of naming as the basic response measure, also limits the conclusions which can be drawn from this research.

Humphreys' Semantically-Based Model for Processing Visual Objects

Following low-level perceptual processing, such as figure-ground segmentation and integration of local and global form description consistent with Marr and Nishihara (1978), Humphreys posits that structural, semantic, and phonological processing stages are activated to permit recognition and naming of visual objects (Humphreys et al., 1987). These three discrete processing system stages are activated in cascade. Humphreys proposes that access to stored structural description is influenced by perceptual distinctiveness in the primary stage. At the secondary stage, he reports that access to functional and associative semantic knowledge is affected by prototypicality. At the final stage, he adds that access to output phonology is affected by naming frequency (Boucart & Humphreys, 1992, 1994; Humphreys & Riddoch, 1987a; Riddoch & Humphreys, 1987b). To further examine this model, Boucart and Humphreys (1994) initiated a series of object matching studies.

In their studies, Boucart and Humphreys (1994) sought to distinguish whether participants attend and match drawings of objects based upon selective dimensions of orientation, size, luminance, and color without semantic information preceding and determining RTs and accuracy. On each trial, participants were initially presented with a reference object, which was immediately followed by a 100 ms pattern mask. Next, participants were shown two objects simultaneously (i.e., a target and a distracter), and were asked to press the left or right key to indicate which of the two objects was the target object. Participants were to choose the object that matched the reference object on the designated dimension (i.e., orientation, size, luminance, or color).

In all of their studies Boucart and Humphreys (1994) found that RTs were fastest and error rates were lowest when the reference and the target were physically identical to the reference stimulus. This finding has been confirmed repeatedly since it was first reported by Posner and Mitchell (1967) who determined that matching was faster when letters were physically identical than when they merely had the same name (see also

Ellis, Allport, Humphreys, & Collis, 1989). Further, Boucart and Humphreys found that in experiments of orientation and size (for outline drawings), there was facilitation when the target was semantically-related to the reference object, but inhibition when the distracter was semantically-related to the reference object. In contrast, they found no effects of semantic relatedness for discrimination of size (for silhouettes), color, luminance with outline, slightly fragmented outline, and highly fragmented "non-nameable" outline forms. They note that their results cannot be due to unequal difficulty of discrimination or task complexity as they sought to control for these factors. As a result, Boucart and Humphreys acknowledge their experiments produced findings which are difficult to interpret based on visual system organization.

Interpretation of Boucart and Humphreys' (1994) findings, unfortunately, are hampered by a range of problems with their experimental design. Items both within and across studies were not consistently counterbalanced or equated for practice, familiarity, typicality, number and orientation of axes. In addition, items were selectively changed, deleted, replaced, added, and redrawn.

Boucart and Humphreys initially asserted that participants cannot refrain from accessing semantic information in the perception and re-perception of objects. Later they modified their view to say that automatic semantic activation and facilitation disappear when tasks are either "too easy or too difficult." Finally, Boucart and Humphreys concluded that, "task difficulty per se does not determine whether semantic effects occur (p. 77)." While they note that increasing RT should enhance semantic processing, their argument, however, does not explain why when stimuli were presented upside down (Boucart & Humphreys, 1992), in incongruent colors (Price & Humphreys, 1989), in non-canonical orientations (Jolicoeur, 1985, 1990), in silhouette (Boucart & Humphreys, 1994), or to a visual agnosic, RTs increased, while the effects of semantic processing were significantly reduced. They suggest that when participants attend to color and luminance, they filter access to orientation and size, which they characterize as high-level form information. Finally, they admit that their model does not explain many inconsistencies in their findings stating:

> Although this proposal explains the lack of semantic effects in the luminance and color matching tasks, it does not explain why semantic effects did occur in the orientation and size matching tasks. Presumably, by attending to these simple properties of form, analyzed early in the visual processing stream, participants ought to filter out access to high level form information. Evidently this did not occur (p. 77).

In the end, they conclude that, "there is automatic access to semantic knowledge from objects, but only when participants attend to global form information. Other properties of objects, such as their color and intensity, can be attended selectively (Boucart & Humphreys, 1994, p. 79)." Thus, conclusions and interpretations from these studies necessitate considerable qualification to account for recent research into the organization of the higher order visual system.

Pilot RT Study of Location and Identification of Visual Objects

This pilot study sought to determine if the pattern of RTs for detection of location, identity, and location+identity of visual objects was consistent with the proposed organization of the dual pathway model.[19] In addition, this study sought to assess whether processing cues presented upon the onset of each trial could meaningfully alter the pattern of RTs for detection of location, identity, and location+identity of visual objects.

Each trial began with the warning, "Trial Begins" in the center of the computer screen. Then, one of four possible cues, (i.e., location, identity, location+identity, and no change) was shown in the center of the screen for 200 milliseconds (ms). Next, the first array was presented, consisting of three horizontal boxes displayed at the center of the screen for 300 ms; during which a digitized line drawing of a single black-and-white object selected from among the set of 260 Snodgrass and Vanderwort (1980) figures was shown for the final 100 ms in one of the boxes.[20] Normative data on the figures permitted counterbalancing items both within and across conditions for imagibility, familiarity, complexity, concept frequency, and name agreement. Then, after a delay of 0, 15, or 30 seconds, in which the screen remained blank, participants were shown a second array of three horizontal boxes displayed in the center of the screen for 2200 ms. Two hundred ms after the onset of this array, a single black-and-white object from among the Snodgrass and Vanderwort figures was shown for 2000 ms in one of the boxes.[21] Participants responded by pressing one of two response keys to verify whether the initial cue was "valid" or "invalid" in predicting the change, if any, between the first array and the second array.

For example, if a participant was presented the cue, "Location Only," and then shown a drawing of a hammer in the far left box of the first array, followed by an identical hammer in the middle or the far right box in the second array, then the cue was "valid" since the object had, indeed, changed location. If in the second array, instead, the hammer had been shown again in the far left box, or if a different object was presented in any of the 3 boxes, then the cue was "invalid" since the initial object (the hammer) had not reappeared at a new location. The different trial types were presented randomly throughout three blocks and each block consisted of 24 trials. Trial type and cue type were randomly paired such that for each trial type, there was a 50% chance of receiving a valid or an invalid cue.

It is notable that participants made few errors (M =.94). The RT data were analyzed as a 4(Trial: location, identity, location+identity, no change) x 4(Cue: location, identity, location+identity, no change) analysis of variance (ANOVA). There were no main effects for Trial or for Cue, but there was a Trial x Cue interaction. This Trial x Cue interaction suggests that cue instructions appear to influence cognitive processes involved when making judgments about visual stimuli. Participants were fastest on all trial types if cues correctly predicted the nature of the trial. Also, the pattern of RTs obtained in the pilot study were consistent with predictions of the dual pathway model since RTs for location judgments preceded identity judgments and, both location and identity alone preceded location+identity judgments.

Additional support for this model was found even when there was no change in the first and second presentation of the array, (which is consistent with Posner and Mitchell, 1967), and when the cue was "invalid" in predicting any change between first and second array. It is notable that responses were faster on location+identity trials when the cue predictions were valid than when the cue predictions led one to expect the other types of trials (i.e., location only, identity only, or no change). This suggests that increased RT for location+identity judgments were not simply a reflection of a more complex two-part judgment, but an accurate reflection of the organization of the higher order visual system.

The differences in RTs for location and identity judgments are consistent with prior research that has indicated 30-200 ms RT advantage for visual stimuli when processed by the dorsal pathway relative to the ventral pathway (Breitmeyer, 1992; Petersen et al., 1985; Richmond et al., 1983; Robinson & Rugg, 1988; Schiller & Logothetis, 1992; Schiller, Logothetis, & Charles, 1991; Silverman et al., 1990). This RT advantage suggests that location information should reach more central processing loci in the PPx prior to arrival of information for object identity which travels along the ventral pathway to IT cortex. The outcome of this pilot study indicates that this methodology for examining RT patterns and for influencing cognitive processes associated with visual object processing is an effective means of providing insight into the organization of the higher order visual system. It is reasonable to conclude that this methodology can be effectively applied in further studies of visual and memory processes.

RT Studies of Location and Identification of Visual Objects

Converging evidence from the animal, clinical, and experimental literature supports the existence of the dual pathway system of visual organization. The dual pathway model proposes that object location and object identity are processed and analyzed independently through separate pathways. In this model, visual location information is carried along the dorsal pathway to the PPx for processing of spatial location (Mishkin & Ungerleider, 1982; Zipser & Andersen, 1988), whereas color and form information are carried by the ventral pathway to the IT cortex for processing of identity (Desimone & Schein, 1987; Gross, 1992; Gross et al., 1984; Zeki, 1992). These centers each then project separately to the hippocampus where both location and identity are conjoined and stored as either fused, or multipart, representations in associated neural network ensembles (Felleman & Van Essen, 1991).

The inherent relation between neural organization and cognitive processing permits assessment of the predictive validity of the dual pathway model of the visual system. Yet, assumptions based on the organization and processing of the human dual pathway model have yet to be investigated directly using RT and accuracy measures. The RTs and accuracy measures derived from the pilot study have provided strong support for the proposed organization of the dual pathway model, and have provided evidence that cues can meaningfully influence cognitive processing.

The proposed experiments will assess the effects of color, quantity, spatial frequency, and speeded response methodology on RT and accuracy to examine the organization of the higher order visual system governing the perception and re-perception of location and identity of visual objects. Based on the parallel sequential nature of the higher order visual system, detection of the location of visual objects should be faster than detection of identity, and each alone should precede judgments of location+identity. RT and accuracy measures in the pilot study support this prediction.

The organization of the dual pathway model suggests that color information should be processed by the ventral pathway (Maunsell, 1987; Schwartz & Loop, 1983; Williams et al., 1991). Researchers, however, are equivocal as to whether color facilitates detection of the identity of visual objects. For example, Ostergaard and Davidoff (1985) have found that color facilitates RT and accuracy for identification of visual objects. Given this view, the addition of color to the stimuli should provide a processing advantage for identity, and location+identity judgments for colored objects relative to the processing of black-and-white objects. In contrast, location information is expected only, at best, to be marginally facilitated by the use of color as location is conveyed along the dorsal pathway to the PPx, which is responsible for spatial location, but exhibits relatively little, or no, sensitivity to color. Thus, the processing advantage provided by color should be limited almost completely to the detection of identity with little, or no, assistance in detection of location.

The degree to which the location, the identity, and the location+identity of visual objects are influenced by "complexity," or are processed serially, or in parallel can be assessed on a variety of levels by these studies. While the pilot study provides strong evidence that complexity could not account for the experimental findings, the proposed studies provide further opportunity to evaluate complexity and processing effects. Analysis of RT and accuracy distributions resulting from an increase in the number of objects from one to two items can further elucidate complexity and processing effects. Analysis of differential RT distributions can illuminate whether directed processing for location, identity, or location+identity results in processing which is serial or parallel. If directed processing is parallel, there should be no increase in RT caused by increasing the number of items subjects must evaluate. However, if the process is sequential, there should longer RTs when the number of items are increased. Further, it is expected that judgments for location or identity alone using one or more objects will produce RT and accuracy distributions which differ from judgments of location+identity together suggesting that these judgments reflect the organization and processing of the higher order visual system, and not the complexity of the judgment itself.

The dual pathway model proposes that low spatial frequency information is conveyed along the dorsal pathway to the PPx for processing of spatial location, while high spatial frequency, color and form information, is carried along the ventral pathway to the IT cortex for processing of object identity (Breitmeyer, 1984, 1992; Humphreys & Quinlan, 1987; Marr & Hildreth, 1980; Pearson & Robinson, 1985; Schwartz & Loop, 1983; Sergent, 1988; Watt, 1988; Watt & Morgan, 1985; Wilson, 1980). Selective filtering of these spatial frequencies, therefore, should influence speed and accuracy for determination of location and identity of visual objects. Use of a highpass digital filter which removes low spatial frequency information, but permits high spatial frequency information to pass through, should produce selective inhibition for judgments of location relative to judgments of identity. In contrast, use of a lowpass digital filter to selectively remove high spatial frequency information, but permit low spatial frequency information to pass through, should produce selective inhibition for judgments of identity relative to judgments of location. Finally, use of selective filters should differentially inhibit judgments of location or identity, respectively, causing the performance of normal subjects to resemble that of neurological patients with selective lesions of PPx and IT respectively.[22]

The use of speed-accuracy tradeoff methodology permits precise examination of the relation between serial and parallel processes underlying determination of the identity and location of visual objects. Dosher and colleagues have demonstrated that this methodology is capable of discriminating the degree to which component processes are serial or parallel in nature by analysis of RT, accuracy, and item capacity distributions (McElree & Dosher, 1993; Meyer, Osman, Irwin, & Yantis, 1988). In this methodology, a response signal is presented at set points in the processing of the stimuli for response. Upon receiving a response tone, participants must interrupt their ongoing processing, leading to a completed response, to respond with their best guess within a brief critical period of time. Analysis of the partial, and complete, accuracy and item capacity distributions for processing single and multiple items by this speeded response methodology permits one to distinguish whether processing of location and identity of visual objects is serial, parallel, or in cascade. The pattern of RTs produced by this methodology is expected to reflect the fundamental organization and processing of the higher order visual system, and is expected to be consistent with the dual pathway model (Greene, 1992; Irwin & Yeomans, 1991; McElree & Dosher, 1993; Meyer et al., 1988).

Footnotes for Introduction and Literature Review

[1] The retino-striate model of visual system organization which proposed that the visual system projected only as far as the primary visual cortex (Kreig, 1975; Lashley, 1948, 1950; Morgan & Stellar, 1950) has been extended for experimental, clinical, and neuroanatomical reasons (Gross, Bender, & Rocha-Miranda, 1969; Gross et al., 1972; Gross et al., 1967; Gross, 1998). The geniculo-striate model of visual system organization (Hubel & Weisel, 1965), which conceptualized the visual system as a feedforward, linear-sequential, hierarchical progression has been extended as well to account for parallel pathways, reciprocal connections, and instances in which middle stages were bypassed before neural projections reconverged at higher levels within the visual system (Maunsell & Van Essen, 1983a, 1983b; DeYoe & Van Essen, 1988). Similarly, the tectofugal model of visual system organization (Ingle, 1967), proposing a visuosensory role for the superior colliculus in humans, has been revised to suggest that the superior colliculus contributes to motoric guidance when shifting eye movements (Bushnell, Goldberg, & Robinson, 1981; Held, 1968; Newcombe & Russell, 1969; Schiller & Stryker, 1972; Trevarthen, 1968). Moreover, Bushnell et al. (1981) demonstrated that complete bilateral collicular ablation failed to cause deficits on spatial location tasks.

Gross has recounted in depth both the contributions and the evolution of developments in the mapping of extrastriate, IT, and PPx in visual processing (Gross, Rodman, Gochin, & Colombo, 1993). As a result, this footnote serves only as a summary of his discussion for the convenience of the reader (see Gross, 1988, pp. 184-6). As described, the obstacle of establishing a corticocortical pathway to IT without severing the optic radiations was surmounted by Kuypers, Szwarcbart, Mishkin, and Rosvold

(1965) through the use of silver degeneration. Kuypers et al. identified the presence of two successive stages within prestriate cortex which neither pulvinar lesions, nor prestriate lesions had produced. At that time, Mishkin demonstrated that interruption of the pathway between prestriate cortex and IT through a crossed lesion paradigm produced profound visual learning deficit.

Mapping of the area surrounding the striate cortex was continued by such researchers as Cowey (1964), who established the visuotopic organization of area V2 in the squirrel monkey. These findings led to a proliferation of visual areas based on research by Allman, Gross, Van Essen, Desimone, Ungerleider, Zeki and their colleagues (e.g., Allman & Kass, 1971) using single-unit recording. Iwai and Mishkin demonstrated a functional subdivision between anterior (TE) lesions causing deficits in concurrent visual discrimination learning and memory, and posterior TEO regions or foveal prestriate cortex, producing perceptual deficits on single-object pattern-discrimination learning tasks. Gross, Bender, Schiller, Gerstein, Cowey, Perrett, Rolls, Caan, and their colleagues in the field of visual processing and perception went on to map the organization and attributes of visual processing within the higher order visual system through animal studies using single unit recording (As noted by Gross, 1998; see also Felleman & Van Essen, 1991; Desimone & Ungerleider, 1989).

These models have clarified conceptions about visual system organization and have been important in their contribution to the development of the dual pathway model as well as accounting for the multiple cortical and subcortical visual areas which have been identified to-date the majority of which occur after primary visual cortex (Andersen et al., 1985; Felleman & Van Essen, 1991; Gross et al., 1984; Livingstone, 1990; Livingstone & Hubel, 1984, 1987; Maunsell, 1987; Mishkin et al., 1983; Pohl, 1973; Rolls, 1990; Schiller & Lee, 1991).

[2] Until Gall and Spurzheim advanced the notion of phrenology in 1810, the "optic" thalamus was considered the highest sensory locus in the brain (Finger, 1994; Gross, 1994). Having observed that the LGN and the superior colliculus atrophied after optic nerve damage, Gall and Spurzheim speculated that visual projections continued further beyond the thalamus to the cortex. Their speculation was supported by Bartolomeo Panizza in 1855, who detected the presence of optic radiations projecting from the thalamus to the visual cortex, and by Flechsig (1895) who confirmed Panizza's findings.

Panizza observed that strokes often were followed by partial or total blindness. He posited that these visual impairments were the result of occipital lobe damage. In support of his view, he produced total blindness in dogs through bilateral occipital lobe ablations, but only partial blindness (restricted to the contralateral visual field) with unilateral occipital lobe lesions. In 1870, Theodor Meynert refined the understanding of the occipital cortex by positing that the calcarine sulcus was the portion most critical for visual processing of the occipital lobe. Although these advances in the understanding of the visual system extended the visual pathway as far the cerebral cortex, the cerebral loci for vision had yet to be determined.

[3] Supporting the speculation of Meynert in 1870, Brown and Schäfer reported that complete bilateral ablation of the ventral surface of the temporal lobes and total removal of both occipital lobes produced complete and permanent blindness. Further, Brown and Schäfer reported that occipital lobe lesions caused significantly greater visual deficits than angular gyrus lesions. They concluded that angular gyrus lesions were neither

necessary, nor sufficient, to produce blindness. Finally, Brown and Schäfer observed that electrical stimulation of the occipital cortex produced far greater contralateral eye movements than angular gyrus stimulation.

[4]An additional striking feature which Brown and Schäfer noted was a significant reduction in aggressive behavior, and they referred to this "animal 6" as the "tame one." This finding of diminished aggressive behavior and visual defects would later be rediscovered by Klüver and Bucy in 1938. Yet this syndrome remained undifferentiated until the 1950's when Josephine Semmes (Nissen, Semmes Blum, & Blum, 1949) and Kao Liang Chow (1951) reported that large lesions involving not only peristriate areas 18 and 19, but also dorsal prestriate areas leading into the parietal lobe with anterior and ventral lesions reaching into the temporal lobe produced profound impairments in visual discrimination learning (i.e., psychic blindness) as well as some deficits in tactile learning (as noted by Gross, 1998: see Ruch, Fulton, & German, 1938; Blum, 1951; and Wilson, Stamm, & Pribram, 1960). Chow's research demonstrated that the temporal cortex underlay visual learning since lesions of the lateral surface of the temporal lobe, particularly the middle temporal gyrus, resulted in visual defects, although adjacent areas did not. Pribram and Bagshaw (1953) reported that through lesions to the amygdala and adjacent cortex they were able to produce tameness and changes in sexual and eating behavior without visual deficits. In 1954, Mishkin and Pribram further localized visual components of the syndrome described by Klüver and Bucy (1938) to the middle and inferior temporal gyri, now termed IT (Mishkin, 1954; see Gross, 1973, 1994, 1998; Dean, 1976).

[5]The interconnections between pathways may explain why the patients described by Benson and Greenberg (1969) and Goldstein and Gelb

(1918) could compensate for their visual agnosia through the use of kinesthetic and movement information.

[6]The ganglion fibers which leave the retina project to 3 basic subcortical regions of the brain:

[a]. Pretectal area: Located rostrally to the superior colliculus, this area uses retinal inputs to respond to overall changes in brightness to control reflexes for pupil dilation and constriction. Specifically, the pretectal area projects to the accessory oculomotor nucleus in the brainstem to inervate ciliary ganglion in both eyes to cause pupil constriction and dilation.

[b]. Superior colliculus: The colliculus uses input regarding moving shapes, visual attention, and broad visual outline to control saccadic (high velocity) eye movements so as to integrate head and eye position in relation to a visual stimulus. The colliculus acts in conjunction with frontal eye fields, which receive input from the occipital cortex concerning fine visual discrimination and are involved in generating saccades to complex visual movements. The superior colliculus projects to the inferior pulvinar, the ventrolateral Pulvinar, the dorsolateral pulvinar, and the medial pulvinar (which, in turn, projects to the PPx). NB: In contrast, the oral pulvinar projects to area 5a of the superior parietal lobe, which along with area 5b of the superior parietal lobe, projects to area 7b (anterior parietal cortex, also called lateral area PF).

[c]. Lateral geniculate nucleus: Principal subcortical region processing visual information for visual perception. The LGN receives input from the retinal ganglion cells of both eyes. Visual input to the nasal portion of the retina crosses over to the contralateral hemisphere, whereas the temporal portion remains ipsilateral without crossing over. The LGN maintains a visuotopic representation of the retina. Moreover, each geniculate neuron

receives relatively untransformed retinal input from only a very small number of ganglion cells, although 90 percent of optic nerve fibers project to the LGN. This ganglion cell axon input represents only a small proportion of input to the LGN, since 80-90 percent of the connections are from other regions including brainstem reticular formation and cortical feedback connections. At the LGN, individual layers receive input from one eye only so that fibers from contralateral nasal hemiretina project to layers 1, 4, and 6; while fibers from the ipsilateral temporal hemiretina project to layers 2, 3, and 5. Axons of M-cells terminate in the lowest layers 5 and 6, and axons of P-cells terminate the uppermost layers 1-4. These six maps are in precise vertical register so that the same location in each layer represents a single orientation in visual space.

In 1965, Hubel and Weisel reported the existence of spot detectors in the retina and LGN. Projecting light patterns onto a screen in front of cats and monkeys, they demonstrated that the receptive fields of LGN neurons are the same as ganglion cells in the retina. Moreover, they provided evidence that these LGN cells have small on-center or off-center concentric circular fields, about one degree in diameter, which respond best to small spots of light. Diffuse illumination of the entire receptive field of the LGN neuron produced only a weak response caused by cancelling out both the center and the surround.

[7]Visual sensory input to the occipital cortex is from the contralateral half of visual space. The six layers of the visual cortex are approximately two millimeters thick and information flows systematically from one layer to another. The stripe of Gennari in layer 4 of the visual cortex contains myelinated axons from the thalamus and other cortical areas. This layer is subdivided into four sublayers: 4-Alpha, 4-Beta, 4C-Alpha, and 4C-Beta.

Axons of M-cells terminate in layer 4C-Alpha which project onward to the broad band region of layer 4B, and axons of P-cells terminate in layer 4C-Beta which project onward to layers 2 and 3 to the blob region involved in color detection and the interblob region involved in form detection.

The cells in layer 4C are the only cells in the visual cortex which respond to small spots of light and, along with the blob region, have circular receptive fields. All other regions of the cortex are completely unresponsive to small spots of light and only respond to stimuli which have linear properties such as a line or a bar. In their research, Hubel and Weisel demonstrated that striate cortex (V1) simple cells responded to a specific retinal position; exhibited discrete excitatory and inhibitory zones which combine multiple stellate cells from layer 4C of the striate cortex to form rectilinear receptive fields; have specific vertical, horizontal, or oblique rectangular axis of orientation for every retinal position; did not respond or responded only weakly to spots of light; did not respond to diffuse light; had larger receptive fields than LGN cells; showed indications that cells in layers 2, 3, and 4B projected onward to higher visual cortical areas; whereas, cells in layer 5 projected to the superior colliculus; and finally showed that layer 6 cells projected back to the LGN and the claustrum.

[8]The striate cortex can be considered to be the beginning of the higher order visual system and, therefore, the beginning of what is termed, the "dorsal pathway." The magnocellular cell input to layer 4B of area V1 then continues onward as the dorsal pathway to synapse upon: perastriate visual association cortex area V2 (also called area 18 and OB); dynamic form area V3v (also called VP), V3d, and V3A which are part of area OA as well as MT (also called V5). Input to area OB projects to the thick dark stripe region within area V2. Moreover, from area VP, V3d, and V3A there is projection

to the color area V4 (also part of OA) in the ventral pathway. From area MT, the pathway synapses upon area MST; as well as upon area VIP (ventral intraparietal area, which projects afterward to area STP of the superior temporal polysensory area), as well as LIP (lateral intraparietal area), and ultimately to area 7a (PPx, also called medial area PG). Area MST, in turn, projects to area VIP and area 7a (PPx). As noted in the text, area 7a represents the pinnacle of the dorsal pathway involved in visual location.

[9] From PPx (area 7a), the dorsal pathway then projects onward to the presubiculum, which projects on to the entorhinal cortex (area 28) and to the principal sulcus of the prefrontal cortex which maintains direct connections with the hippocampus. Area 28 of the entorhinal cortex then projects to three sites within the hippocampus: the dentate gyrus (also called fascia dentata or FD); area CA3 of the Cornu Ammonis; and area CA1 of the Cornu Ammonis, respectively. The dentate gyrus projects to CA3, which, in turn, projects through area CA2 to CA1, which projects to the subiculum. The subiculum then projects back to the entorhinal cortex, which then projects to the parahippocampal cortex gyrus. Specific regions within the PPx project to separate sites within the parahippocampal cortex. Specifically, the ventral caudal region of the PPx projects to the lateral parahippocampal gyrus, while the dorsal inferior PPx projects to the medial parahippocampal gyrus; and the central inferior PPx projects to intermediate parahippocampal gyrus. Furthermore, the parahippocampal gyrus projects to area TE (i.e., AIT), which, in turn, projects to the entorhinal cortex (area 28).

[10] The "ventral pathway" is considered to begin at the striate cortex as well where, from layer 4C-Beta the axons project to layers 2 and 3 of the blob and interblob regions, (based on cytochrome oxidase staining) and are involved, respectively, in detection of color and of form. Cells within the

blob region project onward to the thin dark stripe region of area V2 involved in color, which then project onward to area V4 (part of OA), which is viewed by many as the key "color area" of the ventral pathway. Similarly, cells from the interblob region project onward to the pale lighter interstripe regions within area V2 involved in form detection, which then project onward to separate sites within area V4 (part of OA) which is, for many, the key area involved in "color sensitive form." Both the color and color sensitive form portions of area V4, then project to area TEO (i.e., posterior inferotemporal area, also called PIT). The cells of TEO then project onward to area TE (i.e., anterior inferotemporal area, also called AIT) which, as noted in the main body of this text, serves as the pinnacle of the ventral pathway involved in identification of visual objects.

[11] From IT (area TE), the ventral pathway projects onward to the entorhinal cortex (area 28) as well as to areas 11 and 13 of the orbital surface of the frontal lobe (Chavis & Pandya, 1976; Goldman-Rakic, 1987; Gross, 1994; Gross & Weiskrantz, 1964; Macko et al., 1982; Martin-Elkins & Horel, 1992), and area 12 of the prefrontal convexity (Webster et al., 1994). These connections between the perirhinal and orbital cortices contribute to both recognition memory and performance on delayed-nonmatch-to-sample tasks with long delays (Kowalska et al., 1991) Area 28 of the entorhinal cortex then projects to three sites within the hippocampus: the dentate gyrus (also called FD); area CA3 of the Cornu Ammonis; and area CA1 of the Cornu Ammonis, respectively. The dentate gyrus projects to CA3, which, in turn, projects through area CA2 to CA1, which projects to the subiculum. The subiculum then projects back to the entorhinal cortex, which projects to the parahippocampal cortex gyrus. Finally, the parahippocampal gyrus projects back to area TE (also known as area AIT).

[12] An additional set of fibers travel from PPx via the superior longitudinal fasciculus to the principal sulcus of the dorsolateral prefrontal cortex which contribute to short-term spatial memory and to the dorsomedial frontal lobe to contribute to spatial aspects of vision and egocentric localization (Barbas, 1988; Cavada & Goldman-Rakic, 1989; Funahashi, Bruce, & Goldman-Rakic, 1990, 1993; Gross, 1994; Lawler & Cowey, 1987; Macko et al., 1982; Rodman, 1994; Quintana, Fuster, & Yajeya, 1989; Quintana & Fuster, 1992; Webster, Bachevalier, & Ungerleider, 1994). Projections from the PPx to the frontal eye fields and the superior colliculus are critical for coordination of the guidance of motor sequences necessary for visual saccades for foveation and eye movements (Cohen, 1993; Mesulam, 1981; Watson, Miller, & Heilman, 1978).

[13] An additional set of fibers project from the anterior portion of IT to areas 11 and 13 of the orbital surface of the frontal lobe (Barbas, 1988; Chavis & Pandya, 1976; Goldman-Rakic, 1987; Gross, 1994; Gross & Weiskrantz, 1964; Macko et al., 1982; Martin-Elkins & Horel, 1992; Mishkin & Manning, 1978; Rodman, 1994; Suzuki & Amaral, 1994; Webster et al, 1994; Wilson, O Scalaidhe, & Goldman-Rakic, 1993), and area 12 of the prefrontal convexity, which contribute to the acquisition of the nonmatch rule for shape and color of visual objects (Webster et al., 1994). These connections between the perirhinal and orbital cortices have been shown to contribute to both recognition memory and performance on delayed-nonmatch-to-sample tasks with long delays (Kowalska et al., 1991; Meunier et al., 1993). In addition, the anterior portion of IT has been reported to be essential for concurrent object discrimination in visual memory tasks (Gross, 1973; Overman, Bachevalier, Turner, & Peuster, 1992; Sakai & Miyashita, 1993).

[14] Recent research has demonstrated the existence of a subdivision within the dorsal pathway which subserves stimulus movement, including such motion pathway sites as MST and MT which project to area STP (Bruce et al., 1981; Gross, 1994). Most notably, area MT is a small visuotopically organized area which contains cells specialized for analysis of motion. These cells are selective for direction and speed of stimulus movement as well as expansion and rotation, but evidence little or no sensitivity to form, color or both (Albright, Desimone, & Gross, 1984; Desimone et al., 1985; Desimone & Ungerleider, 1989; DeYoe & Van Essen, 1988; Duffy & Wurtz, 1991; Gattass, Gross, & Sandell, 1981; Gross, 1991; Maunsell, 1987; Maunsell & Newsome, 1987; Maunsell & Van Essen, 1983a, 1983b; Merigan et al., 1991c; Motter & Mountcastle, 1981; Saito et al., 1986; Sakata, Shibutani, Kawano, & Harrington, 1985; Snowden, Treue, Erickson, & Andersen, 1991; Tanaka et al., 1986; Van Essen & Maunsell, 1983; Van Essen & Maunsell, 1983).

Lesions within area MT have been shown to impair detection of shearing motion, movement of random dots, and perception of structure from motion (Newsome & Paré, 1988; Siegel & Andersen, 1986). While large lesions involving portions of MT and MST produce severe and permanent impairment in motion perception (Merigan & Maunsell, 1993; Newsome & Paré, 1988; Yamasaki & Wurtz, 1991). In fact, complete bilateral MT-MST lesions cause persistent disruption to several aspects of motion perception, including speed, direction, and global motion (Pasternak et al., 1991).

[15] Approximately one third of cells in the IT cortex respond selectively to two- and three-dimensional patterned stimuli including hands, brushes, facial profiles, facial parts, or entire faces (Baylis, Rolls, & Leonard, 1985, 1987; Desimone & Gross, 1979; Gross, 1973; Gross et al., 1979;

Gross et al., 1972; Perrett et al., 1985; Richmond et al., 1983; Richmond, Optican, Podel, & Spitzer, 1987; Tovee, Rolls, & Azzopardi, 1994; Sato, Kawamura, & Iwai, 1980). The responses of these selective cells are reduced by removal of facial features which influence recognition of specific features of faces, yet are unaffected by uniform changes of stimulus position, orientation, distance, spatial frequency, direction, and size (Desimone et al., 1984; Desimone & Ungerleider, 1989; Baylis et al., 1985).

[16] The hippocampus was first named by Julius Caesar Arantius, a "rather dull" pupil of Andreas Vesalius. According to Lewis (1923), "The flight of fancy which led Arantius, in 1587, to introduce the term hippocampus is recorded in what is perhaps the worst anatomical description extant." Gross (1998) however, has offered 1564, instead, as the date on which Arantius (Aranzi) first labeled the hippocampus (sea horse). Further, Gross offers the additional historical footnote that for one-half a century, beginning in 1779, the hippocampus came to be known as the "Hippopotamus," in contemporary publications until this error was rectified by Burdach in 1829 (Gross, 1998, p. 143).

[17] Although, Gall and Spurzheim (1810) hypothesized that color blindness might be due to specific cortical organs, their idea remained purely speculative until the 1880's. Their insights are particularly remarkable in that the nature of the phrenological system related to identifying personality characteristics rather than sensory or motor cortical localization. Instead, color vision was believed to occur at the level of the eye rather than the cerebral cortex. Then, in 1883, Swanzy reported the case of a 77-year-old man with chromatic hemianopsia who had no evidence of retinal or optic nerve lesions. Swanzy concluded that this, "proves color perception is in the brain and not the eye, and that in the

brain is a separate center from that for the form sense and for ordinary light perception." Soon after, Wilbrand (as cited in Solms, Kaplan-Solms, & Brown, 1996) suggested that in the three separate layers of the primary visual cortex, "visual projections first go to a light center, then to a form center, and finally to a color center." At this time, Verrey (as cited in Damasio & Damasio, 1986) reported a case of a complete hemiachromatopsia, concluding that color vision took place in the lingual and fusiform gyri of the occipital lobe. According to Verrey, the most dorsal of these neighboring areas was for light, the middle for form, and the central ventral area for color. As a result, deficits in form perception frequently should co-occur with deficits in color perception. By 1923, Poppelreuter had extended these conceptions to suggest that streams of visual information for form, motion, stereopsis, and color were processed in parallel (Cowey, 1979; Finger, 1994; Hawkins, 1969; Saraga & Shallice, 1973; Zeki, 1989).

[18]Marr (1982) proposed a computational approach to visual perception in which vision is organized into an information processing system which comprises successive stages of "modular processes." These processes break visual computation into component parts which proceed relatively independently. The starting point of the process of visual perception occurs at the image stage which is a spatial distribution of intensity values across the retina. This is followed by the primal sketch which takes the raw intensity values of the visual image and makes explicit the spatial, or geometric, distribution of intensity changes, and the manner in which they are organized. This affords surface detection and as such, the M- and P-pathways contribute to the two-dimensional representation. The next stage is termed, "The 2 1/2-D sketch." At this

stage the orientation and rough depth of the visual surface are made explicit producing a "picture of the world." Yet this picture is organized egocentrically with reference to the viewer only and not linked to a stable external world. The final stage is the 3-D representation in which shapes and their orientations are made explicit as tokens of 3-dimensional objects. These tokens are organized in an object-centered framework which is independent of the position and orientation of the image on the retina thereby producing an allocentric (i.e., viewer independent) representation of the external world.

[19] The proposed task design can be traced to human studies including: "Learning-A-Place-In-Space-Test" (Lhermitte & Signoret, 1972); "7/24-Spatial-Location-Test" (Rao et al., 1984); "Toy Location Task" (Smith & Milner, 1981); "Object-Place Association Learning Task" (Squire & Cave, 1991); "Spatial Array Memory Task" (Hirst & Volpe, 1984); "Design Memory Task"(Jones-Gotman, 1986a, 1986b, 1986c); "Visual-Conjunction-Task" (Briand & Klein, 1987). The task design of the proposed studies is also related to prior animal studies including "Delayed-Nonmatch-To-Sample" (DNMTS; Mishkin & Delacour, 1975) and "Food-Search-Task" (Passingham, 1985).

[20] Investigations of early perceptual processes have shown an inverse relation between stimulus duration and apparent brightness for stimuli presented for durations below 100 ms (i.e., Bloch's law).

[21] Increasing the duration between presentation of the first and second stimuli to 30 seconds would serve as a human analog to DNMTS task in which one must discriminate what is new in the second array that was not present in the first array (Mishkin & Delacour, 1975).

[22] Given the organization of the higher order visual system, patients with lesions to the PPx or IT cortex should be expected to show double dissociations for detection of location and identity of visual objects. Patients with damage to PPx should be impaired in detection of location, but show normal ability to detect identity, whereas patients with lesions to IT should evidence impaired detection of identity, while showing that detection of location is intact. Further, if no delay is imposed between the first and second arrays, patients with hippocampal lesions should be able to correctly detect location, identity, and location+identity since their PPx and their IT remain intact permitting them to correctly determine location, identity, and location+identity. However, should a delay be imposed between presentation of the first and the second arrays necessitating involvement of memory, these patients would not be capable of performing these discriminations successfully, as it requires an intact hippocampus to combine and store these traces in memory (Farah, 1990; Meunier et al., 1993; Pohl, 1973; Rueckl et al., 1989).

METHOD

Research Overview

The present investigation of the dorsal and ventral pathways of the higher order visual system derives its foundation from pre-established anatomical, physiological, and neuropsychological findings (Felleman & Van Essen, 1991; Gross, 1973, 1998; Mishkin, Ungerleider, & Macko, 1983; Pohl, 1973). The dorsal pathway projects forward from magnocellular projection sites in occipital cortex through extrastriate regions upward to the posterior parietal cortex for processing spatial location of visual objects (Mishkin, 1972; Andersen, 1989). The ventral pathway projects forward from parvocellular projection sites in occipital cortex through extrastriate regions downward to the inferior temporal cortex for processing hue and form for the identity of visual objects (Macko, Jarvis, Kennedy, et al., 1982; Rocha-Miranda, Bender, Gross, & Mishkin, 1975;).

The origins of the occipital-parietal and occipital-temporal contributions to vision, which are seen now to correspond to the dorsal and ventral processing streams, can be traced, respectively, as far back as 1884, with Ferrier and Yeo's animal "case 8," and to 1888, with Brown and Schäfer's "animal 6." Ferrier and Yeo's case 8 evidenced visuospatial location impairment, without deficits in visual identification; while Brown and Schäfer's "animal 6" showed impairment in visual identity, without deficits in visual location (Gross, 1998). In spite of subsequent clinical descriptions by Holmes and Horax (1916), Goldstein and Gelb (1918), Klüver and Bucy (1936), Brain (1941), Blum (1951), and many others, the initial findings by Ferrier and Yeo and by Brown and Schäfer were often overlooked only to be appreciated once again following further progress in the understanding of the organization and function of the visual system.

It was not until 30 years ago that the extrastriate cortex began to be recognized as the true site of higher order visual processing. In fact, even as recently as 1968, shortly after the groundbreaking work of Hubel and Weisel (1965), Trevarthan was to advance a dual pathway model of vision in which tectal vision served as one of the two major processing pathways for primate vision. However, soon after Trevarthen's novel conception was supplanted by a more precise cortical representation of higher order visual processing based on the work of Mishkin (1972) and followed soon after by Pohl (1973). It is these latest findings that now serve as the cornerstone for future understanding of the dual pathway model of higher order vision. Since that time understanding of the extrastriate role in higher order vision has advanced considerably. Differences have been shown in sites along the dorsal and ventral pathways in facial recognition (Gross & Rodman, 1992), color processing (Gross, 1994; Livingstone & Hubel, 1988), single cell recording (Perrett, Rolls, & Caan, 1982; Williams, Breitmeyer, & Lovegrove, 1991), neurotransmitter distribution (Aston-Jones, Foote, & Bloom, 1984; Posner & Petersen, 1990; Posner & Raichle, 1994), PET and fMRI studies (Mitchell, Johnson, Raye, & D'Esposito, in press) clinical reports (Humphreys & Riddoch, 1987a; Luria, 1973; Smith & Milner, 1981; Warrington & James, 1988), dyslexia (Galaburda & Livingstone, 1993), visual attention (Bisiach et al., 1979; Fuster & Jervey, 1981; Posner, 1992) and in computational and cognitive modeling of these pathways (Kosslyn, Flynn, Amsterdam, & Wang, 1990; Rueckl, Cave, & Kosslyn, 1989) In sum, these reports point to differences which should be measurably reflected through behavioral measures of reaction time and accuracy (Posner & Mitchell, 1967).

The goal of the present research into the detection of identity and location of visual objects is to more fully illuminate the organization and response characteristics of the higher order visual system. To realize this goal, the effect of timing, number, color, and spatial frequency upon human visual object recognition was assessed using the behavioral measures of response time and accuracy. Through explicit control of information flow to intact participants, this paradigm afforded selective facilitation and inhibition of the two processing streams which underlie judgments of identity and location of visual objects.

As shown by Figure 1, preliminary sites which precede the origin of the dorsal and ventral pathways begin as early as the retina through equivalents of w, x, and y cells. These cells lead to the lateral geniculate nuclei and project forward in parallel as the magnocellular and parvocellular pathways to selective sites in primary visual cortex (V1). Differences in Parvocellular and Magnocellular pathway cell characteristics have been reported both neuroanatomically (Schiller et al., 1990a, 1990b) and behaviorally (Merigan, Byrne, & Maunsell, 1991). Parvocellular pathway cells are small, slow responding, slow conducting, sustained response cells, which exhibit poor contrast sensitivity, high spatial frequency, and fine spatial selectivity necessary for high resolution color (i.e., hue) and form perception for pattern discrimination and object recognition (Campbell, 1974; Graham, 1980; Livingstone & Hubel, 1987; Galaburda & Livingstone, 1993). In comparison, Magnocellular pathway cells are large, rapid responding, fast conducting, transient response cells with high contrast sensitivity, low spatial frequency, low spatial resolution and low acuity, which exhibit reportedly little sensitivity to hue and are ideally suited to convey signals relating to movement and spatial location (Cohen, 1993; Derrington, Krauskopf, & Lennie, 1984; Kaplan & Shapley, 1982).

Three research methodologies were brought together to assess responses to visual stimuli processed by the higher order visual system: 1. delayed-nonmatch-to-sample (DNMS) was selected over delayed-match-to-sample (DMS) for reasons of visual processing and anatomical organization (Mishkin & Delacour, 1975; Mishkin & Murray, 1994); 2. speed-accuracy tradeoff (SAT) was used in addition to the traditional RT paradigm to allow assessment of performance during ongoing processing, rather than solely at the point of completion (McElree & Dosher, 1993; Meyer, Osman, Irwin, & Yantis, 1988); and 3. digital filtering of objects was chosen over optical filtering as it afforded significantly greater control over spatial wavelengths of stimuli presented (Breitmeyer & Ganz, 1977; Ginsburg, 1986; Williams et al., 1991).

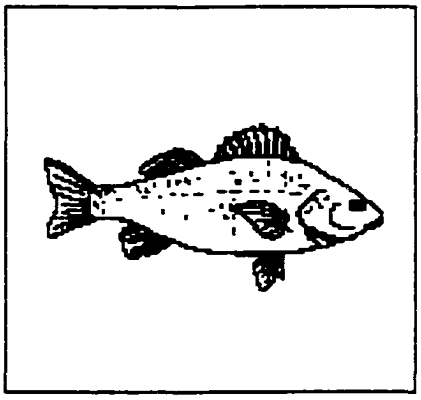
Participants

Fifty-seven college and graduate student volunteers between the ages of 18 and 35 were recruited from universities in New York City; fourteen participated in Experiment 1, seventeen in Experiment 2, and twenty-six in Experiment 3. There were no significant differences between the groups with respect to age, years of education, gender, handedness, and all reported no prior history of substance abuse and reported that they were drug-free at time of testing. Finally, all performed within normal limits on neuropsychological measures and visual acuity was within normal limits with glasses if needed, (see Appendix for elaboration of neuropsychological tests and for descriptions of visual acuity tests).

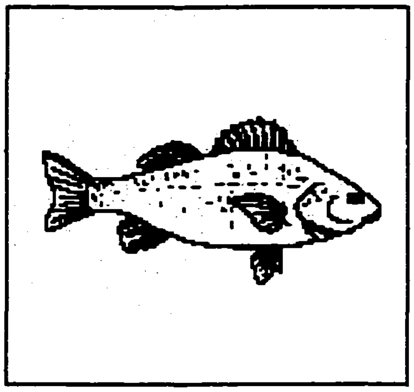
Materials

The experiments were created in the B/C PowerLaboratory programming environment (Chute & Westall, 1996), and were presented utilizing a Macintosh PowerBook 550c computer which was connected to a M1297, 13-inch AppleColor High Resolution (square-pixel) RGB monitor. Images were prepared for display through the program, Image Alchemy. Stimuli consisted of 260 digitized Snodgrass and Vanderwort (1980) line drawings. Normative information on the figures permitted counterbalancing items both within and across conditions for imagibility, familiarity, complexity, concept frequency, and name agreement.

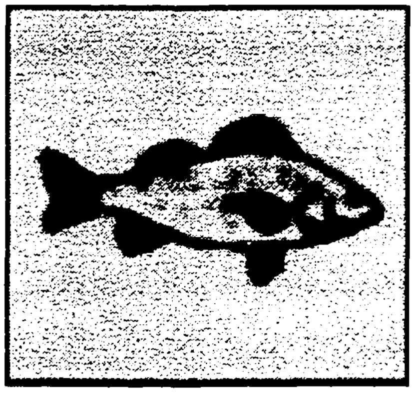
All line drawings of objects were filtered digitally using 2-dimensional butterworth filters. Digital computational processing of image pixels affords a level of bandpass filter precision that is simply unobtainable using optical filters (Maunsell, 1987; Schwartz & Loop, 1983; Williams et al., 1991). There were three sets of objects: the first set comprised unfiltered digitized line drawings (see Figure 2a); the second matching set of line drawings was filtered with a highpass filter, which filtered out all spatial frequencies except those within the range of 9.50 - 11.00 cycles per degree (cpd; see Figure 2b); and the third set of line drawings were filtered with a lowpass filter which filtered out spatial



a. unfiltered object



b. highpass-filtered object



c. lowpass-filtered object

Figure 2. Examples of unfiltered and filtered stimuli.

frequencies outside the range of 0.01 - 1.50 cpd (see Figure 2c). Prior research using spatial frequency gratings has demonstrated that the magnocellular pathway responds to movement and location input from spatial frequencies below 6.0 cpd; whereas, the parvocellular pathway responds to color and form/pattern input from frequencies above 6.0 cpd.

On all trials, a specialized visual pattern mask was shown following each sample stimulus to ensure that no "iconic" representational store obscured the effects of the independent variables on the experimental tasks (di Lollo & Dixon, 1992; Irwin & Yeomans, 1991, 1995). The pattern mask covered the entire screen and consisted of a two-dimensional butterworth bandpass spatial frequency mask of overlapping visual gratings comprising visual frequencies from 0.01 - 11.00 cpd. Each of the two-dimensional gratings consisted of two rows of pixels so as to allow 240 independent rows of visual gratings. Each grating was programmed so as to begin independently at an initial random location at any of the 640 pixels in a particular row of the computer screen and then repeat 29 times across that row. Moreover, the photic power (i.e., energy) of each of the sine waves that comprised the gratings was equated to ensure that there was equal masking effects at all frequencies from 0.01 - 11.00 cpd.

Use of digital filters permitted control over the spatial frequencies presented to participants. The black, red, green, and blue lowpass and highpass filtered Snodgrass and Vanderwort (1980) drawings were filtered using 2-dimensional butterworth filters. Moreover, using photic power spectrum analysis, the energy levels of the filtered line drawings then were assessed to ensure that they were equivalent. The highpass and lowpass digital filters controlled the input to the retinal cell detectors which, in turn, were expected to determine retinal cellular output project to retinal ganglion cells such that by the level of the lateral geniculate nucleus, one could be confident that digital filtering of these selective spatial frequencies, carried by the magnocellular and parvocellular pathways, respectively, would be detectable in higher order visual information processing by response time and accuracy measures.

The selection of the DNMS paradigm was chosen over DMS because the former has been identified as involving occipital, parietal, temporal structures (Mishkin & Murray, 1994), while the latter has been more strongly associated with neural structures relating to frontal lobe and basal ganglia circuits such as found in delayed alternation tasks. A further advantage of DNMS was its extension and clear precedence in animal research associated with location and identity discrimination. Finally, given the high levels of recognition often associated with visual recognition memory tasks, the greater task demands and difficulty of DNMS served as a protection against ceiling effects.

Finally, the SAT methodology was chosen to complement traditional response time and accuracy measures. In spite of the utility of self-terminated RT paradigms, researchers run a greater risk of participant bias as sampling occurs based on participant's subjective understanding of the instruction, "Please answer as quickly and accurately as possible." Not only does this method frequently generate nonlinear data, but also the shorter the response time, the worse the accuracy and conversely, the longer the response time the greater the accuracy with no systematic linear means of comparison for modeling. The advantage of the SAT methodology is that it makes it possible to assess ongoing processing that otherwise might be obscured using traditional self-terminated RT methods in which highest level of accuracy occurs at completion of all processing. The data from these two methodologies can be compared and more precise conclusions can be made regarding the nature of cognitive processing.

PROCEDURES

General experimental procedures: Each trial (see Figures 3-5) in the three experiments began with the presentation of the words, "Trial Begins," in the center of the computer screen for 4000 ms, followed by a blank screen for 1500 ms. Then, one of three possible cues was shown on the screen for 4000 ms, (i.e., IDENTITY ONLY, LOCATION ONLY, or LOCATION+IDENTITY), followed by a blank screen for 1500 ms. Next, four separate, but contiguous, two-inch squares arranged horizontally on the screen were displayed for 300 ms. Horizontally, the images subtended a horizontal visual angle of 30.00 degrees and vertical angle of 7.50 degrees as viewed by a participant 18.26 inches from the screen. Then, 200 ms after the onset of the blank squares, an object was presented for 100 ms in one of

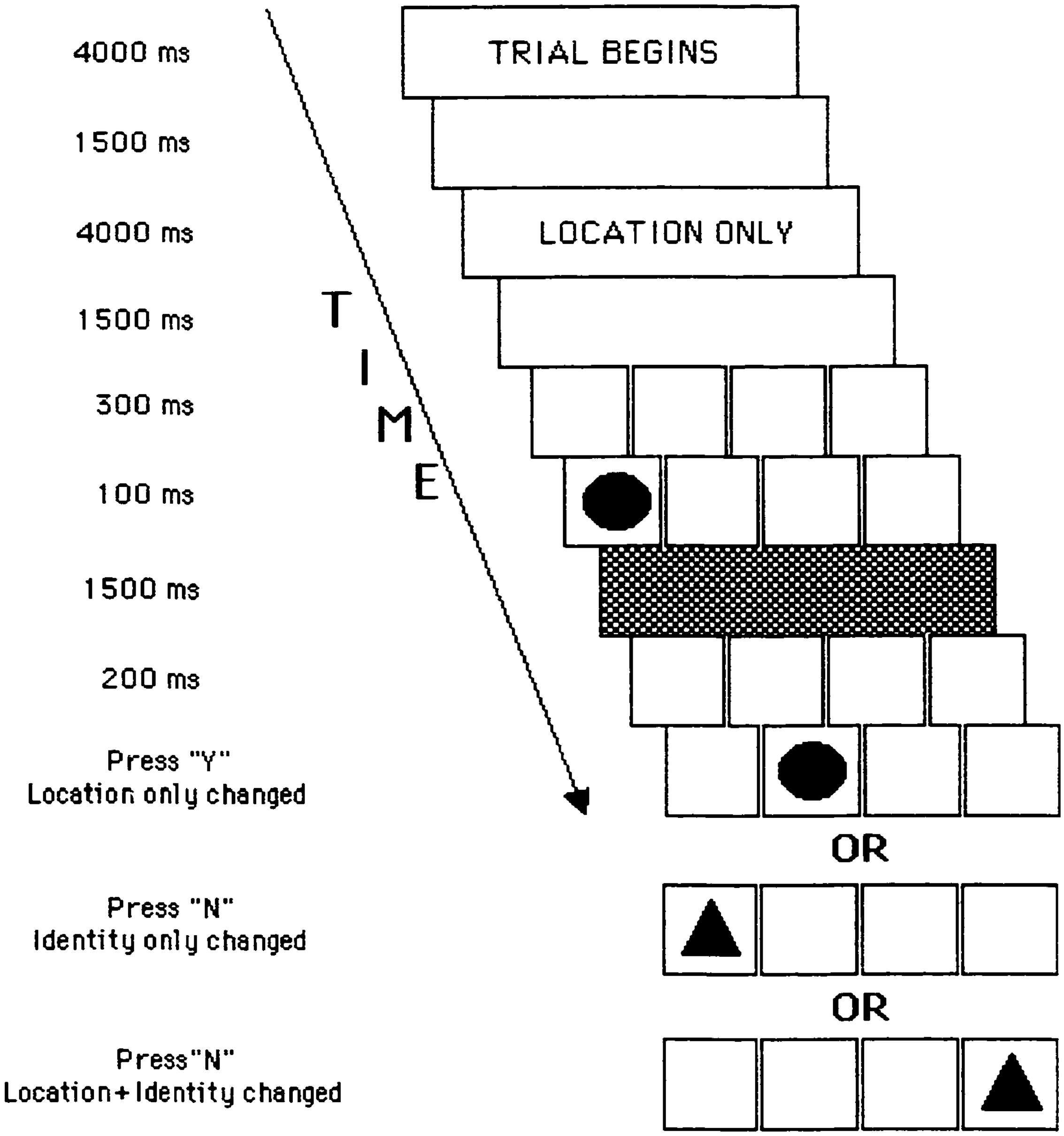


Figure 3. Examples of "location only" trials.

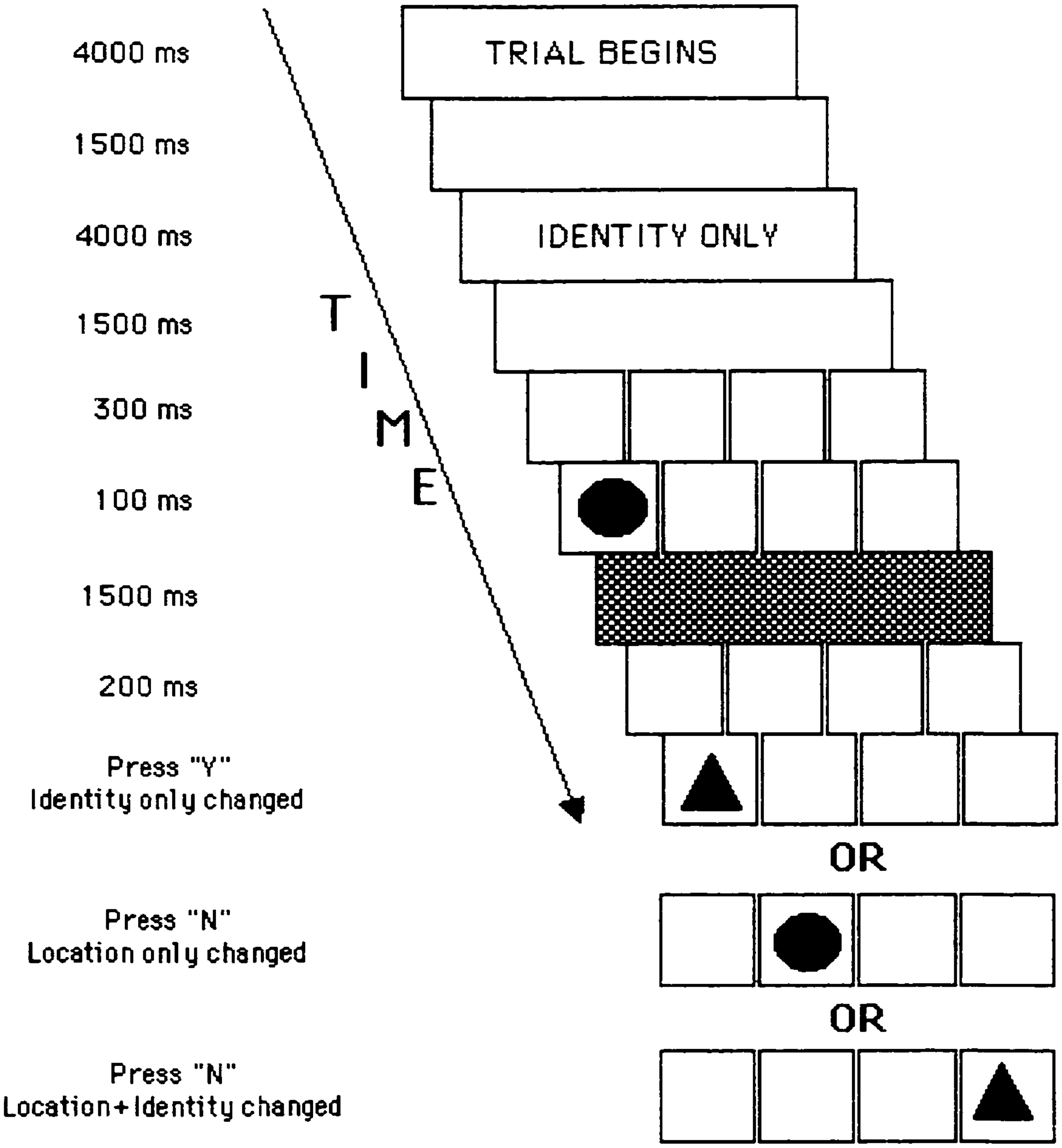


Figure 4. Examples of "identity only" trials.

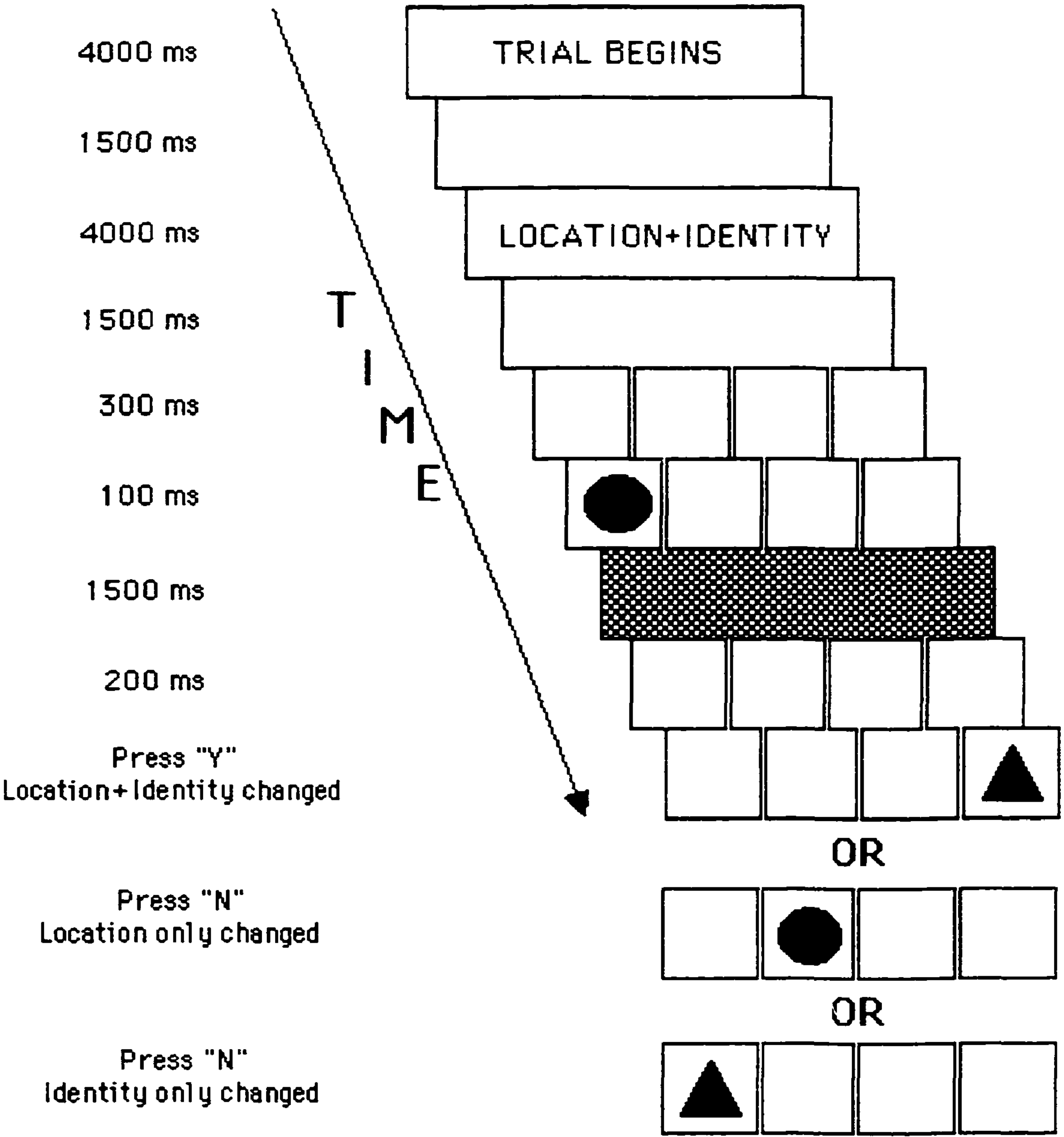


Figure 5. Examples of "location+identity" trials.

the four boxes. Immediately afterward, this display was followed by the presentation of the pattern mask for 1500 ms, that completely occupied the screen. Precisely at the moment the mask disappeared, the array of four squares was presented once again. After 200 ms an object appeared in one of the four squares upon the screen. This time, however, the object remained in one of the four squares until the participant responded with a key press. Participants had been instructed to decide whether the object, or the objects, presented had changed between the sample and the test phase in the manner predicted by the cue. Participants pressed "Y" for "yes" if the change was correctly predicted by the cue, and "N" for "no" if the change was not correctly predicted by the cue which had been presented at the beginning of the trial.

Experiment 1

Experiment 1 manipulated color and number of stimulus items using only unfiltered line drawings of objects to explore whether these parameters differentially influenced response time measures for detection of location, identity, and location+identity. The four conditions administered to each participant consisted of: a single black and white object, a single colored object, two black and white objects, and two colored objects. Participants were administered 24 practice trials, and the objects presented were not reused in the experimental trials. These practice trials consisted of six trials from each of the four conditions. Participants were then administered one block of 72 trials. For the practice trials and in the experiment itself, trials from each condition were equally divided and randomly presented.

Experiment 2

Experiment 2 was identical to Experiment 1, except that performance was assessed under two different filter conditions: highpass and lowpass.

Experiment 3

Experiment 3 was the same as Experiments 1 and 2, except for the following modifications. Stimulus set size comprised only four objects selected from the Snodgrass and Vanderwort (1980) drawings. Four objects were selected so as to equate the number of locations with the number of object identities. At 350, 700, 1050, or 1400 ms after the presentation of the object in the test array, participants were presented with a 100 ms signal tone. At the onset of the tone, the participant was required to answer with his or her "best guess" by pressing one of two response keys. If the participant's response occurred more than 250 ms after the response tone offset, the participant received a 1000 ms warning, "Too Slow" at the end of that trial. Similarly, if the participant's response preceded the onset of the tone, the participant received a 1000 ms warning, "Too Fast" at the end of that trial. When this occurred the trial was not repeated and the data for that trial was excluded from subsequent analyses.

RESULTS AND DISCUSSION

Owing to the inadvertent use of "only" in my instructions, rather than "Location" and "Identity," I am unable to clearly identify the processes that produced my data. Therefore, I can make no unequivocal claims regarding location versus identity processing, and any statements regarding this data must be viewed as speculative. Future research, however, offers the possibility of clarifying these ambiguities.

Despite this limitation as RT studies risk nonlinearity of data, log transformations were performed for all data, with both direction and level of statistical significance maintained in every case. Last, alpha probability level was set at .05 for statistical significance for all calculations. Accuracy for all experiments was analyzed with D-prime (d′) scores. Use of d′ ensures that individual response bias could not be a factor in recognition performance measures.

Response Time for Location and Identity

Considerable animal and human research has led to the hypothesis that in human higher order vision, judgments of location should be processed more rapidly than judgments of identity (REFs). Based on planned comparisons, this speculation was strongly confirmed by the present study with unfiltered stimuli, $\underline{F}(1,26) = 5.59$, $\underline{p} < .03$. Although response time for location ($\underline{M}$ = 1151 ms) was faster than for identity ($\underline{M}$ = 1262 ms) and for location+identity ($\underline{M}$ = 1289 ms) judgments, there existed no statistical difference between judgments of identity and judgments of location+identity. Consistent with this view, a Cue x Filter interaction in Experiment 2, indicated that judgments of "location only" were more accurate for lowpass filtered objects than for highpass filtered objects. Predictions based on the dual pathway model would suggest that lowpass filtering would facilitate processing of location information as it is carried by the dorsal pathway, and that highpass filtering would hamper processing of location information as it selectively removes the spatial frequencies carried the dorsal pathway. The implication of these findings is that location and identity are separable processes, which can be differentially influenced by spatial frequency filtering consistent with the predictions of the dual pathway model.

Quantity

The effect of quantity of visual information on visual processing was examined and participants responded faster for one item than for two items, (M = 1170 vs. M = 1297; $F(1,26) = 11.02$, $p < .01$). However, number of items did not interact with cue type. This absence of an interaction indicates that although two visual stimuli require more time to process than one visual stimulus, the response time for judging two location items or two identity items is not proportionally faster than for two location+identity items. In other words, the cognitive operations involved in the processing of conjoined location+identity judgments are not more complex than the processing of each judgment individually.

Further support for this finding comes from the finding that for trials in which two objects were shown simultaneously, comparison of early block trials with late block trials revealed that subjects continued to monitor both items. These results indicate that complexity cannot account for the data in this study.

Finally, on trials in which two items were presented simultaneously, a suggestion was made to have trials in which only one item changed rather than both change or not change in the same manner. Although there was a risk of experimental redundancy as participants could monitor just one of the two items on these trials, it is notable that the participants continued to monitor both items in analysis of early and late block trials. Moreover, the reason both items changed, or did not change in the same manner, was that to have do otherwise would have produced a situation in which participants would have had to give contradictory responses.

Hue

Prior research literature suggests that hue impacts visual object recognition under unfiltered conditions solely in instances in which objects are less prototypical or are highly similar in category or structure. However, the effect of hue on object recognition of spatially-filtered items was yet to be determined. This issue was of particular note in the domain of visual object processing as the ventral pathway contains sites for hue and for hue-form (area V4), whereas the dorsal pathway exhibits little (slight sensitivity to red only in area ST), or no color sensitivity. In Experiment 2, the effect of color and cue and filter was analyzed as a 2(Hue: black & white (bw), red & green & blue (rgb) x 3(Cue: identity, location, location+identity) x 3(Filter: highpass, lowpass, unfiltered) repeated measures analysis of variance (ANOVA). There was a main effect of Hue, $\underline{F}(1,28) = 9.88$, $\underline{p} <.01$, with participants exhibiting higher levels of recognition for bw objects ($\underline{M} = 4.34$) than for rgb objects ($\underline{M} = 4.00$).

This effect of hue indicates that the presentation of rgb items does not facilitate processing of visual identity information for highpass or for lowpass filtered objects. Thus, the limited situations in which color assists in object recognition remains unchanged by this study. These findings suggest that the processing advantage for bw stimuli indicates that the rapid processing of the dorsal pathway has an essential contribution for both location and identity of visual objects.

Spatial Frequency Filtering

The regression analyses of the d′ scores for Experiment 1 and 2 lend support to the idea that the processing of cues over time is sensitive to the spatial frequency of the material to-be-remembered (see Figure 6). When stimuli are unfiltered and trials are self-terminated, as was the case in Experiment 1, "location only" judgments declined rapidly, $\underline{F}(1,26) = 5.45$, $\underline{p} <.01$, relative to the comparatively flat and consistently high levels of accuracy for judgments of "identity only" and "location+identity." A similar pattern was evident with the highpass filter in Experiment 2:

accuracy for location remained constant, but accuracy for identity judgments declined over time and the change approached significance, $F(1,12) = 4.17$, $p < .08$. In contrast, in the lowpass filter condition in Experiment 2, accuracy for "identity only" declined rapidly, $F(1,18) = 5.98$, $p < .01$, whereas, accuracy for "location only" and for "location+identity" remained relatively flat, consistently high, and did not change significantly over time. In addition, as is evident from Figure 7, Cue interacted with Filter, $F(4,56) = 2.72$, $p < .04$; judgments of location were more accurate for lowpass filtered stimuli ($M = 4.37$) than highpass filtered stimuli ($M = 3.66$).

In sum, with lowpass filtered items, there was a rapid decline for "identity only" judgments compared to the relatively flat and consistently high levels of accuracy for "location only" and "location+identity" judgments. As all trials were self-terminated in Experiments 1 and 2, the apparent similarity in slopes both for unfiltered and highpass filtered stimuli could lead one to the mistaken inference that highpass filtering of stimuli has no effect on processing, and that only the lowpass filter is capable of producing the double dissociation noted above. Alternatively, one might infer that the ventral pathway predominates processing under unfiltered conditions, and it is only under the lowpass filtered conditions that the effects of the dorsal pathway became apparent. The lowpass filter, therefore, aids processing of location information which increases signal strength to improve accuracy for location+identity judgments. This can be

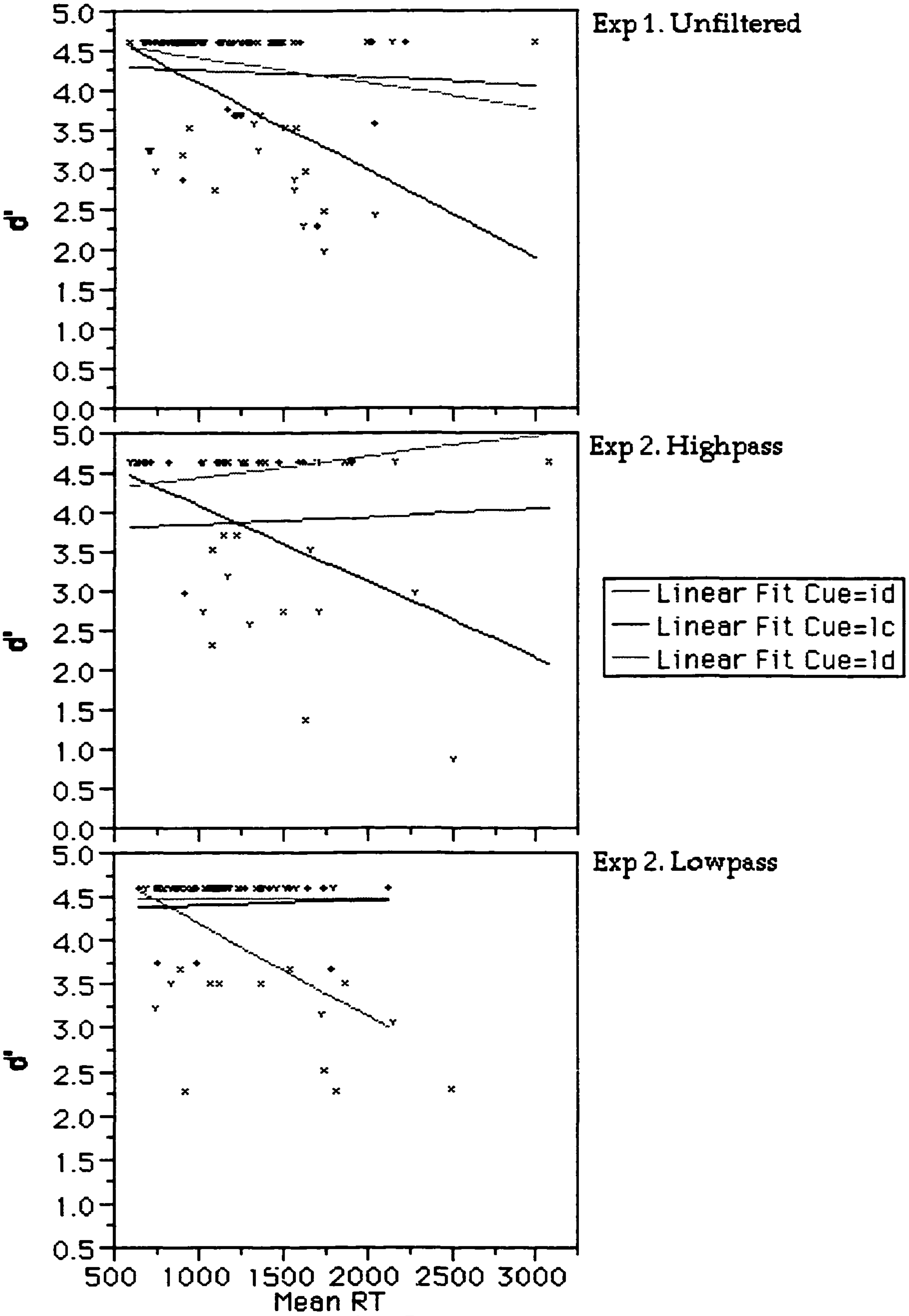


__Figure 6__. Experiments 1 and 2: Regression of RTs and d' by filter.

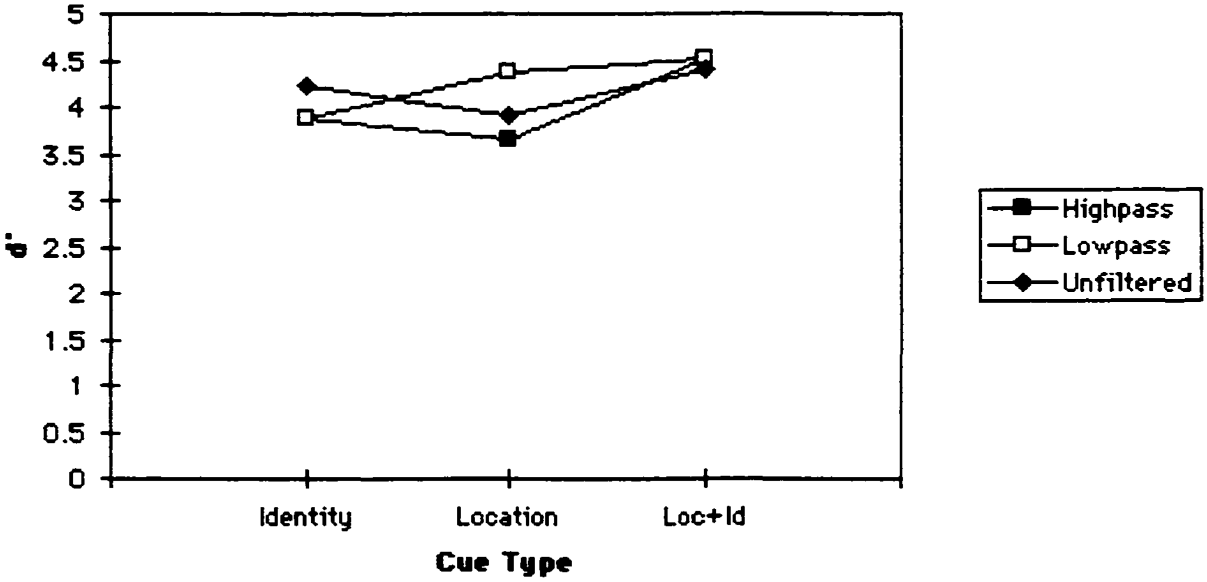


Figure 7. Experiments 1 and 2: Accuracy for consistent cue-test by filter.

better understood by examining the SAT data of Experiment 3, resulting from the interruption of processing at specific time intervals.

Speed-Accuracy Tradeoff

In Experiment 3 the time course for making location, identity, and location+identity judgments was interrupted at specific time intervals after the onset of processing. The resulting d′ data was analyzed as a 3 (Cue: location, identity, location+identity) x 4 (Interval: 1-350 ms, 351-700 ms, 701-1050 ms, 1051-1400 ms) x 3 (Filter: highpass, lowpass, unfiltered) repeated measures ANOVA. There was a main effect of Interval, $\underline{F}(3,66) = 5.03$, $\underline{p} < .003$, accuracy was lowest at the 1-350 ms interval ($\underline{M} = 1.35$), and peaked during the 351-700 ms ($\underline{M} = 2.20$) and 701-1050 ms ($\underline{M} = 1.98$) intervals. These results indicated that selection of four time intervals were sufficient to effectively discriminate the different phases in processing location, identity, and location+identity.

In addition, there was a main effect of Cue, $\underline{F}(2,44) = 9.96$, $\underline{p} < .001$; location ($\underline{M} = 1.91$) and location+identity judgments ($\underline{M} = 2.11$) were more accurate than identity judgments ($\underline{M} = 1.45$). Notably, the conjoined judgment of "location+identity" is more accurate than that of "identity only" which suggests that location+identity benefits from the contribution of processing location information. Consistent with this notion, Cue interacted with Interval, $\underline{F}(6,132) = 2.33$, $\underline{p} < .04$; (see Figure 8), location ($\underline{M} = 2.59$) and location+identity judgments ($\underline{M} = 2.45$) were more accurate than identity judgments ($\underline{M} = 1.56$) at the 351-700 ms interval.

In addition, there was a tendency toward a three-way interaction of Cue x Interval x Filter, $F(12,132) = 1.70$, $p = .07$ (see Figure 9). Further analysis revealed that during the 1-350 ms interval, location+identity judgments were more accurate in the unfiltered condition ($M = 1.86$) than the lowpass condition ($M = .91$; $F(1,13) = 9.81$, $p < .01$). The fact that the conjoined location+identity judgment is more accurate for unfiltered than lowpass filtered items at this early interval suggests that identity predominates in the unfiltered condition. At the 351-700 ms interval, however, location+identity judgments were more accurate in the highpass condition ($M = 2.92$) relative to the unfiltered condition ($M = 1.84$; $F(1,17) = 4.37$, $p < .05$). This finding suggests that highpass filtering of items enhances the signal strength of identity. Finally, at the 1051-1400 ms interval, judgments of identity, $F(1,14) = 8.44$, $p < .01$, and location+identity, $F(1,14) = 4.88$, $p < .04$, were more accurate with the highpass than the lowpass filter indicating that highpass filter maintains the accuracy for the identity information rather than decline as would be expected with the lowpass filter.

The d′ data for inconsistent cue-test pairs was also analyzed. As is evident from Figure 9, at the 701-1050 ms interval, there was greater accuracy for the highpass than the unfiltered condition for "identity at cue and location at test" ($M = 1.96$ vs. $M = 1.16$; $F(1,17) = 5.16$, $p < .04$), and "location at cue with identity at test" ($M = 3.94$ vs. $M = 2.06$; $F(1,17) = 7.58$, $p < .01$). This finding suggests not only that under unfiltered conditions

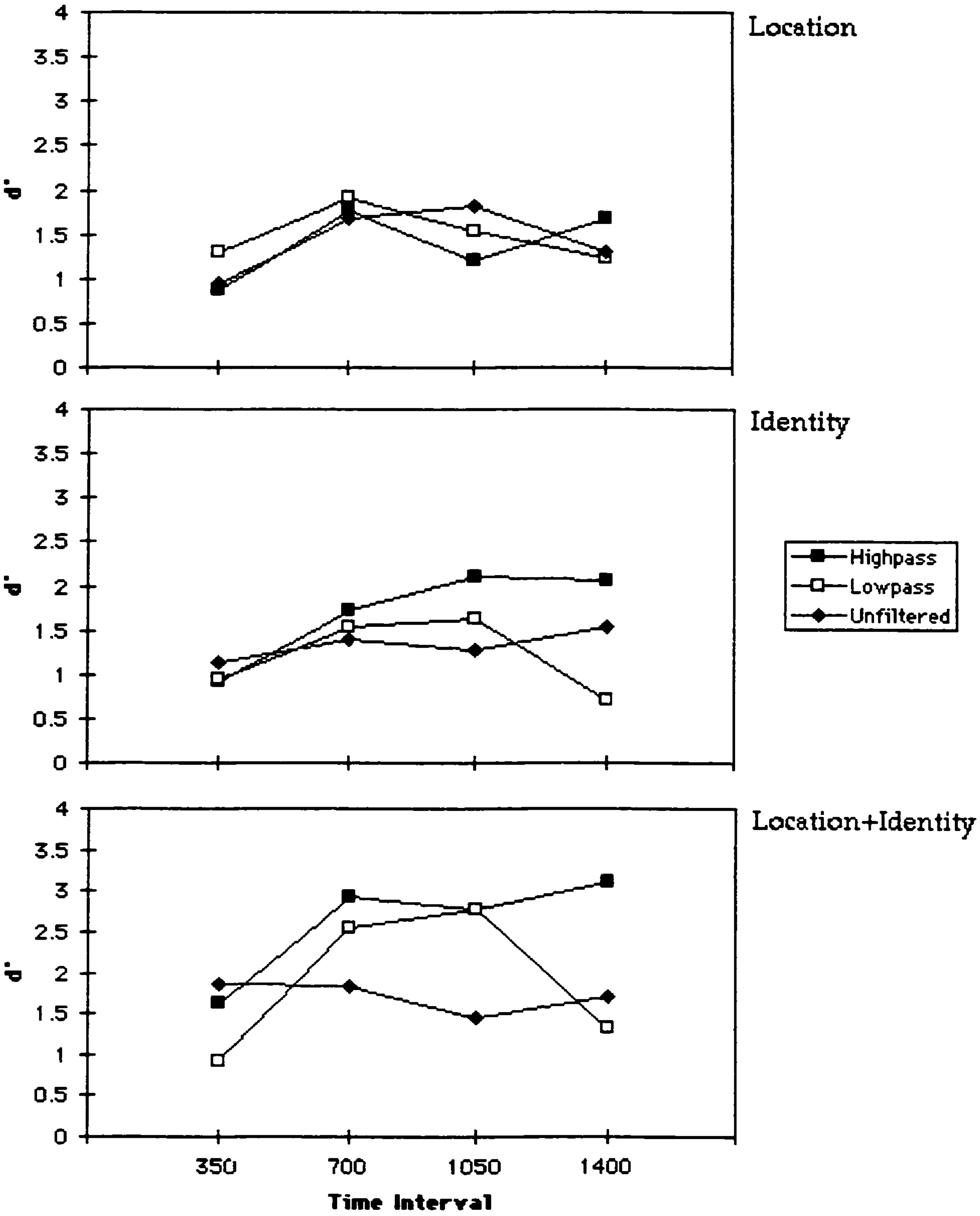


Figure 8. Experiment 3: Accuracy for filter and interval by cue.

that identity predominates, but that highpass causes location judgments to sustain an additional interval until 1050 ms rather than begin to fall off by the preceding interval 700 ms. A similar pattern at the 1050 ms interval was evident for location+identity cues (see Figure 10) with the highpass ($\underline{M} = 3.48$) relative to the unfiltered condition ($\underline{M} = 1.12$). Highpass filtered items at 1050 ms were more accurate than unfiltered items for "location+identity at cue" paired with "identity at test" ($\underline{F}(1,17) = 8.03$, $\underline{p} < .01$), "location at test" ($\underline{F}(1,17) = 10.12$, $\underline{p} < .01$), and "no change at test" ($\underline{F}(1,17) = 4.55$, $\underline{p} < .05$). These results indicate that highpass filtering maintains location processing, rather than decline rapidly. Finally, accuracy for trials with "location+identity at cue and location at test" was higher with the lowpass filter ($\underline{M} = 3.09$) than the unfiltered condition ($\underline{M} = 1.03$; $\underline{F}(1,17) = 4.89$, $\underline{p} < .05$) at the 1050 ms interval. This finding indicates that when the cue and test do not match, the cue influences the processing strategy participants adopt in anticipation of the test. Thus, the "location+identity" cue prepares participants to expect a conjoint judgment despite being tested on "location only" and the resulting accuracy curve closely matches that of consistent "location+identity" cue and test trials.

Processing of location and identity in the higher order visual system is determined by spatial frequency. Under normal unfiltered conditions, location is a rapid process that occurs by 350 ms, peaks by 700 ms, and declines markedly by 1050 ms. In comparison, identity is a process that

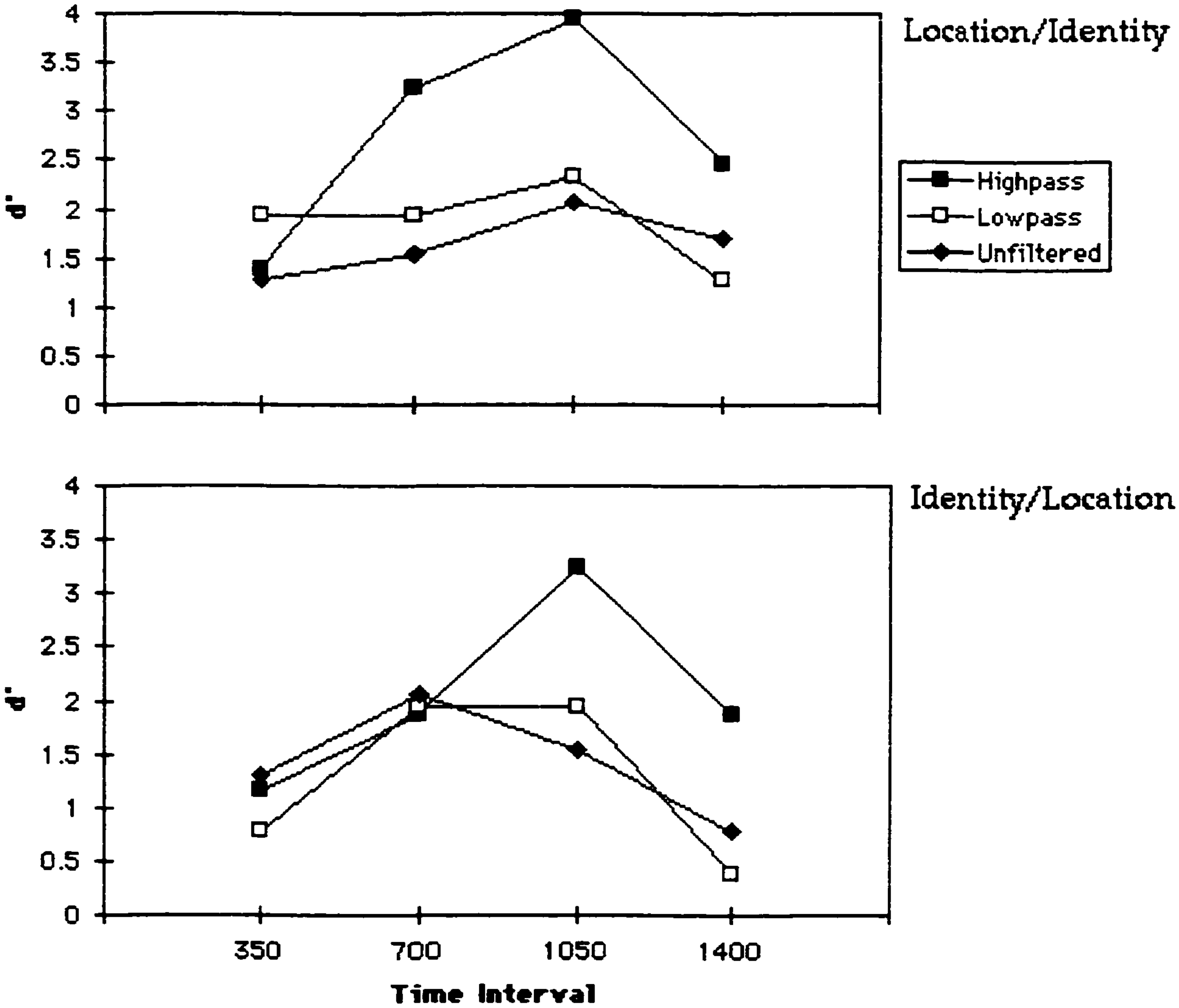


Figure 9. Accuracy for location/identity and identity/location by filter and interval.

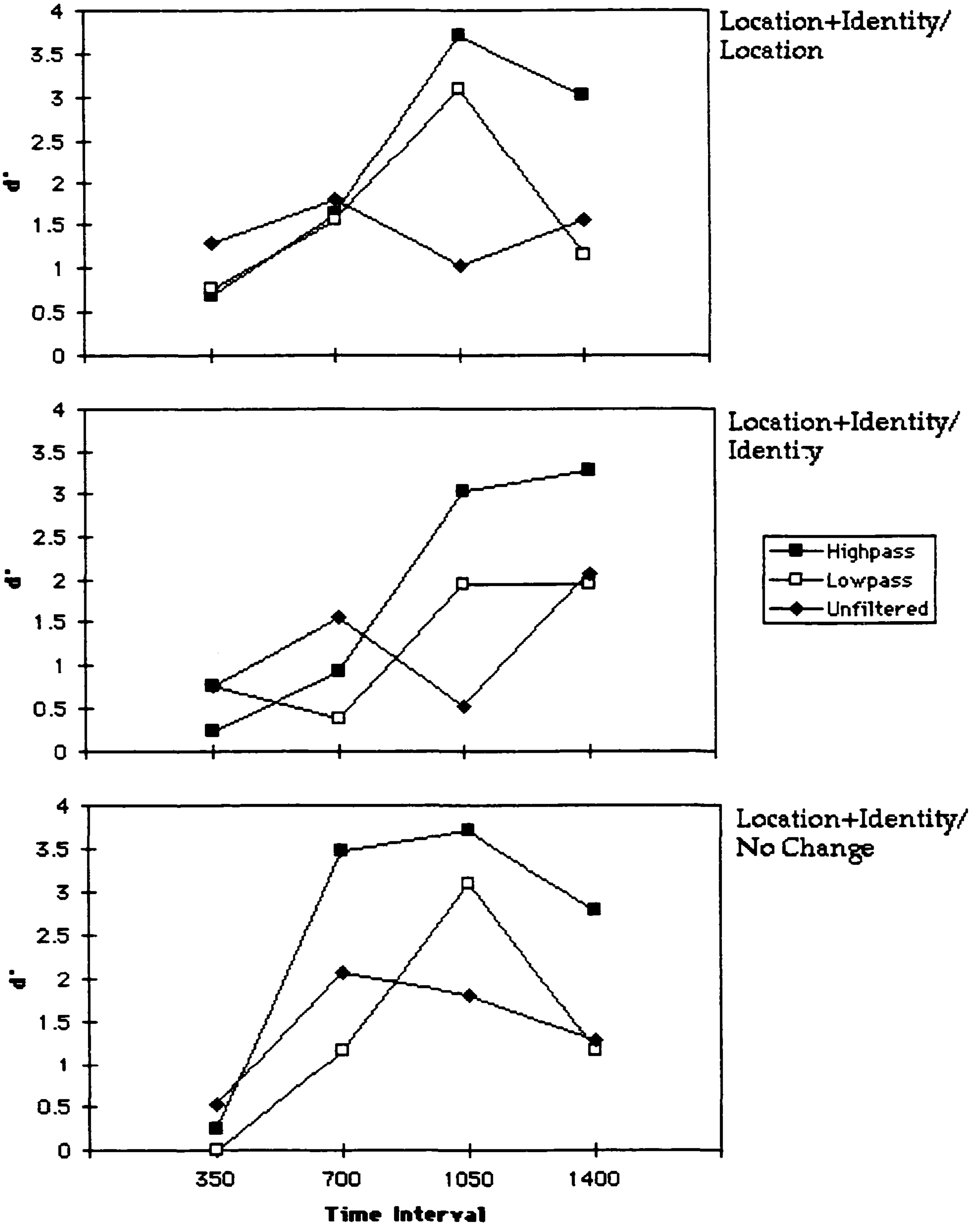


Figure 10. Accuracy for location+identity: Inconsistent cue-pairs by filter and interval.

rises more gradually to peak and predominate processing fully by 1050 ms and then continue to maintain accuracy. Conjoined location+identity judgments reflect the influence of location until 700 ms and then the contribution of identity through later stages of processing. Use of an highpass filter causes location judgments to resemble the unfiltered pattern of identity, while enhancing accuracy levels for judgments of identity. The same occurs for conjoined location+identity judgments in which location resembles the unfiltered pattern of identity, however, identity judgments peak earlier and then continue to maintain accuracy. By contrast, lowpass filtering enhances accuracy of location judgments, but makes identity judgments decline rapidly at 1050 ms resembling the pattern of identity judgments under lowpass filtered conditions. Together these findings show that location and identity are strongly influenced by filter.

The significant effect of cue is also important to consider as there is evidence that cue directs the order of processing in that consistent cue-test pairs are processed faster than inconsistent cue-test pairs. Further, trials with inconsistent cue-test pairs in which location is the cue are processed more rapidly than those in which identity is the cue. This means that to expect location and receive identity should be processed faster than trials in which one expects identity and receives location. The reason for this discrepancy is that location processing has already occurred in the former, and can access limited identity information to respond rapidly, whereas in the latter identity information must be processed fully before responding. On inconsistent trials in which one is presented with conjoined location and identity cues, but either no change, location, or identity, alone occur as the test item, one would expect location information to be processed more rapidly than identity.

GENERAL DISCUSSION

Both Ratcliff and McKoon as well as Townsend have proposed memory search models which employ a search algorithm that compares limited and exhaustive search fields. Although they differ in the degree to which processing is serial or parallel, in both models search continues until a match occurs between the target and the memory set. All possible comparisons must be made between the target and the memory set to determine that there is "no match." As long as either the target set or the memory set contain more than one item, the time required to detect a match between these two sets (i.e., limited search) is shorter than the time needed to determine there is "no match," (i.e., exhaustive search).

Data from the present study of higher order visual processing does not support an interpretation consonant with limited versus exhaustive dichotomy models. According to the predictions from these models, participants should be fastest when cue and test items match as neither element changed, requiring only a limited search to match items as would be the case with all "no change" test items. Conversely, participants should be slowest when cue and test items fail to match as all pairings between cue and test items must be made "exhaustively" to discover there is no match, as would be the case with all location+identity test items.

In the present investigation of location and identity processing, the "no change" test condition requires only limited search for both elements, but the "location+identity" test condition requires exhaustive search of both location and identity items. Factor analysis of the limited versus exhaustive searches (match/mismatch) both in detail and via cluster analysis show no statistical differences between exhaustive vs. limited searches for all categories of comparison.

Relation to the Dual Pathway Model

Figure 11 diagrams the cognitive operations for the DNMS task used in this study, providing both task decomposition and corresponding cognitive processes requisite for all trials. Overall, the task for the participant is to verify the type of change from the sample phase to the test phase of the trial. As such, all trials require four fundamental stages of processing: 1. the cue generates a pattern of predicted changes, which is then held in memory; 2. participants separately detect changes in location and changes in identity; 3. participants compare the pattern of these changes with the pattern of changes held in memory predicted by the cue; 4. the output of this decision expresses the participant's response.

Cue Phase: The trial commences when a verbal cue ("location only", "identity only", "location+identity") is presented visually. This cue is processed by a linguistic transducer that generates semantic information from the cue. This semantic information will be used to select a pattern pair from four possible relations which will occur in the trial (location change or location no change) with (identity change or identity no change). The resulting selection is an outcome maintained by a hold function throughout the sample and test phases.

<u>Detection and Comparison Phases:</u> A sample pattern is presented followed by a visual test pattern, and are compared to each other. A difference detection module compares location and identity information to determine the type of change in pattern between the sample and the test phase. There are four outcomes possible in this comparison: 1. change in location with change in identity; 2. change in location with no change in identity; 3. no change in location with change in identity; 4. no change in location with no change in identity.

<u>Decision and Response Phases:</u> Once the type of pattern change has been detected, the output of this module is fed to a decision module. A "yes" response indicates that the change in pattern from sample to test matches that predicted by the cue. A "no" response indicates that the change in pattern from sample to test does not match that predicted by the cue.

In order to determine whether the inputs from sample and test match, the Decision and Response Phase comparator must search four elements in order to indicate "no match." Should the sample pattern and outcome pattern match (i.e., consistent), search is terminated. The model in Figure 11 predicts that 'consistent' cue-test trials should occur faster than inconsistent trials. At the Decision and Response Phase, magnocellular and parvocellular systems which provide input for the dorsal and ventral pathways sample and test array comparators become important. The input signal (s) over time (t) to the Detection and Comparison Phase comparator module is ($s/s+a$ vs.$1/s+a$ where, s of "location only" » s of "identity only" and t of "identity only" » t of "location only"). Until the Detection and Comparison Phase modules have performed their tasks, the Decision and Response Phase module cannot complete its comparisons.

Both the parvocellular and magnocellular pathways can be characterized as "leaky integrators" whereby the signal loses amplitude over time. Signal amplitude conducted by the magnocellular system rises more rapidly than in the parvocellular system. However, signal amplitude also decreases at a faster rate in the magnocellular system relative to the parvocellular system whose signal amplitude rises more slowly and lasts longer. Thus, one should expect that the output of the Detection and Comparison Phase will closely parallel signal amplitude.

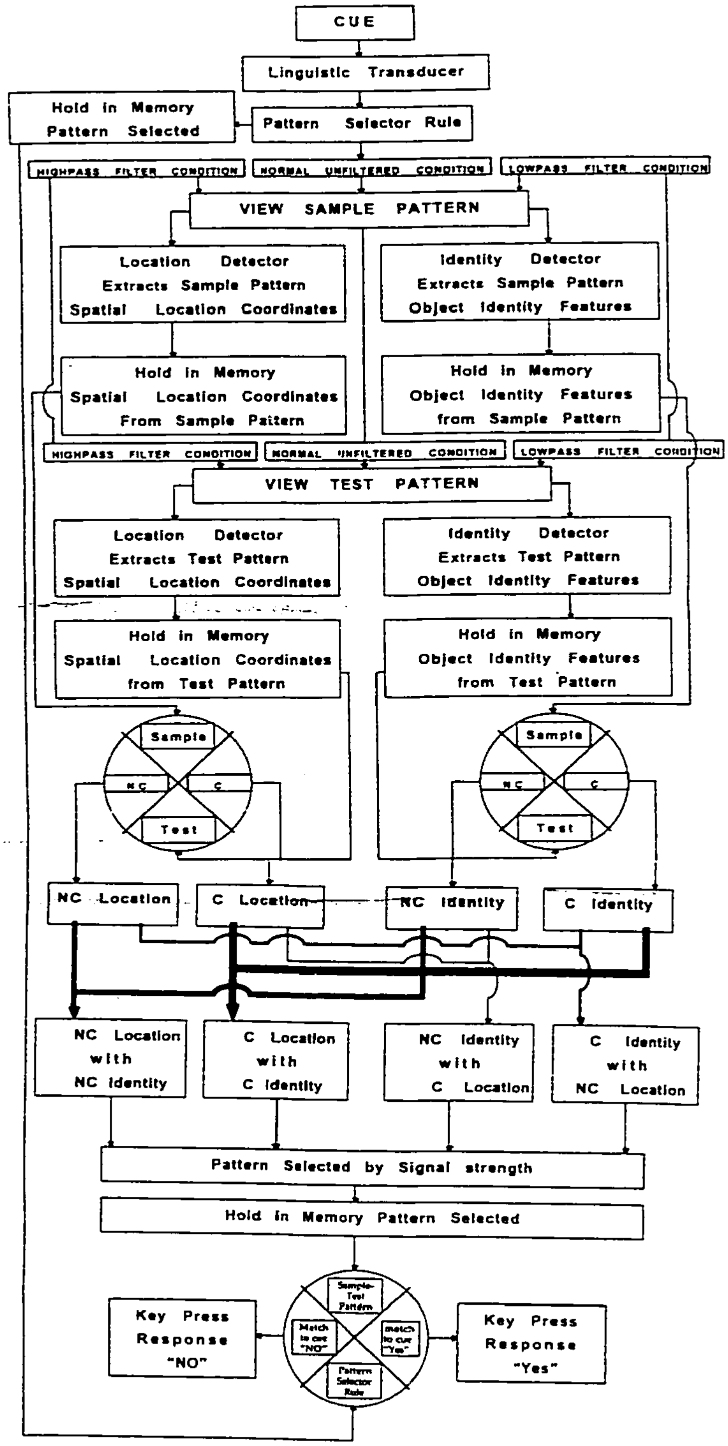


Figure 11. Cognitive operations underlying performance of the DNMTS task.

Summary and Conclusion

These visual processing experiments support and elaborate understanding of the dual pathway model of higher visual system function and the contribution of location and identity processing to visual object recognition. They reveal location and identity judgments are largely independent, with "location only" judged faster than "identity only." In addition, speed-accuracy tradeoff methodology reveals critical differences in the timing between the pathways: location rapidly rises and then declines; identity rises more slowly and then continues at the same level; and conjoined location+identity judgments reflect the initial influence of location, followed by the later influence of identity.

The effect of filter on this pattern of accuracy is that the lowpass filter enhances location and causes the slope of identity to decline rather than to continue at the same level; while the highpass filter enhances identity and causes the slope of location to continue at the same level rather than to decline.

This study found that there was no effect of rgb hue on the processing of visual objects in unfiltered, highpass, and lowpass filter conditions, and that bw stimuli were processed more rapidly suggest that the dorsal pathway has have an essential contribution in the processing of visual objects. Furthermore, participants judged a single item faster than two items, and response time for judging two location only items, or two identity only items, was not proportionally faster than judging two location+identity items.

Further, the integration of standard RT methodology with speed-accuracy tradeoff methodology provided an deeper glimpse into the nature of processing in the higher order visual system. Not only did it reveal a greater level of interaction between the pathways in modulating visual object location and identification, but it also revealed the natural function and time course of such processes. Moreover, this study provided firm grounds for describing a process model which describes higher order visual system and gives strong support to the dual pathway model of visual system function.

Although these experiments serve as the cornerstone of future experimentation, an limitation of this design was that participants were given the instructions "location only" and "identity only," rather than "location" or "identity." This meant that participants had to verify both location and identity in every case to respond to the cue. Thus, additional conditions would lay this issue to rest by removing the word "only," and simply have participants detect changes in "location" or changes in "identity," regardless of the state of the other attribute.

Intriguing potential for further research is suggested in the area of dyslexia, also. Recent studies with visual dyslexics have posited a mismatch in synchrony between the dorsal and the ventral pathways as the cause for the dyslexics failure in letter and word synchrony. By use of letter combinations, real and nonsense words, and phonemic and semantic manipulations, one could explore the precise nature of these dyslexic errors, and point to new approaches to remediation of visual dyslexic errors. Finally, a deficit in spatial frequency processing has been suggested in individuals with Multiple Sclerosis and Alzheimer's dementia (Turner, 1990). Thus, this methodology opens new avenues in the area of detection for these significant neurological disorders as well.

Appendix

After obtaining informed consent, all participants were administered a screening questionnaire of relevant personal, educational, psychological, and medical history as well as a handedness inventory (Nebes & Briggs, 1975). A series of tests of visual perception were presented to ensure that participants had the visual skills necessary to perform the experimental tasks. Upon completion of the tests of visual perception, individuals were presented the computer-based reaction time study. Once the computer-based reaction time was completed, participants were administered a series of neuropsychological tests to ensure that they had the basic skills necessary to provide meaningful data as well as to serve as a source of validation for the computer-based experimental tasks.

Visual perception tests:

1. Visual acuity was assessed through administration of the Lighthouse Near Acuity Test. Participants viewed sixteen rows of Sloan letters of decreasing size from a distance of 16 inches. The last row of letters identified without errors was considered the participants' level of visual acuity. To qualify for participation, participants had to have corrected visual acuity at levels of 20/80 or better. 2. Next, contrast sensitivity was assessed by administration of the Vision Contrast Test System (VCTS) 6000 (Ginsburg, 1986). Participants viewed and indicated the contents of five rows of 9 circles from a distance of 16 inches. Each circle consisted of evenly-spaced, circular sinewave

Table A1

Group Performance on Neuropsychological Tests

	Experiment 1		Experiment 2		Experiment 3	
	n = 14[a]		n = 17[b]		n = 25[a]	
Test	M	SD	M	SD	M	SD
BNT	54.43	3.63	53.93	3.96	52.65	5.32
WAIS-R Vocabulary	11.50	1.91	10.77	2.46	10.42	2.62
Raven SPM	55.71	3.07	53.59	3.43	52.92	5.63
BVRT-R (Copy)	9.86	0.36	9.53	0.51	9.80	0.41
BVRT-R (Memory)	8.43	1.09	8.35	1.12	8.36	1.25

Note. BNT = Boston Naming Test (Kaplan, Goodglass, & Weintraub, 1983); WAIS-R = Wechsler Adult Intelligence Scale - Revised (Wechsler, 1981); Raven SPM - Short Form = Raven Standard Progressive Matrices - Short Form (Raven, Raven, & Court, 1995); BVRT-R = Benton Visual Retention Test - Revised (Sivan, 1992).

[a] Two participants from Experiment 1 and two participants from Experiment 3 did not complete the BNT.

[b] One participant did not complete the WAIS-R Vocabulary.

gratings which appeared as finely-blurred, gray bars randomly tilted to the left, to the right, vertically upright, or simply blank. Each contrast grating indicated sensitivity to a specific spatial frequency expressed in cycles per degree (cpd).

3. Finally, color vision was assessed using the PV-16 Quantitative Color Vision Test. Participants were shown 16 plastic caps, each of a different color wavelength. A specific "pilot" cap was then designated and participants were instructed to select the cap which was closest in color to the pilot cap. The chosen cap was then placed next to the pilot cap and participants were asked to continue to select and place successive caps in the same manner until all caps had been used.

Following completion of the vision tests, the computer-based reaction time study was presented (see Procedures). After completing the reaction time study on the computer, participants were administered four standardized neuropsychological tests:

Neuropsychological tests:

1. The first of the neuropsychological tests administered was the Boston Naming Test (BNT; Kaplan, Goodglass, & Weintraub, 1983) which was used to assess participants' ability to recognize and name line drawings of common visual objects. Research findings by Van Gorp, Satz, Kiersch, and Henry (1986) indicate that performance on the BNT is highly-correlated with general naming ability.

2. The next test administered was the Vocabulary Subtest of the Wechsler Adult Intelligence Scale-Revised (WAIS-R; Wechsler, 1981) was given to determine the ability to define words. The Vocabulary subtest of the WAIS-R was chosen because the subtest exhibits the highest reliability coefficient (.96) and intercorrelation with verbal IQ score (.85) of all subtests on the WAIS-R the normative sample on which the test is based (Wechsler, 1981). As such, the Vocabulary subtest can be considered to represent the single best brief measure of both verbal and general mental ability and is considered a "hold" score as it is little affected by academic motivation or achievement or diffuse or bilateral brain injury (Lezak, 1983; McFie, 1975).

3. The third test administered was the Raven Standard Progressive Matrices (SPM)-Short Form (Raven, Raven, & Court, 1995). On the Raven SPM, participants were required to select the best item to complete each complex visual pattern. This visually presented test of problem solving ability requires that participants conceptualize visual, spatial, design, and numerical relationships to solve the patterns. The Raven SPM is correlated with overall IQ score on the WAIS-R (.7), and has traditionally been viewed as a supportive measure to assess general reasoning ability and to provide an IQ estimate (Raven, Court, & Raven, 1976). According to Lezak (1995), the Raven SPM is "considered more culture-fair than the Wechsler for measuring IQ," and evidences the strongest relationship with the Block Design subtest of the WAIS-R, involving visuospatial

skills. Given the diversity of the population for this study, it was considered a useful tool for providing a less biased measure of intellectual ability (Mills, Ablard, & Brody, 1993; O'Leary, Rusch, & Guastello, 1991).

4. The last test administered to participants was the Benton Visual Retention Test (BVRT). Participants were presented Administration A, (Form C) of the BVRT, in which participants were shown line drawings of abstract geometric shapes for ten seconds and then immediately afterward required to draw these figures from memory. Moreover, participants were given Administration C (Form D) of the BVRT, in which they were required to copy line drawings of abstract geometric stimuli while it remained in front of them allowing one to distinguish between visual memory and graphomotor difficulty. The BVRT is considered an effective test of "visual memory, visual perception, and visuoconstructive abilities" (Lezak, 1995). According to Lezak interscorer agreement for administration A is above .95, with retest reliability of .79 (Form D) and .85 (Form C); internal consistency coefficients .80. The BVRT evidences moderate correlation with IQ (Benton, 1974; Benton, Eslinger, & Damasio, 1981) with a strong correlation with lifetime occupation regardless of educational level (Dartigues, Gagnon, Mazaux, & Barberger-Gateau, 1992).

References

Aggleton, J.P., Burton, M.J., Passingham, R.E. (1980). Cortical and subcortical afferents to the amygdala of the rhesus monkey (Macaca mulatta). Brain Research, 190, 347-368.

Allman, J.M., & Kaas, J.H. (1971). A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (Aotus trivirgatus). Brain Research, 31, 85-101.

Andersen, R.A. (1987). Inferior parietal lobule function in spatial perception and visuomotor integration. In V.B. Mountcastle, F. Plum, & S.R. Geiger (Eds.), Handbook of physiological section 1: The nervous system (pp. 483-518). Bethesda, MD: American Physiological Society.

Andersen, R.A. (1989). Visual and eye movement functions of the posterior parietal cortex. Annual Review of Neuroscience, 12, 377-403.

Andersen, R.A., Essick, G.K., & Siegel, R.M. (1985). The encoding of spatial location by posterior parietal neurons. Science, 230, 456-458.

Andersen, R.A., Essick, G.K., & Siegel, R.M. (1987). Neurons of area 7 activated by both visual stimuli and oculomotor behavior. Experimental Brain Research, 67, 316-322.

Andersen, R.A., & Siegel, R.M. (1988). Motion processing in primate cortex. In G.M. Edelman, W.E. Gall, & W.M. Cowan (Eds.), Signal and sense: Local and global order in perceptual maps. New York: Wiley Press.

Andersen, R.A., Snyder, L.H., Li, C.-S., Stricanne, B. (1993). Coordinate transformations in the representation of spatial information. Current Opinion in Neurobiology, 3, 171-176.

Aston-Jones, G., & Bloom, F.E. (1981). Norepinephrine-containing locus coeruleus neurons in behaving rats exhibit pronounced responses to non-noxious environmental stimuli. The Journal of Neuroscience, 1, 887-900.

Aston-Jones, G., Foote, S.L., & Bloom, F.E. (1984). Anatomy and physiology of locus coeruleus neurons: Functional implications. In M.G. Ziegler & C.R. Lake (Eds.), Frontiers in clinical neuroscience: Vol. 2. Norepinephrine: Clinical aspects (pp. 92-116). Baltimore, MD: Williams & Wilkins.

Balint, R. (1909). Seelenlahmung des "Schauens," optische Ataxie, raumliche Storung der Auf merksamhiet. Monatsschrift für Psychiatrie und Neurologie, 25, 51-81.

Ballard, D.H. (1986). Cortical connections and parallel processing: Structure and function. Behavioral and Brain Sciences, 9, 67-120.

Barbas, H. (1988). Anatomic organization of basoventral and mediodorsal visual recipient prefrontal regions in the rhesus monkey. Journal of Comparative Neurology, 276, 313-342.

Barnes, C.A. (1988). Spatial learning and memory processes: The search for their neurobiological mechanisms in the rat. Trends in the Neurosciences, 11, 163-169.

Barnes, C.A., & McNaughton, B.L. (1983). Where is the cognitive map? Neuroscience Abstracts, 9, A191.16

Bauer, R.M. (1993). Agnosia. In K.M. Heilman & E. Valenstein, Clinical neuropsychology (3rd ed.). New York: Oxford University Press.

Baylis, G.C., Rolls, E.T., & Leonard, C.M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. Brain Research, 342, 91-102.

Baylis, G.C., Rolls, E.T., & Leonard, C.M. (1987). Functional subdivisions of temporal lobe neocortex, Journal of Neuroscience, 7, 330-342.

Benson, D.F. (1989). Disorders of visual agnosis. In J.W. Brown (Ed.), Neuropsychology of visual perception (pp. 59-78). Hillsdale, NJ: Lawrence Erlbaum Associates.

Benson, D.F., & Greenberg, J.P. (1969). Visual form agnosia. Archives of Neurology, 20, 82-89.

Benton, A.L. (1974). Revised Visual Retention Test (4th ed.). New York: The Psychological Corporation.

Benton, A.L., Eslinger, P.J., & Damasio, A.R. (1981). Normative observations on neuropsychological test performances in old age. Journal of Clinical Neuropsychology, 3, 33-42.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. Psychological Review, 94, 115-147.

Biederman, I., & Cooper, E.E. (1991a). Priming contour-deleted images: Evidence for intermediate representations in visual object recognition. Cognitive Psychology, 23, 393-419.

Biederman, I., & Cooper, E.E. (1991b). Evidence for complete transformational and reflectional invariance in visual object priming. Perception, 20, 585-593.

Biederman, I., & Cooper, E.E. (1992). Size invariance in visual object priming. Journal of Experimental Psychology: Human Perception and Performance, 18, 121-133.

Biederman, I., Hummel, J.E., Cooper, E.E., & Gerhardstein, P.C. (1993). Shape recognition in mind, brain, and machine. In P. Rudomin, M. A. Arbib, F. Cervantes-Pérez, & R. Romo (Eds.), Neuroscience: From neural networks to artificial intelligence (pp. 282-293). New York, NY: Springer-Verlag.

Biederman, I., & Ju, G. (1988). Surface versus edge-based determinants of visual recognition. Cognitive Psychology, 20, 38-64.

Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. Cortex, 14, 129-133.

Bisiach, E., Luzzatti, C., & Perani, D. (1979). Unilateral neglect, representational schema, and consciousness, Brain, 102, 609-618.

Blum, J.S. (1951). Cortical organization in somesthesis: Effects of lesions in posterior associative cortex on somatosensory function in Macaca mulatta. Comparative Psychology Monographs, 20, 219-249.

Boucart, M., & Humphreys, G.W. (1992). Global shape cannot be attended without object identification. Journal of Experimental Psychology: Human Perception and Performance, 18, 785-806.

Boucart, M., & Humphreys, G.W. (1994). Attention to orientation, size, luminance, and color: Attentional failure within the form domain. Journal of Experimental Psychology: Human Perception and Performance, 20, 61-80.

Brain, W.R. (1941a). Visual object agnosia with special reference to the gestalt theory. Brain, 64, 43-62.

Brain, W.R. (1941b). Visual disorientation with special reference to lesions of the right cerebral hemisphere. Brain, 64, 224-272.

Breitmeyer, B.G. (1984). Visual masking: An integrated approach. New York: Oxford University Press.

Breitmeyer, B.G. (1992). Parallel processing in human vision: History, review, and critique. In J.R. Brannan (Ed.), Applications of parallel processing in vision. New York: North-Holland.

Breitmeyer, B.G., & Breier, J.I. (1994). Effects of background color on reaction time to stimuli varying in size and contrast: Inferences about human M channels. Vision Research, 34, 1039-1045.

Breitmeyer, B.G., & Julesz, B. (1975). The role of on and off transients in determining the psychological spatial frequency response. Vision Research, 15, 411-415.

Briand, K.A., & Klein, R.M. (1987). Is Posner's "beam" the same as Treisman's "glue?" On the relation between visual orienting and feature integration theory. Journal of Experimental Psychology: Human Perception & Performance, 13, 228-241.

Brody, B.A., & Pribram, K.H. (1978). The role of frontal and parietal cortex in cognitive processing. Tests of spatial and sequence functions. Brain, 101, 607-633.

Brown, J.W. (1989). Essay on perception. In J.W. Brown (Eds.), Neuropsychology of visual perception (pp. 233-255). Hillsdale, NJ: Lawrence Erlbaum Associates.

Brown, S., & Schäfer, E.A. (1888). An investigation into the functions of the occipital and temporal lobes of the monkey's brain. Philosophical Transactions of the Royal Society of London, 179, 303-327.

Bruce, C.J., Desimone, R., & Gross, C.G. (1977). Large receptive fields in a polysensory area in the superior temporal sulcus of the macaque. Society of Neuroscience Abstracts, 3, 1756.

Bruce, C.J., Desimone, R., & Gross, C.G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. Journal of Neurophysiology, 46, 369-384.

Bushnell, M.C., Goldberg, M.E., & Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I.

Modulation in posterior parietal cortex related to selective visual attention. Journal of Neurophysiology, 46, 755-772.

Butters, N., Soeldner, C., & Fedio, P. (1972). Comparison of parietal and frontal lobe spatial deficits in man: Extrapersonal vs. personal (egocentric) space. Perceptual and Motor Skills, 34, 27-34.

Campbell, F.W. (1974). The transmission of spatial information through the visual system. In F.O. Schmidt & F.W. Worden (Eds.), The neurosciences third study program (pp. 95-103). Cambridge, MA: MIT Press.

Cavada, C., & Goldman-Rakic, P.S. (1989). Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. Journal of Comparative Neurology, 287, 422-445.

Chavis, D., & Pandya, D.N. (1976). Further observations on corticofrontal connections in the rhesus monkey. Brain Research, 117, 369-386.

Chow, K-L. (1951). Effects of partial extirpations of the posterior association cortex on visually mediated behavior. Comparative Psychology Monographs, 20, 187-217.

Chute, D.L. & Westall, R.F. (1996). Fifth-generation research tools: Collaborative development with PowerLaboratory. Behavior Research Methods, Instruments and Computers, 28, 311-314.

Cohen, H.J. (1984). Preserved learning capacity in amnesia: Evidence for multiple memory systems. In L. Squire & N. Butters (Eds.), Neuropsychology of memory (pp. 83-103). New York: Guilford Press.

Cohen, R.A. (1993). The neuropsychology of attention. New York: Plenum Press.

Conley, M., & Fitzpatrick, D. (1989). Morphology of retinogeniculate axons in the macaque. Visual Neuroscience, 2, 287-296.

Coppin, C.M.L., & Jack, J.J.B. (1972). Journal of Physiology, 222, 91P.

Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L., & Petersen, S.E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. Journal of Neuroscience, 11, 2383-2402.

Corkin, S. (1984). Lasting consequences of bilateral medial temporal lobectomy: Clinical course and experimental finds in H.M. Seminars in Neurology, 4, 249-259.

Cowey, A. (1964). Projection of the retina onto striate and prestriate cortex in the squirrel monkey, Saimiri sciureus. Journal of Neurophysiology, 27, 366-393.

Cowey, A. (1979). Cortical maps and visual perception: The Grindley Memorial Lecture. Quarterly Journal of Experimental Psychology, 31, 1-17.

Critchley, M. (1966). The parietal lobes. New York: Hafner.

Damasio, A.R., & Benton, A.L. (1979). Impairments of hand movements under visual guidance. Neurology, 29, 170-178.

Damasio, A.R., & Damasio, H. (1983). Localization of lesions in achromatopsia and prosopagnosia. In A. Kertesz (Ed.), Localization in neuropsychology (pp. 182-197). Orlando, FL: Academic Press.

Damasio, A.R., & Damasio, H. (1986). Hemianopia, hemiachromatopsia and the mechanisms of alexia. Cortex, 22, 161-169.

Damasio, A.R., & Damasio, H., & Van Hoesen, G.W. (1982). Prosopagnosia: Anatomic basis and behavioral mechanisms. Neurology, 32, 331-341.

Dartigues, J.F., Gagnon, M., Mazaux, J.M., & Barberger-Gateau, P. (1992). Occupation during life and memory performance in nondemented French elderly community residents. Neurology, 42, 1697-1701.

Davidoff, J. (1991). Cognition through color. Cambridge, MA: MIT Press.

Davidoff, J.B., & Ostergaard, A.L. (1988). The role of colour in categorical judgments. Quarterly Journal of Experimental Psychology, 40A, 533-544.

Dean, P. (1976). Effects of inferotemporal lesions on the behavior of monkeys. Psychological Bulletin, 83, 41-71.

Delaney, R.C., Rosen, A.J., Mattson, R.H., & Novelly, R.A. (1980). Memory function in focal epilepsy: A comparison of nonsurgical, unilateral temporal lobe and frontal lobe samples. Cortex, 16, 103-117.

DeMonasterio, F.M., & Schein, S.J. (1980). Protan-like spectral sensitivity of foveal Y ganglion cells of the retina of macaque monkeys. Journal of Physiology, 299, 385-396.

Denny-Brown, D., & Chambers, R.A. (1958). The parietal lobe and behavior. Research Publication of the Association for the Research of Nervous and Mental Diseases, 36, 35-117.

De Renzi, E. (1985). Disorders of spatial orientation. In J.A.M. Frederiks (Eds.), Handbook of clinical neurology, vol. 1 (45): Clinical neuropsychology (pp. 405-422). Amsterdam: Elsevier Science Publishers.

Derrington, A.M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in the lateral geniculate nucleus of macaque. Journal of Physiology, 357, 241-265.

Derrington, A.M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurons in lateral geniculate nucleus of macaque. Journal of Physiology, 357, 219-240.

Desimone, R. (1991). Face-selective cells in the temporal cortex of monkeys. Journal of Cognitive Neuroscience, 3, 1-8.

Desimone, R., Albright, T.D., Gross, C.G., & Bruce, C.J. (1980). Responses of inferior temporal neurons to complex visual stimuli. Society for Neuroscience Abstracts, 6, 581.

Desimone, R., Albright, T.D., Gross, C.G., & Bruce, C.J. (1984). Stimulus selective properties of inferior temporal neurons in the macaque. Journal of the Neurosciences, 4, 2051-2062.

Desimone, R., & Gross, C.G. (1979). Visual areas in the temporal cortex of the macaque. Brain Research, 178, 363-380.

Desimone, R., Schein, S.J., Moran, J., & Ungerleider, L.G. (1985). Contour, color and shape analysis beyond the striate cortex. Vision Research, 25, 441-452.

Desimone, R., & Schein, S.J. (1987). Visual properties of neurons in Area V4 of the macaque: Sensitivity to stimulus form. Journal of Neurophysiology, 57, 835-868.

Desimone, R., & Ungerleider, L.G. (1986). Multiple visual areas in the caudal superior temporal sulcus of the macaque. Journal of Comparative Neurology, 248, 164-189.

Desimone, R., & Ungerleider, L.G. (1989). Neural mechanisms of visual processing in monkeys. In F. Boller & J. Grafman (Eds.), Handbook of neuropsychology (pp. 267-299). New York: Elsevier Science Publishers.

DeYoe, E.A., & Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. Trends in the Neurosciences, 11, 219-226.

di Lollo, V., & Dixon, P. (1992). Is the icon's worth apples and oranges? Some fruitful thoughts on Loftus, Duncan, and Gehrig (1992). Journal of Experimental Psychology: Human Perception and Performance, 18, 550-555.

DiMattia, B.V., & Kesner, R.P. (1988). The role of the posterior parietal association cortex in the processing of spatial event information. Behavioural Neurosciences, 102, 397-403.

Dreher, B., Fukada, Y., & Rodieck, R.W. (1976). Identification, classification and anatomical segregation of cells with X-like and Y-like properties in the lateral geniculate nucleus of old-world primates. Journal of Physiology, 258, 433-452.

Duffy, C.J., & Wurtz, R.H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. Journal of Neurophysiology, 65, 1329-1345.

Ellis, R., Allport, D.A., Humphreys, G.W., & Collis, J. (1989). Varieties of object constancy. Quarterly Journal of Experimental Psychology, 41A, 775-796.

Farah, M.J. (1984). The neurological basis of mental imagery: A componential analysis. Cognition, 18, 245-272.

Farah, M.J. (1985). Psychophysical evidence for a shared representational medium for mental images and percepts. Journal of Experimental Psychology: General, 114, 91-103.

Farah, M.J. (1990). Visual agnosia: Disorders of object recognition and what they tell us about normal vision. Cambridge, MA: MIT.

Farah, M.J. (1992). Is an object an object an object? Cognitive and neuropsychological investigations of domain specificity in visual object recognition. Current Directions in Psychological Science, 1, 164-169.

Felleman, D.J., & Van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex, 1, 1-47.

Ferrier, D. (1886). The functions of the brain (2nd ed.). New York: Putnam.

Ferrier, D., & Yeo, G.F. (1884). A record of the experiments on the effects of lesions of different regions of the cerebral hemispheres. Philosophical Transactions of the Royal Society of London, 175, 479-564.

Finger, S. (1994). Origins of neuroscience: A history of explorations into brain function. New York: Oxford University Press.

Flechsig, P.E. (1896). Gehirn und Steele. Leipzig: Veit.

Flechsig, P.E. (1920). Anatomies des menschlichen Gehirns und Ruckenmarks. Leipzig: Thieme.

Foote, S.L., Berridge, C.W., Adams, L.M., & Pineda, J.A. (1991). Electrophysiological evidence for the involvement of the locus coeruleus in alerting, orienting, and attending. In C.D. Barnes & O. Pompeiano (Eds.), Progress in brain research (Vol. 88) (pp. 521-532). Amsterdam: Elsevier.

Freud, S. (1953). Zur auffasun der aphasien: Eine kritische studie [On aphasia: A critical study] (E. Stengel, Trans.). New York: International Universities Press. (Original work published in 1891).

Friedman-Hill, S.R., Robertson, L.C., & Treisman, A. (1995). Parietal contributions to visual feature binding: Evidence from a patient with bilateral lesions. Science, 69, 853-855.

Funahashi, S., Bruce, C.J., & Goldman-Rakic, P.S. (1990). Visuospatial coding in primate prefrontal neurons revealed by oculomotor paradigms. Journal of Neurophysiology, 63, 814-831.

Funahashi, S., Bruce, C.J., & Goldman-Rakic, P.S. (1993). Dorsolateral prefrontal lesions and oculomotor delayed-response performance: Evidence for mnemonic "scotomas." Journal of Neuroscience, 13, 1479-1497.

Fuster, J.M. (1995). Memory in the cerebral cortex: An empirical approach to neural networks in the human and nonhuman primate. Cambridge, MA: MIT Press.

Fuster, J.M., & Jervey, J.P. (1981). Inferotemporal neurons distinguish and retain behaviorally relevant features of visual stimuli. Science, 212, 952-955.

Gaffan, D., & Harrison, S. (1989). A comparison of the effects of fornix transection and sulcus principalis ablation upon spatial learning by monkeys. Behavioural Brain Research, 31, 207-220.

Galaburda, A.M. (1993). Neuroanatomical basis of developmental dyslexia. Behavioral Neurology, 11, 161-173.

Galaburda, A.M., & Livingstone, M. (1993). Evidence for a magnocellular defect in developmental dyslexia. Annals of the New York Academy of Science, 682,70-81.

Gall, F.J., & Spurzheim, J.C. (1910). Anatomie et physiologie du systeme nerveux. Paris: Schoell.

Gattass, R., Gross, C.G., & Sandell, J.H. (1981). Visual topography of V2 in the macaque. Journal of Comparative Neurology, 201, 519-539.

Gerhardstein, P.C., & Biederman, I. (1991, May). 3D orientation invariance in visual object recognition. Paper presented at the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, FL.

Ginsburg, A.P. (1986). Spatial filtering and visual form perception. In K.R. Boff (Ed.), Handbook of perception and human performance, Vol. 2: Cognitive processes and performance (pp. 1-41). New York: John Wiley & Sons.

Glickstein, M. (1985). Ferrier's mistake. Trends in the Neurosciences, 8, 341-344.

Goldberg, M.E., & Robinson, D.L. (1977). Visual responses of neurons in inferior parietal lobule: The physiological substrate of attention and neglect. Neurology, 27, 350-362.

Goldberg, M.E., & Robinson, D.L. (1980). The significance of enhanced visual responses in posterior parietal cortex. Behavioral and Brain Sciences, 3, 503-505.

Goldberg, M.E., & Seagraves, M.A. (1987). Visuospatial and motor attention in the monkey. Neuropsychologia, 25, 107-118.

Goldman-Rakic, P.S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In V.B. Mountcastle (Ed.), Handbook of physiology, The Nervous system, Vol. 5 (pp. 373-417). Bethesda, MD: American Physiological Society.

Goldman-Rakic, P.S. (1988). Topography of cognition: Parallel distributed networks in primate association cortex. Annual Review of Neuroscience, 11, 137-156.

Goldman-Rakic, P.S. (1992). Working memory and the mind. Scientific American, 267, 110-117.

Goldstein, K., & Gelb, A. (1918). Psychologische Analysen hirnpathologischer Falle auf Grund von Untersuchungen Hirnverletzter. Z. Gesamte Neurol Psychiatr, 41, 1-142.

Goodale, M.A., & Milner, A.D. (1992). Separate visual pathways for perception and action. Trends in Neurosciences, 15, 20-25.

Goodale, M.A., Milner, A.D., Jakobson, L.S., & Carey, D.P. (1991). A neurological dissociation between perceiving objects and grasping them. Nature, 349, 154-156.

Gouras, P. (1969). Antidromic responses of orthodromically identified ganglion cells in monkey retina. Journal of Physiology, 204, 407-419.

Graham, N. (1980). Spatial-frequency channels in human vision: Detecting edges without edge detectors. In C.S. Harris (Ed.), Visual coding and adaptability. Hillsdale, NJ: Erlbaum.

Greene, R.L. (1992). Human memory: Paradigms and paradoxes. Hillsdale, NJ: Erlbaum.

Gross, C.G. (1973). Visual functions of inferotemporal cortex. In H. Autrum, R. Jung, W.R. Lowenstein, D.M. McKay, & H.L. Teuber (Eds.), Handbook of sensory physiology: Vol. 7, Part 3B (pp. 451-481). Berlin: Springer-Verlag.

Gross, C.G. (1991). Contribution of striate cortex and the superior colliculus to visual function in area MT, the superior temporal polysensory area and inferior temporal cortex. Neuropsychologia, 29, 497-515.

Gross, C.G. (1992). Representation of visual stimuli in inferior temporal cortex. Philosophical Transactions of the Royal Society of London, B335, 3-10.

Gross, C.G. (1994). How inferior temporal cortex became a visual area. Cerebral Cortex, 5, 455-469.

Gross, C.G. (1998). Brain, vision, memory: Tales in the history of neuroscience. Cambridge, MA: MIT Press.

Gross, C.G., Bender, D.B., & Gerstein, G.L. (1979). Activity of inferior temporal neurons in behaving monkeys. Neuropsychology, 17, 215-229.

Gross, C.G., Bender, D.B., & Rocha-Miranda, C.E. (1969). Visual receptive fields of neurons in inferotemporal cortex of the monkey. Science, 166, 1303-1306.

Gross, C.G., Desimone, R., Albright, T.D., & Schwartz, E.L. (1984). Inferior temporal cortex as a visual integration area. In F. Reinoso-Suarez & C. Ajmone-Marsan (Eds.), Cortical integration. New York: Raven Press.

Gross, C.G., & Mishkin, M. (1977). The neural basis of stimulus equivalence across retinal translation. In S. Harnad, R. Doty, J. Jaynes, L. Goldstein, & G. Krauthamer (Eds.), Lateralization in the nervous system. New York: Academic Press.

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, 96-111.

Gross, C.G., & Rodman, H.R. (1992). Inferior temporal cortex: Neuronal properties and connections in adult and infant macaques. In R. Lent (Ed.), The visual system from genesis to maturity (pp. 245-266). Boston: Birkhauser.

Gross, C.G., Rodman, H.R., Gochin, P.M., & Colombo, M. (1993). Inferior temporal cortex as a pattern recognition device. In E.B. Baum (Ed.), Computational Learning and Cognition: Proceedings of the Third NEC Research Symposium. Philadelphia: Siam.

Gross, C.G., Schiller, P.H., Wells, C., & Gerstein, G.L. (1967). Single unit activity in temporal association cortex of the monkey. Journal of Neurophysiology, 30, 833-843.

Gross, C.G., & Weiskrantz, L. (1964). Some changes in behavior produced by lateral frontal lesions in the macaque. In J.M. Warren & K. Akert (Eds.), The frontal granular cortex and behavior (pp. 74-98). New York: McGraw-Hill.

Hawkins, H.L. (1969). Parallel processing in complex visual discrimination. Perception & Psychophysics, 5, 56-64.

Hécaen, H., & de Ajuriaguerra, J. (1954). Balint's syndrome. Brain, 77, 373-400.

Hécaen, H., Penfield, W., Bertrand, C., & Malmo, R. (1956). The syndrome of apractagnosia due to lesions of the minor cerebral hemisphere. Archives of Neurology and Psychiatry, 75, 400-434.

Heilman, K.M., Pandya, D.N., Karol, E.A., & Geschwind, N. (1971). Auditory inattention. Archives of Neurology, 24, 323-325.

Heilman, K.M., & Valenstein, E. (1972). Frontal lobe neglect in man. Neurology, 22, 660-664.

Heilman, K.M., Watson, R.T., & Valenstein, E. (1985). Neglect and related disorders. In K.M. Heilman & E. Valenstein (Eds.), Clinical neuropsychology (2nd Ed.) (pp. 243-293). New York: Oxford University Press.

Heilman, K.M., & Watson, R.T. (1977). Mechanisms underlying the unilateral neglect syndrome. In E.A. Weinstein & R.P. Friedland (Eds.), Advances in Neurology (pp. 93-106). New York: Raven Press.

Held, R. (1968). Dissociation of visual function by deprivation and rearrangement. Psychology Forschung, 31, 338-348.

Hicks, T.P., Lee, B.B., & Vidyasagar, T.R. (1983). The responses of cells in the macaque lateral geniculate nucleus to sinusoidal gratings. Journal of Physiology, 337, 183-200.

Hirst, W., & Volpe, B.T. (1984). Encoding of spatial relations with amnesia. Neuropsychologia, 22, 631-634.

Holmes, E.J., & Gross, C.G. (1984). Stimulus equivalence after inferior temporal lesions in monkeys. Behavioural Neuroscience, 98, 898-901.

Holmes, G. (1918). Disturbances of visual orientation. British Journal of Opthamology, 2, 449-486.

Holmes, G., & Horrax, G. (1919). Disturbances of spatial orientation and visual attention, with loss of stereoscopic vision. Archives of Neurology and Psychiatry, 1, 385-407.

Holmes, G., & Lister, W.T. (1916). Disturbances of vision from cerebral lesions, with special reference to the cortical representation of the macula. Brain, 39, 34-73.

Horel, J.A., Keating, E.G., & Misantone, L.J. (1975). Partial Klüver-Bucy syndrome produced by destroying temporal neocortex or amygdala. Brain Research, 94, 349-359.

Hubel, D.H., & Livingstone, M.S. (1990). Color and contrast sensitivity in the lateral geniculate body and primary visual cortex of the macaque monkey. Journal of Neuroscience, 10, 2223-2237.

Hubel, D.H., & Weisel, T.N. (1965). Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. Journal of Neurophysiology, 18, 229-289.

Humphreys, G.W. (1989). Parallel distributed processing and psychology. In R.G.M. Morris (Ed.), Parallel distributed processing:

Implications for psychology and neuroscience. New York: Oxford University Press.

Humphreys, G.W., & Quinlan, P.T. (1987). Normal and pathological processes in visual object constancy. In G.W. Humphreys & M.J. Riddoch (Eds.), Visual object processing: A cognitive neurological approach. London: Lawrence Erlbaum Associates.

Humphreys, G.W., & Riddoch, M.J. (1987a). The fractionation of visual agnosia. In G.W. Humphreys & M.J. Riddoch (Eds.), Visual object processing: A cognitive neuropsychological approach. London: Lawrence Erlbaum Associates.

Humphreys, G.W., & Riddoch, M.J. (1987b). To See But Not To See: A Case Study of Visual Agnosia. London: Lawrence Erlbaum Associates.

Hursh, J.B. (1939). Conduction velocity and diameter of nerve fibers. American Journal of Physiology, 127, 131-139.

Hyvärinen, J. (1981). Regional distribution of functions in parietal association area 7 of the monkey. Brain Research, 206, 287-303.

Hyvärinen, J. (1982). Posterior parietal lobe of the primate brain. Physiological Reviews, 62, 1060-1129.

Hyvärinen, J., Poranen, A., & Jokinen, Y. (1980). Influence of attentive behavior on neuronal responses to vibration in primary somatosensory cortex of the monkey. Journal of Neurophysiology, 43, 870-882.

Ingle, D. (1967). Two visual mechanisms underlying the behavior of fish. Psychologische Forschung, 31, 44-51.

Irwin, D.E., & Yeomans, J.M. (1991). Duration of visible persistence in relation to stimulus complexity. Perception & Psychophysics, 50, 475-489.

Iwai, E., & Mishkin, M. (1968). Two visual foci in the temporal lobe of monkey. In N. Yoshii, & N.A. Buchwald (Eds.), Neurophysiological basis of learning and memory (pp. 23-33). Osaka: Osaka University Press.

Jackson, J.H. (1932). Case of large cerebral tumor without optic neuritis and with left hemiplegia and imperception. In I. Taylor (Ed.), Selected writings of John Hughlings Jackson, Vol. 2. London: Hodder and Stoughton. (Original work published in 1876).

Jacobson, S., & Trojanowski, J.Q. (1977). Prefrontal granular cortex of the rhesus monkey. I. Intrahemispheric cortical afferents. Brain Research, 132, 209-233.

James, W. (1950). Principles of psychology. New York: Dover. (Original work published in 1890).

Jarred, L.E. (1978). Selective hippocampal lesions: Differential effects on performance by rats of a spatial task with preoperative versus postoperative training. Journal of Comparative Physiological Psychology, 92, 1119-1127.

Jarred, L.E. (1983). Selective hippocampal lesions and behavior: Effects of kainic acid lesions on performance of place and cue tasks. Behavioural Neurosciences, 97, 873-889.

Jarred, L.E. (1986). Selective hippocampal lesions and behavior: Implications for current research and theorizing. In R.L. Isaacson & K. Pribram (Eds.), The hippocampus. New York: Plenum Press.

Jarred, L.E., Okaichi, H., Steward, O., & Goldschmidt, R.B. (1984). On the role of hippocampal connections in the performance of place and cue tasks: Comparisons with damage to hippocampus. Behavioural Neurosciences, 98, 946-954.

Johnson, M.K., & Chalfonte, B.L. (1994). Binding complex memories: The role of reactivation and the hippocampus. In D.L. Schacter & E. Tulving (Eds.), Memory systems 1994 (pp. 311-350). Cambridge, MA: MIT Press.

Jolicoeur, P. (1985). The time to identify disoriented natural objects. Memory and Cognition, 13, 289-303.

Jolicoeur, P. (1990). Orientation congruency effects on the identification of disoriented shapes. Journal of Experimental Psychology: Human Perception and Performance, 16, 351-364.

Jones, E.G., & Powell, T.P.S. (1970). An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain, 93, 793-820.

Jones-Gotman, M. (1986a). Memory for designs: The hippocampal contribution. Neuropsychologia, 24, 193-203.

Jones-Gotman, M. (1986b). Right hippocampal excision impairs learning and recall of a list of abstract designs. Neuropsychologia, 5, 659-670.

Jones-Gotman, M. (1986c). Psychological evaluation: Testing hippocampal function. In J. Engle (Ed.), Surgical treatment of the epilepsies. New York: Raven Press.

Kaplan, E., & Shapley, R.M. (1982). X and Y cells in the lateral geniculate nucleus of macaque monkeys. Journal of Physiology, 330, 125-143.

Kaplan, E.F., Goodglass, H., & Weintraub, S. (1983). The Boston Naming Test (2nd ed.). Philadelphia: Lea & Febiger.

Kesner, R.P. (1989). Retrospective and prospective coding of information: Role of the medial prefrontal cortex. Journal of Experimental Brain Research, 74, 163-167.

Kesner, R.P., & DiMattia, B.V. (1984). Posterior parietal association cortex and hippocampus: Equivalency of mnemonic function in animals and humans. In L.R. Squire & N. Butters (Eds.), Neuropsychology of memory (pp. 385-398). New York: Guilford Press.

Kesner, R.P., Farnsworth, G., & DiMattia, B.V. (1989). Double-dissociation of egocentric and allocentric space following medial prefrontal and parietal cortex lesions in the rat. Behavioural Neurosciences, 103, 907-910.

Klüver, H., & Bucy, P.C. (1938). An analysis of certain effects of bilateral temporal lobectomy in the rhesus monkey, with special reference to "psychic blindness." Journal of Psychology, 5, 33-54.

Klüver, H., & Bucy, P.C. (1939). Preliminary analysis of the temporal lobes in monkeys. Archives of Neurology and Psychiatry, 42, 979-1000.

Kolb, B., & Whishaw, I.Q. (1990). Fundamentals of human neuropsychology (3rd ed.). New York: W.H. Freeman.

Kosslyn, S.M. (1987). Seeing and imaging in the cerebral hemispheres: A computational approach. Psychological Review, 94, 148-175.

Kosslyn, S.M. (1991). A cognitive neuroscience of visual cognition: Further developments. In R.H. Logie & M. Denis (Eds.), Mental images in human cognition (pp. 351-381). Amsterdam: North-Holland.

Kosslyn, S.M., Flynn, R.A., Amsterdam, R.B., & Wang, G. (1990). Components of high-level vision: A cognitive neuroscience analysis and accounts of neurological syndromes. Cognition, 34, 203-277.

Kosslyn, S.M., & Koenig, O. (1992). Wet mind. New York: Maxwell Macmillian Canada, Inc.

Kowalska, D.M., Bachevalier, J., Mishkin, M. (1991). The role of the inferior prefrontal convexity in performance of delayed nonmatching-to-sample. Neuropsychologia, 29, 583-600.

Krieg, W.J.S. (1975). Interpretive atlas of the monkey's brain. Evanston, IL: Brain Books.

Kuypers, H.G.J.M., Szwarcbart, M.K., Mishkin, M., & Rosvold, H.E. (1965). Occipito-temporal cortico-cortical connections in the rhesus monkey. Experimental Neurology, 11, 245-262.

LaMotte, R.H., & Acuna, C. (1978). Defects in accuracy of reaching after removal of posterior parietal cortex in monkeys. Brain Research, 139, 309-326.

Lansdell, H. (1970). Relation of extent of temporal removal to closure and visuomotor factors. Perceptual and Motor Skills, 31, 491-498.

Lashley, K.S. (1948). The mechanism of vision: XVIII. Effects of destroying the visual "associative areas" of the monkey. Genetics and Psychological Monographs, 37, 107-166.

Lashley, K.S. (1950). In search of the engram. Symposium of Experimental Biology, 4, 45-48.

Lawler, K.A., & Cowey, A. (1987). On the role of posterior parietal and prefrontal cortex in visuo-spatial perception and attention. Experimental Brain Research, 65, 695-698.

Lennie, P. (1980). Parallel visual pathways: A review. Vision Research, 20, 561-594.

Leventhal, A.G., Rodieck, R.W., & Dreher, B. (1981). Retinal ganglion cell classes in the old-world monkey: Morphology and central projections. Science, 213, 1139-1142.

Levine, D.N., Warach, J., & Farah, M.J. (1985). Two visual systems in mental imagery: Dissociation of "what" and "where" in imagery disorders due to bilateral posterior cerebral lesions. Neurology, 35, 172-196.

Lewis, F.T. (1923). The significance of the term hippocampus. Journal of Comparative Neurology, 35, 213-230.

Lezak, M.D. (1983). Neuropsychological Assessment (2nd ed.). New York: Oxford University Press.

Lezak, M.D. (1995). Neuropsychological Assessment (3rd ed.). New York: Oxford University Press.

Lhermitte, F., & Signoret, J.L. (1972). Analyse neuropsychologique et différenciation des syndromes amnésiques. Revue Neurologique, 126, 161-178.

Livingstone, M. (1990). Segregation of form, colour, movement and depth in the visual system: Anatomy, physiology, art, illusion. In B. Cohen & I. Bodis-Wollner (Eds.), Vision and the brain (pp. 119-138). New York: Raven Press.

Livingstone, M.S., & Hubel, D.H. (1984). Anatomy and physiology of a color system on the primate visual cortex. Journal of Neuroscience, 4, 309-356.

Livingstone, M.S., & Hubel, D.H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement and depth. Journal of Neuroscience, 7, 3416-3468.

Livingstone, M.S. & Hubel, D.H. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. Science, 240, 740-749.

Livingstone, M.S., Rosen, G.D., Drislane, F.W., & Galaburda, A.M. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. Proceedings of the National Academy of Sciences, 88, 7943.

Lovegrove, W. (1993). Weakness in the transient visual system: A casual factor in dyslexia? Annals of the New York Academy of Science, 682, 57-69.

Lovegrove, W.J., Billing, G., & Slaghuis, W. (1978). Processing of visual contour orientation information in normal and disabled reading children. Cortex, 14, 268-278.

Lovegrove, W.J., Garzia, R.P., & Nicholson, S.B. (1990). Experimental evidence for a transient system deficit in specific reading disability. Journal of the American Optomology Association, 61, 137.

Lovegrove, W., Martin, F., & Slaghuis, W. (1986). A theoretical and experimental case for a residual deficit in specific reading disability. Cognitive Neuropsychology, 3, 225-267.

Lund, J.S. (1988). Anatomical organization of macaque monkey striate visual cortex. Annual Review of Neuroscience, 11, 253-288.

Luria, A.R. (1972). The man with a shattered world. New York: Basic Books.

Luria, A.R. (1973). The working brain. New York: Basic Books.

Lynch, J.C. (1980). The functional organization of posterior parietal association cortex. Behavioral and Brain Sciences, 3, 485-534.

Macko, K.A., Kennedy, C., Sokoloff, L., & Mishkin, M. (1981). Society of Neuroscience Abstracts, 7, 832.

Macko, K.A., Jarvis, C.D., Kennedy, C., Miyaoka, M., Shinohara, M., Sokoloff, L., & Mishkin, M. (1982). Mapping the primate visual system with [2-14C] deoxyglucose. Science, 218, 394-397.

Marr, D. (1982). Vision: A computational investigation into the human representation and processing of visual information. San Francisco: W.H. Freeman.

Marr, D., & Hildreth, E. (1980). Theory of edge detection. Proceedings of the Royal Society of London, B207, 187-217.

Marr, D., & Nishihara, H.K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. Proceedings of the Royal Society of London, B204, 301-328.

Marrocco, R.T., McClurkin, J.W., & Young, R.A. (1982). Spatial summation and conduction latency classification of cells of the lateral geniculate nucelus of macaques. Journal of Neurosciences, 2, 1275-1291.

Martin, F., & Lovegrove, W. (1987). Flicker contrast sensitivity in normal and specifically-disabled readers. Perception, 16, 215-221.

Martin-Elkins, C.L., & Horel, J.A. (1992). Cortical afferents to behaviorally defined regions of the inferior temporal and parahippocampal gyri as demonstrated by WGA-HRP. Journal of Comparative Neurology, 321, 177-192.

Maunsell, J.H.R. (1987). Physiological evidence for two visual subsystems. In L. Vaina (Ed.), Matters of intelligence (pp. 59-87). Dordrecht, Holland: Reidel.

Maunsell, J.H.R., Nealey, T.A., & DePriest, D.D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. Journal of Neuroscience, 10, 3323-3334.

Maunsell, J.H.R., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. Annual Review of Neuroscience, 10, 363-401.

Maunsell, J.H.R., & Van Essen, D.C. (1983a). Anatomical connections of the middle temporal visual area in the macaque monkey and their relationship to a hierarchy of cortical areas. Journal of Neuroscience, 3, 2563-2586.

Maunsell, J.H.R., & Van Essen, D.C. (1983b). Functional properties of neurons in the middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientations. Journal of Neurophysiology, 49, 1148-1167.

McCarthy, R.A., & Warrington, E.K. (1986). Visual associative agnosia: A clinico-anatomical study of a single case. Journal of Neurology, Neurosurgery, and Psychiatry, 49, 1233-1240.

McCarthy, R.A., & Warrington, E.K. (1987). Understanding: A function of short term memory? Brain, 110, 1565-1578.

McCarthy, R.A., & Warrington, E.K. (1990). Object recognition. In Cognitive neuropsychology. New York: Academic Press.

McElree, B., & Dosher, B.A. (1993). Serial retrieval processes in the recovery of order information. Journal of Experimental Psychology: General, 122, 291-315.

McFie, J. (1975). Assessment of organic intellectual impairment. New York: Academic Press.

McFie, J., & Zangwill, O.L. (1960). Visuo-constructive disabilities associated with lesions of the right cerebral hemisphere. Brain, 82, 243-259.

McNaughton, B.L., Barnes, C.A., Meltzer, J., & Sutherland, R.J. (1989). Hippocampal granule cells are necessary for spatial learning but not for spatially-selective pyramidal cell discharge. Experimental Brain Research, 76, 485-496.

McNaughton, B.L., Barnes, C.A., Rao, G., Baldwin, J., & Rasmussen, M. (1986). Long-term enhancement of hippocampal synaptic transmission and the acquisition of spatial information. Journal of Neuroscience, 6, 563-571.

McNaughton, B.L., & Morris, R.G.M. (1987). Hippocampal synaptic enhancement and information storage within a distributed memory system. Trends in the Neurosciences, 10, 408-415.

Meadows, J.C. (1974). The anatomical basis of prosopagnosia. Journal of Neurology, Neurosurgery and Psychiatry, 37, 489-501.

Merigan, W.H., Byrne, C., & Maunsell, J.H.R. (1991). Does primate motion perception depend on the magnocellular pathway? Journal of Neuroscience, 11, 3422-3429.

Merigan, W.H., & Maunsell, J.H.R. (1993). How parallel are the primate visual pathways? Annual Review of Neuroscience, 16, 369-402.

Mesulam, M.-M. (1981). A cortical network for directed attention and unilateral neglect. Annals of Neurology, 10, 309-325.

Mesulam, M.-M., Van Hoesen, G.W., Pandya, D.N., & Geschwind, N. (1977). Limbic and sensory connections of the inferior parietal lobule (area PG) in the rhesus monkey: A study with a new method for horseradish peroxidase histochemistry. Brain Research, 136, 393-414.

Meunier, M., Bachevalier, J., Mishkin, M., & Murray, E.A. (1993). Effects on visual recognition of combined and separate ablations of the entorhinal and perirhinal cortex in rhesus monkeys. Journal of Neuroscience, 13, 5418-5432.

Meyer, D.E., Osman, A.M., Irwin, D.E., & Yantis, S. (1988). Modern mental chronometry. Biological Psychology, 26, 3-67.

Mignard, M., & Malpeli, J.G. (1991). Paths of information flow through visual cortex. Science, 251, 1249-1251.

Mikami, A. & Kubota, K. (1980). Inferotemporal neuronal activities and color discrimination with delay. Brain Research, 182, 65-78.

Mills, C.J., Ablard, K.E., & Brody, L.E. (1993). The Raven's Progressive Matrices: Its usefulness for identifying gifted/talented students. Roeper Review, 15, 183-186.

Milner, A.D., Ockleford, E.M., & Dewar, W. (1977). Visuospatial performance following posterior parietal and lateral frontal lesions in stumptail macaques. Cortex, 13, 350-360.

Milner, B. (1965). Visually-guided maze learning in man: Effects of bilateral hippocampal, bilateral frontal, and unilateral cerebral lesions. Neuropsychologia, 3, 317-338.

Milner, B. (1968). Visual recognition and recall after right temporal lobe excision in man. Neuropsychologia, 6, 191-209.

Milner, B. (1972). Disorders of learning and memory after temporal lobe lesions in man. Clinical Neurosurgery, 19, 421-446.

Milner, P.M. (1989). A cell assembly theory of hippocampal amnesia. Neuropsychologia, 27, 23-30.

Mishkin, M. (1954). Visual discrimination performance following partial ablations of the temporal lobe. II. Ventral surface vs. hippocampus. Journal of Comparative Physiological Psychology, 47, 187-193.

Mishkin, M. (1972). Cortical visual areas and their interaction. In A.G. Karezmar & J.C. Eccles (Eds.), Brain and human behavior. New York: Springer-Verlag.

Mishkin, M. (1978). Memory in monkeys severely impaired by combined but not by separate removal of amygdala and hippocampus, Nature, 273, 297-8.

Mishkin, M. (1982). A memory system in the monkey. Philosophical Transactions of the Royal Society of London, B298, 85-95.

Mishkin, M., & Appenzeller, T. (1987). The anatomy of memory. Scientific American, 256, 80-89.

Mishkin, M., & Delacour, J. (1975). An analysis of short-term visual memory in the monkey. Journal of Experimental Psychology: Animal Behavior Processes, 1, 326-334.

Mishkin, M., Lewis, M.E., & Ungerleider, L.G. (1982). Equivalence of parieto-preoccipital subareas for visuospatial ability in monkeys. Behavioural Brain Research, 6, 41-55.

Mishkin, M., Malamut, B., & Bachevalier, J. (1984). Memories and habits: Two neural systems. In G. Lynch, J.L. McGaugh, & N.M. Weinberger (Eds.), Neurobiology of learning and memory (pp. 65-77). New York: Guilford Press.

Mishkin, M., & Manning, F.J. (1978). Nonspatial memory after selective prefrontal lesions in monkeys. Brain Research, 143, 313-323.

Mishkin, M., & Murray, Elisabeth, A. (1994). Stimulus recognition. Current Opinion in Biology, 4, 200-206.

Mishkin, M., & Underleider, L.G. (1982). Contributions of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. Behavioural Brain Research, 6, 57-77.

Mishkin, M., Ungerleider, L.G., & Macko, K. (1983). Object vision and spatial vision: Two cortical pathways. Trends in the Neurosciences, 6, 414-417.

Mitchell, K.J., Johnson, M.K., Raye, C.L., & D'Esposito, M. (in press). Neural correlates of binding deficits. Cognitive Brain Research.

Morgan, C.T., & Stellar, E. (1950). Physiological psychology (2nd ed.). New York: McGraw-Hill.

Morris, R.G.M. (1983). An attempt to dissociate "spatial-mapping" and "working memory" theories of hippocampal function. In W. Seifert (Ed.), Neurobiology of the hippocampus. New York: Academic Press.

Morris, R.G.M., Garrud, P., Rawlins, J.N.P., & O'Keefe, J. (1982). Place navigation impaired in rats with hippocampal lesions. Nature, 297, 681-683.

Motter, B.C., & Mountcastle, V.B. (1981). The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: Foveal sparing and opponent vector organization. Journal of Neuroscience, 1, 3-26.

Mountcastle, V.B. (1975). The view from within: Pathways to the study of perception. Johns Hopkins Medical Journal, 136, 109-131.

Mountcastle, V.B. (1978). Brain mechanisms for directed attention. Journal of the Royal Society of Medicine, 71, 14-27.

Mountcastle, V.B. (1979). An organizing principle for cerebral function: The unit module and the distributed system. In F.O. Schmitt & F.G. Worden (Eds.), The neurosciences (pp. 21-42). Cambridge, MA: MIT Press.

Mountcastle, V.B., Anderson, R.A., & Motter, B.C. (1982). The influence of attentive fixation upon the excitability of the light-sensitive neurons of the posterior parietal cortex. Journal of Neuroscience, 1, 1218-1235.

Mountcastle, V.B., Lynch, J., Georgopoulos, A., Sakata, H., & Acuña, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. Journal of Neurophysiology, 38, 871-908.

Mountcastle, V.B., Motter, B.C., Steinmetz, M.A., & Duffy, C.J. (1984). Looking and seeing: The visual functions of the parietal lobe. In G. Edelman, W.E. Gall, & W.M. Cowan (Eds.), Dynamic aspects of neocortical function (pp. 160-193). New York: Wiley.

Movshon, J.A., Thompson, I.D., & Tolburst, D.J. (1978a). Spatial summation in the receptive fields of simple cells in the cat's striate cortex. Journal of , 283, 53-77.

Movshon, J.A., Thompson, I.D., & Tolburst, D.J. (1978b). Receptive field organization of complex cells in the cat's striate cortex. Journal of , 283, 79-99.

Movshon, J.A., Thompson, I.D., & Tolburst, D.J. (1978c). Spatial and temporal contrast sensitivity of neurones in area 17 and 18 of the cat's visual cortex. Journal of , 283, 101-120.

Munk, H. (1960). Über die Funktionen der Grosshirnrinde [On functions of the cortex]. In G. von Bonin (Ed. and Trans.), Some papers on the cerebral cortex (pp. 97-117). Springfield, IL: Thomas. (Original work published in 1923).

Nadel, L. The hippocampus and space revisited. Hippocampus, 1, 221-229.

Nebes, R.D., & Briggs, G.G. (1975). Handedness and the retention of visual material. Cortex, 10, 209-214.

Newcombe, F., & Russell, W.R. (1969). Dissociated visual perceptual and spatial deficits in focal lesions of the right hemisphere. Journal of Neurology, Neurosurgery, and Psychiatry, 32, 73-81.

Newsome, W.T., & Paré, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). Journal of Neuroscience, 8, 2201-2211.

Newsome, W.T., Wurtz, R.H., Dürsteler, M.R., & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. Journal of Neuroscience, 5, 825-840.

Newsome, W.T., Wurtz, R.H., & Komatsu, H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. Journal of Neurophysiology, 60, 604-620.

Nissen, M.J. (1985). Accessing features and objects: Is location special? In M.I. Posner, & D.S. Marin (Eds.), Attention and performance XI (pp. 205-219). Hillsdale, NJ: Erlbaum.

Nissen, H.W., Blum, J.S., & Blum, R.A. (1949). Conditional matching behavior in chimpanzee; implications for the comparative study of intelligence. Journal of Comparative & Physiological Psychology, 42, 339-356.

O'Keefe, J. (1983). Spatial memory within and without the hippocampal system. In W. Seifert (Ed.), Neurobiology of the Hippocampus, (pp. 375-403). New York: Academic Press.

O'Keefe, J., & Nadel, L. (1978). The hippocampus as a cognitive map. Oxford, England: Oxford University Press.

O'Leary, U-M., Rusch, K.M., & Guastello, S.J. (1991). Estimating age-stratified WAIS-R IQs from scores on the Raven's Standard Progressive Matrices. Journal of Clinical Psychology, 47, 277-284.

Olton, D.S. (1983). Memory functions and the hippocampus. In W. Seifert (Ed.), Neurobiology of the hippocampus (pp. 335-373). New York: Academic Press.

Olton, D.S., & Pappas, B.C. (1979). Spatial memory and hippocampal system function. Neuropsychologia, 17, 669-681.

Olton, D.S., Becker, J.T., & Handelmann, G.E. (1979). Hippocampus, space and memory. Behavioral and Brain Sciences, 2, 313-365.

Ono, T., Nakamura, K., Fukuda, M., & Tamura, R. (1991). Place recognition responses of neurons in monkey hippocampus. Neuroscience Letters, 121, 194-198.

Ostergaard, A.L., & Davidoff, J.B. (1985). Some effects of color on naming and recognition of objects. Journal of Experimental Psychology: Learning, Memory, and Cognition, 11, 579-587.

Overman, W., Bachevalier, J., Turner, M., Peuster, A. (1992). Object recognition versus object discrimination: Comparison between human infants and infant monkeys. Behavioral Neuroscience, 106, 15-29.

Parkinson, J.K., Murray, E.A., & Mishkin, M. (1988). A selective mnemonic role for the hippocampus in monkeys: Memory for the location of objects. Journal of Neuroscience, 8, 4159-4167.

Passingham, R.E. (1985). Memory for monkeys (macaca mulatta) with lesions in prefrontal cortex. Behavioral Neuroscience, 99, 3-21.

Pasternak, T., Maunsell, J.H.R., Polashenski, W., & Merigan, W.H. (1991). Deficits in global motion perception after MT/MST lesions in a macaque. Investigations in Ophthalmology and Visual Science (Supplement), 32, 824.

Paul, S.M. (1985). The advanced progressive matrices: Normative data for an American university population and an examination of the relationship with Spearman's g. Journal of Experimental Education, 54, 95-100.

Pearson, D.E., & Robinson, J.A. (1985). Visual communication at very low data rates. Proceedings of the IEEE, 73.4.

Perrett, D.I., Rolls, E.T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. Experimental Brain Research, 47, 329-342.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., & Jeeves, M.A. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. Proceedings of the Royal Society London, B223, 293-317.

Perry, V.H., Oehler, R., Cowey, A. (1984). Retinal ganglion cells which project to the dorsal lateral geniculate nucleus in the macaque monkey. Neuroscience, 12, 1101-1123.

Petersen, S.E., Robinson, D.L., & Keys, W. (1985). Pulvinar nuclei of the behaving rhesus monkey: Visual responses and their modulation. Journal of Neurophysiology, 54, 867-886.

Petersen, S.E., Robinson, D.L., & Morris, J.D. (1987). Contributions of the pulvinar to visual spatial attention. Neuropsychologia, 25, 97-105.

Petrides, M., & Iversen, S.D. (1979). Restricted posterior parietal lesions in the rhesus monkey and performance on visuospatial tasks. Brain Research, 161, 63-77.

Pohl, W. (1973). Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys. Journal of Comparative and Physiological Psychology, 82, 227-239.

Posner, M.I. (1992). Attention as a cognitive and neural system. Current Directions in Psychological Science, 1, 11-14.

Posner, M.I., & Cohen, Y. (1984). Components of performance. In H. Bouma & D. Bouwhuis (Eds.), Attention and performance (pp. 531-556). Hillsdale, NJ: Erlbaum.

Posner, M.I., & Mitchell, R. (1967). Chronometric analysis of classification. Psychological Review, 74, 392-409.

Posner, M.I., & Petersen, S.E. (1990). The attention system of the human brain. Annual Review of Neuroscience, 13, 25-42.

Posner, M.I., Petersen, S.E., Fox, P.T., & Raichle, M.E. (1988). Localization of cognitive operations in the human brain. Science, 240, 1627-1631.

Posner, M.I., & Raichle, M.E. (1994). Images of mind. New York: Scientific American Library.

Posner, M.I., Walker, J.A., Friedrich, F.A., & Rafal, R.D. (1984). Effects of parietal lobe injury on covert orienting of visual attention. Journal of Neuroscience, 4, 1863-1874.

Posner, M.I., Walker, J.A., Friedrich, F.A., & Rafal, R.D. (1987). How do the parietal lobes direct covert attention. Neuropsychologia, 25, 135-145.

Pribram, K.H., & Bagshaw, M. (1953). Further analysis of the temporal lobe syndrome utilizing fronto-temporal ablations. Journal of Comparative Neurology, 99, 347-375.

Price, C.J., & Humphreys, G.W. (1989). The effects of surface detail on object categorisation and naming. Quarterly Journal of Experimental Psychology, 41A, 797-828.

Quintana, J., & Fuster, J.M. (1992). Mnemonic and predictive functions of cortical neurons in a memory task. NeuroReport, 3, 721-724.

Quintana, J., & Fuster, J.M. (1993). Spatial and temporal factors in the role of prefrontal and parietal cortex in visuomotor integration. Cerebral Cortex, 3, 122-132.

Quintana, J., Fuster, J.M., & Yajeya, J. (1989). Effects of cooling parietal cortex on prefrontal units in delay tasks. Brain Research, 503, 100-110.

Rao, S.M., Hammeke, T.A., McQuillen, M.P., et al. (1984). Memory disturbance in chronic progressive multiple sclerosis. Archives of Neurology, 41, 625-631.

Ratcliff, G., & Davies-Jones, G.A.B. (1972). Defective visual localization in focal brain wounds. Brain, 95, 49-60.

Raven, J.C., Court, J.H., & Raven, J. (1976). Manual for Raven's Progressive Matrices. London: H.K. Lewis.

Raven, J., Raven, J.C., & Court, J.H. (1976). General Overview (1995 ed.). Oxford: Oxford Psychologists Press Ltd.

Richmond, B.J., & Sato, T. (1982). Visual responses of inferior temporal neurons are modified by attention to different stimulus dimensions. Society of Neuroscience Abstracts, 8, 812.

Richmond, B.J., Sato, T., & Wurtz, R.H. (1982). Behavioral and visual modulation of visual responses of single cells in monkey inferior temporal cortex. Investigations in Ophthalmological Vision Sciences, Supplement 21, 238.

Richmond, B.J., & Wurtz, R.H. (1982). Inferotemporal cortex in awake monkeys. In A.R. Morrison & P.L. Strick (Eds.), Changing concepts of the nervous system. New York: Academic Press.

Richmond, B.J., Wurtz, R.H., & Sato, T. (1983). Visual responses of inferior temporal neurons in awake rhesus monkey. Journal of Neurophysiology, 50, 1415-1432.

Richmond, B.J., Optican, L.M., Podel, M., & Spitzer, H. (1987). Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. Journal of Neurophysiology, 57, 132-162.

Riddoch, M.J., & Humphreys, G.W. (1987a). A case of integrative visual agnosia. Brain, 110, 1431-1461.

Riddoch, M.J., & Humphreys, G.W. (1987b). Picture naming. In G.W. Humphreys & M.J. Riddoch (Eds.), Visual object processing: A cognitive neuropsychological approach (pp. 107-142). Hillsdale, NJ: Lawrence Erlbaum.

Ridley, R.M., & Ettlinger, G. (1973). Visual discrimination performance in the monkey: The activity of single cells in infero-temporal cortex. Brain Research, 55, 179-182.

Robinson, D.L., & Rugg, M.D. (1988). Latencies of visually responsive neurons in various regions of the rhesus monkey brain and their relation to human visual responses. Biological Psychology, 26, 111-116.

Rocha-Miranda, C.E., Bender, D.B., Gross, C.G., & Mishkin, M. (1975). Visual activation of neurons in inferotemporal cortex depends on striate cortex and forebrain commissures. Journal of Neurophysiology, 38, 475-491.

Rockland, K.S., & Pandya, D.N. (1981). Cortical connections of the occipital lobe in the rhesus monkey: Interconnections between areas 17, 18, 19 and the superior temporal gyrus. Brain Research, 212, 249-270.

Rodman, H.R. (1994). Development of inferior temporal cortex in the monkey. Cerebral Cortex, 4, 484-498.

Rolls, E.T. (1989). Parallel distributed processing in the brain: Implications for the functional architecture of neuronal networks in the hippocampus. In R.G.M. Morris (Ed.), Parallel distributed processing: Implications for psychology and neurobiology (pp. 286-388). Oxford: Clarendon Press.

Rolls, E.T. (1990). Functions of neuronal networks in the hippocampus and of backprojections in the cerebral cortex in memory. In J.L. McGaugh, N.M. Weinberger, & G. Lynch (Eds.), Brain organization and memory: Cells, systems, and circuits. New York: Oxford University Press.

Rolls, E.T., Baylis, G.C., & Leonard, C.M. (1977). Role of low and high spatial frequencies in the face-selective responses of neurons in the cortex in the superior temporal sulcus in the monkey. Vision Research, 25, 1021-1035.

Rolls, E.T., Miyashita, Y., Cahusac, P.M.B., Kesner, R.P., Niki, H., Feigenbaum, J., & Bach, L. (1989). Hippocampal neurons in the monkey with activity related to the place in which a stimulus is shown. Journal of Neuroscience, 9, 1835-1844.

Ruch, T.C., Fulton, J.F., & German, W.J. (1938). Sensory discrimination in monkey, chimpanzee and man after lesions of the parietal lobe. Archives of Neurology and Psychiatry, 39, 919-938.

Rueckl, J.G., Cave, K.R., & Kosslyn, S.M. (1989). Why are "what" and "where" processed by separate cortical systems? A computational investigation. Journal of Cognitive Neuroscience, 1, 171-186.

Rupniak, N.M.J., & Gaffan, D. (1987). Monkey hippocampus and learning about spatially directed movements. Journal of Neuroscience, 7, 2331-2337.

Sacks, O. (1995). An anthropologist on mars: Seven paradoxical tales. New York: Alfred A. Knopf.

Sagi, D., & Julesz, B. (1985). "Where" and "what" in vision. Science, 228, 1217-1219.

Saito, H., Yukio, M., Tanaka, K., Hikosaka, K., Fukada, Y., & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. Journal of Neuroscience, 6, 145-157.

Sakai, K., & Miyashita, Y. (1993). Memory and imagery in the temporal lobe. Current Opinion in Neurobiology, 3, 166-170.

Sakai, K., Naya, Y., & Miyashita, Y. (1994). Neuronal tuning and associative mechanisms in form representation. Learning and Memory, 1, 83-105.

Sakata, H., Shibutani, H., & Kawano, K. (1980). Spatial properties of visual fixation neurons in posterior parietal association cortex of the monkey. Journal of Neurophysiology, 43, 1654-1672.

Sakata, H., Shibutani, H., Kawano, K., & Harrington, T. (1985). Neuronal mechanisms of space vision in the parietal association cortex of the monkey. Vision Research, 25, 453-464.

Saraga, E., & Shallice, T. (1973). Parallel processing of the attributes of single stimuli. Perception & Psychophysics, 13, 261-270.

Sato, T., Kawamura, T., & Iwai, E. (1980). Responsiveness of inferotemporal single units to visual pattern stimuli in monkeys performing discrimination. Experimental Brain Research, 38, 313-319.

Schiller, P.H. (1993). Parallel pathways in the visual system. In B. Gulyás, D. Ottoson, & P.E. Roland (Eds.), Functional organisation of the human visual cortex (pp. 43-58). New York: Pergamon.

Schiller, P.H., & Lee, K. (1991). The role of the primate extrastriate area V4 in vision. Science, 251, 1251-1253.

Schiller, P.H., & Logothetis, N.K. (1990). The color-opponent and broad-band channels of the primate visual system. Trends in the Neurosciences, 13, 392-398.

Schiller, P.H., Logothetis, N.K., & Charles, E.R. (1990a). Role of the color-opponent and broad-band channels in vision. Visual Neuroscience, 5, 321-346.

Schiller, P.H., Logothetis, N.K., & Charles, E.R. (1990b). Functions of the colour-opponent and broad-band channels of the visual system. Nature, 343, 68-70.

Schiller, P.H., Logothetis, N.K., & Charles, E.R. (1991). Parallel pathways in the visual system: Their role in perception at isoluminance. Neuropsychologia, 29, 433-441.

Schiller, P.H., & Malpeli, J.G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. Journal of Neurophysiology, 41, 788-797.

Schiller, P.H., & Stryker, M. (1972). Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. Journal of Neurophysiology, 35, 915-924.

Schwartz, S.H., & Loop, M.S. (1983). Differences in temporal appearance associated with activity in the chromatic and achromatic systems. Perception & Psychophysics, 33, 388-390.

Schneider, G.E. (1969). Two visual systems: Brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. Science, 163, 895-902.

Seltzer, B. & Pandya, D.N. (1978). Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. Brain Research, 149, 1-24.

Seltzer, B. & Pandya, D.N. (1984). Further observations on parieto-temporal connections in the rhesus monkey. Experimental Brain Research, 55, 301-312.

Sergent, J. (1988). Face perception and the right hemisphere. In L. Weiskrantz (Ed.), Thought without language. Oxford: Oxford University Press.

Shallice, T. (1985). Impairments of semantic processing: Multiple dissociations. In M. Coltheart, R. Job, & G. Sartori (Eds.), The cognitive neuropsychology of language. London: Erlbaum.

Shapley, R., Kaplan, E., Soodak, R. (1981). Spatial summation and contrast sensitivity of X and Y cells in the lateral geniculate nucleus of the macaque. Nature, 292, 543-545.

Shibutani, H., Sakata, H., & Hyvärinen, J. (1984). Saccade and blinking evoked by microstimulation of the posterior parietal association cortex of the monkey. Experimental Brain Research, 55, 1-8.

Siegel, R.M., & Andersen, R.A. (1986). Motion perceptual deficits following ibotenic acide lesions of the middle temporal area (MT) in the behaving rhesus monkey. Society of Neuroscience Abstracts, 12, 1183.

Silverman, S.E., Trick, G.L., & Hart, W.M., Jr. (1990). Motion perception is abnormal in primary open-angle glaucoma and ocular hypertension. Investigative Ophthalmology & Visual Science, 31, 722-729.

Sivan, A.B. (1992). Benton Visual Retention Test (5th ed.). San Antonio: The Psychological Corporation.

Smith, M.L. (1988). Recall of spatial location by the amnesic patient H.M. Brain and Cognition, 7, 178-183.

Smith, M.L., & Milner, B. (1981). The role of the right hippocampus in the recall of spatial location. Neuropsychologia, 19, 781-793.

Snodgrass, J.G., & Vanderwort, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. Journal of Experimental Psychology: Human Learning and Memory, 6, 174-215.

Snowden, R.J., Treue, S., Erickson, R.G., & Andersen, R.A. (1991). The response of area MT and V1 neurons to transparent motion. Journal of Neuroscience, 11, 2768-2785.

Solms, M., Kaplan-Solms, K., & Brown, J.W. (1996). Wilbrand's case of "mind-blindness." In C. Code, & C.W. Wallesch (Eds.), Classic cases in neuropsychology, (pp.89-110). Hove, England: Erlbaum.

Sparks, D.L., & Mays, L.E. (1980). Movement of saccade-related burst neurons in the monkey superior colliculus. Brain Research, 190, 39-50.

Squire, L.R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. Psychological Review, 99, 195-231.

Squire, L.R., & Zola-Morgan, S. (1988). Memory: Brain systems and behavior. Trends in the Neurosciences, 11, 170-175.

Squire, L.R., & Cave, C.B. (1991). The hippocampus, memory, and space. Hippocampus, 1, 269-271.

Stanton, G.B., Cruce, W.L.R., Goldberg, M.E., & Robinson, D.L. (1977). Some ipsilateral projections to areas PF and PG of the inferior parietal lobule in monkeys. Neuroscience Letters, 6, 243-250.

Stein, J.F. (1978). Effects of parietal lobe cooling on manipulative behavior in the conscious monkey. In G. Gordon (Eds.), The mechanisms of recognition of objects by manipulation: A multidisciplinary approach (pp. 79-90). Oxford: Pergamon Press.

Sugishita, M., Ettlinger, G., & Ridley, R.M. (1978). Disturbance of cage finding in the monkey. Cortex, 14, 431-438.

Sutherland, R.J., & Rudy, J.W. (1989). Configural association theory: The role of the hippocampal formation in learning, memory, and amnesia. Psychobiology, 17, 129-144.

Suzuki, W.A., & Amaral, D.G. (1994). The perirhinal and parahippocampal cortices of the monkey: Cortical afferents. Journal of Comparative Neurology,

Tanaka, K., Hikosaka, K., Saito, J.-A., Yukie, M., Fukada, Y., & Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. Journal of Neuroscience, 6, 134-144.

Tanaka, K., Saito, H.-A., Fukada, Y, & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. Journal of Neurophysiology, 66, 170-189.

Teyler, T.J., & DiScenna, P. (1986). The hippocampal memory indexing theory. Behavioural Neurosciences, 100, 147-154.

Treisman, A. (1992). Perceiving and re-perceiving objects. American Psychologist, 47, 862-875.

Treisman, A.M., & Gormican, S. (1988). Feature analysis in early vision: Evidence from search asymmetries. Psychological Review, 95, 15-48.

Treisman, A., & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. Cognitive Psychology, 14, 107-141.

Trevarthen, C.B. (1968). Two mechanisms of vision in primates. Psychology Forschung, 31, 299-337.

Trojanowski, J.Q., & Jacobson, S. (1976). A real and laminar distribution of some pulvinar cortical efferents in rhesus monkey. Journal of Comparative Neurology, 169, 371-392.

Tsal, Y., & Lavie, N. (1988). Attending to color and shape: The special role of location in selective visual processing. Perception & Psychophysics, 44, 15-21.

Tsal, Y., & Lavie, N. (1993). Location dominance in attending to color and shape. Journal of Experimental Psychology: Human Perception and Performance, 19, 131-139.

Turner, J.A.B. (1990). Visual perception in normal aging and Alzheimer's disease: Influences on picture naming and recognition. Unpublished doctoral dissertation, Case Western Reserve University, Ohio.

Ungerleider, L.G. (1985). The corticocortical pathways for object recognition and spatial perception. In C. Chagas, R. Gattas, & C. Gross (Eds.), Pattern recognition mechanisms (pp. 21-37). Vatican City: Pontifical Academy of Sciences.

Ungerleider, L.G., & Brody, B.A. (1977). Extrapersonal spatial orientation: The role of posterior parietal, anterior frontal, and inferotemporal cortex. Experimental Neurology, 56, 265-280.

Ungerleider, L.G., & Desimone, R. (1986). Cortical connections of visual area MT in the macaque. Journal of Comparative Neurology, 248, 190-222.

Ungerleider, L.G., & Mishkin, M. (1982). Two cortical visual systems. In D.J. Ingle, M.A. Goodale, & R.J.W. Mansfield (Eds.), Analysis of visual behavior (pp. 549-580). Cambridge, MA: MIT.

Van Essen, D.C., Felleman, D.J., Deyoe, E.A., & Knierim, J.J. (1993). Probing the primate visual cortex: Pathways and perspectives. In B. Gulyás, D. Ottoson, & P.E. Roland. Functional organisation of the human visual cortex (pp. 29-41) New York: Pergamon.

Van Essen, D.C., & Maunsell, J.H. (1983). Hierarchical organization and functional streams in the visual cortex. Trends in Neurosciences, 6, 370-375.

Van Gorp, W.G., Satz, P., Kiersch, M.E., & Henry, R. (1986). Normative data on the Boston Naming Test for a group of normal older adults. Journal of Clinical and Experimental Neuropsychology, 8, 702-705.

Warrington, E.K. (1982). Neuropsychological studies of object recognition. Proceedings, Royal Society of London, Series B, 298, 15-33.

Warrington, E.K., & James, M. (1988). Visual apperceptive agnosia: A clinico-anatomical study of three cases. Cortex, 24, 13-32.

Warrington, E.K., & Shallice, T. (1979). Semantic access dyslexia. Brain, 102, 43-63.

Warrington, E.K., & Taylor, A.M. (1973). Contribution of the right parietal lobe to object recognition. Cortex, 9, 152-164.

Wasserstein, J., Zappulla, R., Rosen, J., Gerstman, L., & Rock, D. (1987). In search of closure: Participantive contour illusions, gestalt completion tests, and implications. Brain and Cognition, 6, 1-14.

Watson, R.T., Miller, B.D., & Heilman, K.M. (1978). Nonsensory neglect. Annals of Neurology, 3, 505-508.

Watt, R.J. (1988). Visual processing: Computational, psychophysical and cognitive research. London, England: Lawrence Erlbaum Associates.

Watt, R.J., & Morgan, M.J. (1985). A theory of the primitive spatial code in human vision. Vision Research, 25, 1661-1674.

Weber, J.T., & Yin, T.C.T. (1984). Subcortical projections of the inferior parietal cortex (area 7) in the stump-tailed monkey. Journal of Comparative Neurology, 224, 206-230.

Webster, M.J., Bachevalier, J., & Ungerleider, L.G. (1994). Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. Cerebral Cortex, 4, 470-483.

Wechsler, D. (1981). Wechsler Adult Intelligence Scale - Revised. New York: Psychological Corporation.

Weiskrantz, L. (1987). Neuroanatomy of memory and amnesia: A case for multiple memory systems. Human Neurobiology, 6, 93-105.

Whiteley, A.M., & Warrington, E.K. (1977). Prosopagnosia: A clinical, psychological, and anatomical study of three patients. Journal of Neurology, Neurosurgery and Psychiatry, 40, 395-403.

Wible, C.G., Shiben, J.R., & Olton, D.S. (1991). Hippocampus, fimbrialfornit, amygdala and memory: Object discrimination in rats. Behavioural Neurosciences, Wiesel, T.N., & Hubel, D.H. (1966). Spatial and chromatic interactions in the lateral geniculate body of the rhesus monkey. Journal of Neurophysiology, 29, 1115-1156.

Williams, M.C., Breitmeyer, B.G., & Lovegrove, W.J. (1991). Metacontrast with masks varying in spatial frequency and wavelength. Vision Research, 31, 2017-2023.

Wilson, H.R. (1980). Spatiotemporal characterization of a transient mechanism in the human visual system. Vision Research, 20, 443-452.

Wilson, M., & DeBauche, B.A. (1981). Inferotemporal cortex and categorical perception of visual stimuli by monkeys. Neuropsychologia, 19, 29-41.

Wilson, F.A.W., O Scalaidhe, S.P., & Goldman-Rakic, P.S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. Science, 260, 1955-1958.

Wilson, M., Stamm, J.S., & Pribram, K.H. (1960). Deficits in roughness discrimination after posterior parietal lesions in monkeys. Journal of Comparative Physiological Psychology, 53, 535-539.

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, 899-911.

Wurtz, R.H., Goldberg, M.E., & Robinson, D.L. (1980). Behavioral modulation of visual responses in the monkey: Stimulus selection for attention and movement. In J. Sprague & A. Epstein (Eds.), Progress in psychobiology and physiological psychology (pp. 43-83). New York: Academic Press.

Wurtz, R.H., Goldberg, M.E., & Robinson, D.L. (1982). Brain mechanisms of visual attention. Scientific American, 246, 124-135.

Yamasaki, D.S., & Wurtz, R.H. (1991). Recovery of function after lesions in the superior temporal sulcus in the monkey. Journal of Neurophysiology, 66, 651-673.

Zeki, S.M. (1975). The functional organization of projections from striate to prestriate visual cortex in the rhesus monkey, 40, 591-600.

Zeki, S.M. (1980). The representation of colours in the cerebral cortex. Nature, 284, 412-418.

Zeki, S.M. (1989, July). Functional specialisation and multi-stage integration in the visual cortex. Paper presented at the Fifth International Symposium of the Northern Eye Institute, Bristol, UK.

Zeki, S.M. (1990). Colour vision and functional specialisation in the visual cortex. Discussions in Neuroscience, 6, 7-64.

Zeki, S.M. (1992). The visual image in mind and brain. Scientific American, 267, 68-76.

Zihl, J., & von Cramon, D. (1979). The contribution of the "second" visual system to directed visual attention in man. Brain, 102, 835-856.

Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. Brain, 106, 313-340.

Zipser, D. (1985). A computational model of hippocampal place fields. Behavioral Neuroscience, 99, 1006-1018.

Zipser, D. (1991). Recurrent network model of the neural mechanism of short-term active memory. Neural Computation, 3, 178-192.

Zipser, D., & Andersen, R.A. (1988). A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. Nature, 331, 679-684.

Zola-Morgan, S., Squire, L.R., & Amaral, D.G. (1986). Human amnesia and the medial temporal region: Enduring memory impairment

following a bilateral lesion limited to field CA1 of the hippocampus. Journal of Neuroscience, 6, 2950-2957.

Zola-Morgan, S., Squire, L.R., Amaral, D.G., & Suzuki, W.A. (1989). Lesions of perirhinal and parahippocampal cortex that spare the amygdala and hippocampal formation produce severe memory impairment. Journal of Neuroscience, 9, 4355-4370.