Single Trial EEG and MEG Recorded During Spontaneous Reversals of the Necker Cube:

A Non-linear Distributed Systems Approach

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Single Trial EEG and MEG Recorded During

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Abstract

According to Edelman's (1989) theory of neuronal group selection (TNGS), reentrant cortical connections are proposed as the basis for processing complex information. Reentry is not simply feedback, but parallel signalling in the time domain between spatially disparate maps made of groups of neurons. These connections can be reciprocal or from a geometric range, and can be convergent or divergent. Reentry has variable properties existing in time and space that liken it more to a process of correlation between distributed systems. Processing of a Necker cube is an interesting example of complex visual information processing since the perceptual change occurs spontaneously while the stimulus remains constant. Based on the reentrant cortical integration (RCI) model, it would be expected that during spontaneous reversals of the Necker cube, increased correlations between distributed non-linear systems would be present in cortex. The purpose of this thesis then, is to determine if patterns of EEG and MEG activity during reversals are different than processing a figure in two dimensions. Since the correlation patterns are possibly complex and non-linear, a generalised regression neural network (GRNN) was used to classify the two groups. The thesis included an electroencephalography EEG (n=5) and a magnetoencephalography (MEG) phase (n=5). The experimental questions posed were 1) Can non-linear cortical patterns, present during perceptual reversals be classified as different compared to a two-dimensional figure? and 2) Are patterns of correlated cortical activity significantly higher in the Necker cube reversal condition? One second single trial EEG and MEG records were analyzed using the GRNN. A model based on cortico-cortical connections was developed to assess the level of correlations from a subset in each condition. The GRNN significantly classified Necker cube reversal single trials as different compared to perception of a two dimensional figure for both EEG and MEG. Significantly higher patterns of correlations were also observed in the Necker cube reversal condition in both the EEG and MEG phases. The results are interpreted to be in agreement with the RCI model. Non-linear patterns unique to perceptual reversals and correlations of distributed neuronal groups may be fundamental to visual information processing.

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Introduction

Ambiguous figures have attracted the attention of scientists for over a century . They warrant interest because their physical properties remain constant, while the perception of the figure changes. Necker first described an ambiguous figure which eventually appropriated his name, as an optical observation which "has often occurred to me while examining figures and engraved plates of crystalline forms: I mean a sudden and involuntary change in the apparent position of a crystal or solid" figure, (Necker 1832, p.336). Since first descriptions, researchers from a variety of fields have used the Necker cube as a perceptual tool, with the hope of discovering why the brain alters perception of a constant stimulus, and perhaps more importantly, how it allows for this perceptual vacillation to occur.

Psychophysicists have used the Necker cube in attempts to discover different aspects of how the brain processes complex visual information. Specifically, the research has been directed towards determining the nature of how new perceptions are formed from ambiguous or incomplete stimuli. Various theories have been generated based on this research, however, rarely are these theories linked to actual experimental evidence of brain function. The limited number of studies that do attempt to address the question of how the brain functions during reversals of ambiguous figures, tend to modify the stimulus, therefore altering the phenomenon that occurs continually during perception. An experiment that monitors brain function during spontaneous reversals of an ambiguous figure is required to address this question properly.

Recently, a theory of brain function has evolved from research on the cat visual system that offers a fresh perspective on how complex visual information processing occurs in mammalian cortex. The theory proposes that during visual information processing, local neuronal groups oscillate synchronously, and eventually recruit distal neuronal groups that link similar information into a comparable oscillatory pattern. Activity of this nature recorded at cortex, is purported to be

one of the mechanisms responsible for the binding of discrete segments of visual information such as depth and line orientation into perceptual wholes (Gray & Singer, 1989). Cellular models have been proposed to explain this synchronous phenomenon, though to oscillate in the gamma band (approximately between 30-70 Hz) (Llinas, 1989). However, some models extend beyond the standard descriptions of gamma band activity and discuss a functional model that incorporates correlations of cortical and subcortical sites simultaneously, through a process termed reentry (Edelman, 1989). Therefore, this newly developed theory may provide insight into the neuronal processes that occur during complex visual information processing. The Necker cube may be a useful tool to elicit the attributes of sensory feature binding, since newly formed perceptions are constantly being produced. Before a full treatment of the theoretical perspectives however, detailed coverage of stimulus properties should provide an appropriate foundation for the discussion to follow.

Properties of the Necker Cube

Necker cube properties have been studied by perception researchers since Necker's first report in 1832. In the article, he discussed specific figures and crystalline forms as having properties that when " looking repeatedly at the same figure, you will perceive that at times the

> apparent position of the rhomboid is so changed that the solid angle X will appear the nearest, and the solid angle A will appear the furthest; and that the (near face) will recede behind the (far face), which will come forward; which effect gives to the whole solid a quite contrary apparent inclination. I have been a long time at a loss to understand the reason of the apparent accidental and involuntary change which I always witnessed in all sorts of forms in books on crystallography. The only thing I could observe was, that at the time the change took place, a particular sensation was felt in the eye (for it takes place as well when seen with only one eye, as with both eyes), which proved to me that it was an optical, and not merely as I had first thought a mental, operation which was performed " (Necker 1832, p.336) .

Since then, much has been learned about the perceptual properties of the Necker cube, and how human behaviour is patterned during reversals of the figure, including characteristic eye movements. Eye movements immediately before or after cube reversals have been studied to determine whether specific patterns of eye movement are correlated to reversal onset. In 1978, Ellis and Stark used eye scanning data to investigate the underlying cognitive processes used to generate 3-D interpretations of the cube. Their methodology included analysis of the loci and

duration of fixations during perceived reversals. Experimental subjects showed a significant increase in fixation duration at the onset of the cube's reversal when compared to the control subjects. During non-directed viewing, the subject's gaze is attracted to cube loci interpreted as external corners, therefore the subject's scanning behaviour may be described as shifting back and forth diagonally between temporally changing externally appearing corners (Ellis & Stark, 1978).

Complementary results were reported by Kawabata (1986) who hypothesized that the two vertices (points where three lines intersect) in the central area of the Necker cube are determinants of which perception will occur, whereas other vertices are not important in this process. In other words, the three dimensional interpretation of the Necker cube that occurs may be decided via attention to local vertex features. The results suggest that the specific three-dimensional depth perceived is determined by which angle is attended at a vertex. If attention is paid to an angle composed of neighbouring lines, this angle is perceived as the near surface when attention is paid to the vertex angle (Kawabata, 1986). However, Scotto, Olivia and Tuccio (1990) observed that eye positioning was not the only important variable in the determination of subsequent reversal rates. The purpose of their study was to determine whether differences in reversal rates would occur during conditions where the eyes were voluntarily stabilised versus a condition allowing spontaneous eye movements. A decrease in the frequency of saccadic eye movements and an increase in reversal rates was observed during imperfectly stabilised viewing versus unrestricted viewing (Scotto et al., 1990), suggesting that the condition where eyes are allowed to move spontaneously does not consistently guarantee the maximum number of reversals. Therefore, the studies on eye movements during Necker cube perception are informative as to the nature of their effects on reversal rates and tri-dimensionality. They are also important in that they warn of pervasive eye movement related contaminants of EEG and MEG that occur during spontaneous reversals.

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In addition to eye movements, changes in luminance have been reported to affect spontaneous Necker cube reversals. Babich and Standing (1981) measured the effects of changes in luminance using a two adjacent Necker cube stimulus. When the luminance was constant for either cube, adjacent cubes reverse in synchrony. However, when luminance for either cube differed, the reversals become asynchronous (Babich & Standing, 1981). The effects of extreme variance of luminance was studied by Riani, Olivia, Selis, Ciurlo, and Rossi (1984). The authors were interested in answering the question of whether perceptual alteration of the Necker cube would occur when luminance was altered to where only a rod population is responsible for perception, or conversely, when only the cones were responsible for the perception. The results indicate that perceptual alteration is not influenced by a variation in the stimulus luminance over a broad range of values, ranging from inactivation of the rods to inactivation of the cones in retina (Riani et al., 1984). Therefore, limited support exists for the notion that changes in luminance affect Necker cube perception. To avoid possible confounds in the experiment, however, attempts to maintain luminance levels constant should be considered.

Attentional states have been reported to modify perceptions of Necker cube reversals. Reisberg and O'Shaunessy (1984) reported that during a distraction task, two significant effects on the Necker cube reversal rate were found. First, the initial reversal of the figure was delayed and second, fewer reversals were reported compared to a condition with no distraction. The authors conclude that attention modulates reversal rates of the Necker cube (Reisberg & O'Shaunessy, 1984). Some investigators have indirectly reported the effects of attention on reversal rates via studying age effects on perception of ambiguous figures. Camp, Markley and Danielson (1982) were interested in replicating previous results that suggested elderly individuals residing in a retirement homes had fewer reversals compared to a group of younger adults. The findings of their partial replication (partial because they used an all female sample) were interpreted to mean that middle aged women had slightly more spontaneous reversals than either the young women or an elderly group of women not residing in a retirement home (Camp et al., 1982), which conflicted with the results of the previous study. The opposing results obtained using elderly

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subjects seem to depend on whether the subject resided in the community or in a retirement home, and therefore, the question of whether cognitive decline has an effect on Necker cube perception remains open to interpretation.

In fact, it does appear that a decrease in cognitive functioning affects perception of Necker cube reversals. Interesting results are reported by Cohen (1959) who studied reversal rates in brain injured populations using a double Necker cube stimulus. Compared to control subjects, head-injured individuals reported fewer reversals of the Necker cube and the Rubin Vase. Within the brain injured population, those with right hemisphere lesions reported fewer reversals that did those with left hemisphere damage. In frontal lobe damaged populations, no difference was reported between individuals with right or left frontal lobe damage, unless the damage was bilateral, where an increase in reversal rates was observed (Teuber, 1964; Yacorzynski, 1965 in Lezak, 1976, p. 294), indicating that inhibition and control of reversal rates may involve frontal lobe functioning.

Therefore, attentional status of the subject (and whether or not he or she is head injured) should be considered when designing an experiment that employs reversible figures. Another consideration thought to have modulating effects on subject attention is the instructions given to the subject prior to commencement of the experiment. When the instructions to the subject omitted explicit statements about the ambiguous properties of the Necker cube, subjects were often unaware of the figure's reversible properties until they were explicitly stated (Girgus, Rock and Egatz, 1977). Exposure to ambiguous figures is also believed to affect subsequent reversal rates. When subjects are instructed to attend to a particular facet of the figure during an adaptation phase, subsequent reversals are influenced by a bias toward perception of the opponent perception (Schulman, 1993). However, differences in the pattern of exposure in massed practice or distributed practice sessions does not appear to have an effect on ensuing perceptions (Schellinger & Beer, 1993).

Accordingly, several factors must be considered when entering into research using ambiguous figures. In a paradigm where spontaneous eye movements are allowed and encouraged in order to facilitate a spontaneous reversal process, eye movement artifact in the EEG and MEG must be considered prior to analysis. Luminance should be maintained at constant levels and attempts should be made to maintain a constant level of attention in the subject. As with most research endeavours, instructions to the subject should be consistent across subjects, since variations could result in varied perceptions of the figure.

The studies discussed above have discovered many important stimulus properties of the Necker cube, however, what can research of this nature reveal about the underlying neuronal organization which allows for ambiguities in perception? One of the earliest and most popular theories stems from Gestalt principles that focus on passive mechanisms in visual cortex. Proponents of this position, dubbed the fatigue model, suggest that reversals of ambiguous figures are modulated by channels of cortical neurons that initially perceive the image, and then fatigue and give way to the second perspective (Long, Toppino, Kostenbauder, 1983). Central to this theory is the assumption that processing in visual cortex during reversals is serial in nature and therefore the neural system is incapable of complex interactions between distributed systems. In later studies, this position has been modified to include processing in parallel in multiple independent "neural channels" (Toppino & Long, 1987, p. 46). Other theoretical perspectives suggest linear relationships between various learning and memory centres are necessary for the perception of multistable figures (Girgus et al., 1977).

Still others have proposed more complex non-linear dynamical models for multistable figure perception (Ta'eed, Ta'eed, & Wright, 1988). The authors summarised three fundamental points that theories of visual ambiguities should acknowledge:

(1) The illusions are not conceptual but are perceptual (the knowledge that an illusion exists does not diminish the strength of that illusion). (2) That illusions do not result from eye movements, and do not originate in the retina. (3) That prior and past experience play a part in resolving the equivocal sensory image when the resolving information is absent, present, or reduced (Ta'eed et al., 1988, p.97).

The authors propose that some illusions such as the multistable perception of reversible figures cannot be understood within the limitations of linear mathematics. As a result, a non-linear catastrophe model was created using several stimulus parameters thought to be important for oscillations of multistable stimuli. Two abstract factors, Necker cube shape and change in detail from two to three dimensions were essential to their non-linear model. By varying the two parameters, the experimenters were able to fit a non-linear pattern to the data that provided a closer fit than the nearest linear model. The results indicate that shading and bias are decisive factors in perception of the cube, exerting their effects in opposition, neither reinforcing the other (Ta'eed et al., 1988).

This mode of non-linear modelling focuses primarily on stimulus properties and not the underling cortical organization that may also be part of an dynamical non-linear system. Many recent lines of evidence suggest that distributed non-linear systems exist in the brain, and that they may be the basis for various forms of complex information processing. The dynamical systems are not limited to local neuronal groups or *channels* but include local networks connected to other distributed networks via cortico-cortical and subcortical systems. Coupled with the principles of non-linear mathematics and theories of neuronal organization extending beyond common feedback systems, this line of research holds out the promise of explaining how perceptions are processed at the cellular level and are eventually realised at the level of human awareness. The focus of this thesis will now turn to an overview of evidence for these systems in the mammalian brain, with an emphasis on theories of non-linear systems and procedures that are the tools of this emerging perspective.

Non-linear Distributed Systems in the Mammalian Brain

It was once considered that information processing in the mammalian brain was a serial process, operating similar to a message travelling along a telephone wire. Over the past quarter century this perspective has changed dramatically as a considerable amount of evidence has surfaced suggesting that a complex anatomical organization exists at the cortical level with parallel streams of information being integrated via intricate connections. Among the first to engage in enlightened descriptions of complex cortical organization were Hubel and Wiesel (1962), who provided a description of how the visual system in particular had a columnar organization, with cells between pia and white matter having common functional properties such as ocular dominance, orientation specificity and similar receptive fields. However, questions remained about the nature of horizontal connections in cortex between columns, and their role in integrating information.

The horizontal connections in visual cortex were initially described by Gilbert and Wiesel (1983). The authors injected horseradish peroxidase into individual cells in cat striate cortex to provide a detailed analysis of intrinsic cortical connections at the cellular level. This methodology resulted in the reconstruction of 47 cells in various layers of cat visual cortex. The results showed that collaterals extending from the columns did not have a uniform radial distribution but were clustered in a manner similar to the collaterals of thalamic afferents. The cells with the longest collaterals were primarily pyramidal and spiny stellate cells. Individual cortical cells were said to form numerous projections of remarkable intricacy and extent, and when axons extend over considerable cortical areas, collaterals were observed to form a number of distinct repeating clusters. Axonal projections extending up to four mm tangentially tended to be asymmetric, branching further along a specific cortical axis, and axonal fields and were more elongated than their dendritic fields. From the horseradish peroxidase reconstruction it was discovered that many of the axons extended beyond the receptive field area of the cells from which they originated (Gilbert & Wiesel, 1983).

These results were extended by Gilbert (1985) who observed that horizontal cortical connections may extend beyond wide cortical columns and in fact, extended beyond hypercolumns. A hypercolumn in this case was defined in primates as "a full cycle of orientation of ocular dominance columns," in the primate being approximately 700-800 micrometers wide. Gilbert's position was that collaterals projecting more than 4 mm tangential to the cortical surface were presumably connecting non-overlapping areas of the visual field. Further, he stated that collateral organization originally observed in V1 has been shown in several areas of extrastriate cortex. The purpose of these lengthy extensions is therefore thought to represent some form of intrinsic connectivity in cortex, possibly between columns separated by considerable distances that respond to similar forms of information, and were thought to be excitatory in nature. Evidence of the functional significance of tangential collaterals is that, retinotopically, a much larger number of cells may be labelled in area 17 than are labelled in area 18, indicating considerable convergence. Other features of the projections are that they are clustered and distinct, projecting to specific layers of V2 and V3. Experimental evidence of their functional significance was reported in that when slices were made one mm apart, thereby severing the extended tangential connections, a reduction in contour orientation acuity was observed (Gilbert, 1985). Subsequent studies tended to reveal a consistent organization of these tangential connections. When retrograde tracing techniques were employed, the cells appeared to connect in what looked like a honeycomb lattice, indicating the existence of consistent organization (Gilbert & Wiesel, 1989).

The existence of extensive horizontal connections extending over 4 mm and several hypercolumns is worthy of emphasis, since they are obvious candidates in a system that could integrate visual information. Therefore the question to ask at this point is what function do these tangential connections serve? As stated previously, the collaterals are convergent, organised in a honeycomb lattice and project to areas V2 and V3. The convergent nature of these connections and their projections to cortical areas involved in "higher" processing is similar to the convergent nature of three parallel pathways of visual information processing described by

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Livingstone and Hubel (1988). The retino-geniculo-striate pathway contains considerable divisions of the type of information it processes. The distinction is evident early in the pathway as the larger type A retinal ganglion cells project to the magnocellular (M) division while the smaller type B cells project to the parvocellular (P) division of the lateral geniculate nucleus of thalamus (LGN). The M and P divisions differ in four major ways - colour, acuity, speed, and contrast sensitivity. The authors describe three pathways, one extending from primarily P input, one with M input and one with both M and P input. Each of the parallel paths, after the initial interface with layer 4C in striate cortex, tend to show a convergent organization, beginning with projections to simple and complex cells within columns and eventually extending to areas of specialized processing such as mid-temporal lobe (MT) and parietal association cortex. It is possible then, that the horizontal cortical connections provide a system of interaction between each of these distinct parallel paths.

Consistency of cortical connections was one of the focal tenets discussed by Zeki and Shipp (1988). One point discussed by the authors was that many of the connections that exist in one level of the visual system are found to exist at several other levels. Further, some of the anatomical strategies observed in visual cortex are observed repeatedly in other cortical areas. Common principles regarding the functional logic of cortical connections also allow predictions about the general functional organization of uncharted cortical areas. One common principle of cortex is the increase of complex response properties of cells within a specialized pathway accompanied by spatially convergent connections repeated at each successive stage (i.e. spiny stellate-simple-complex-hypercomplex model of cells). Another is the complex unification of hierarchical and parallel strategies supplying cortex with connectivity able to facilitate intricate interactions between different specialisations. The third involves intercommunication between specialized systems which quite possibly involves horizontal connections between parallel paths. Zeki and Shipp stated that the anatomical mechanism for assembling information is convergence. Two types of convergence were discussed, topical and confluent, with four types of convergent directions, forward, backward, lateral and intrinsic. Through the combination of

convergence types and directions, including horizontal collaterals between parallel systems, the authors concluded that the functional logic of cortical connections is to first achieve segregation (the retino-geniculo-striate pathway), and then integration (via convergence) (Zeki & Shipp, 1988).

The complex nature of neural organization discussed thus far is incomplete without the addition of an important factor - non-linearity. One of the first authors to discuss non-linearities in sensory systems was Freeman (1979). His model, based on the mammalian olfactory bulb and limbic system, used the known anatomy and physiology of the bulb and paleocortex as design criteria to synthesize, evaluate and solve a set of non-linear differential equations that represented grouped bulbar dynamics. In a subsequent article (Freeman, 1981), he described a method of modelling invertebrate olfactory and limbic system processes to discuss non-linear principles common to perceptual systems. The level of brain hierarchy discussed in his model was masses of neurons operating in parallel. Freeman suggested that for the activation of single neurons to be transduced to actual perceptions, a degree of co-operation or co-ordination must exist between the neurons within a system. His work centred on 40-80 Hz filtered oscillations (within the gamma band) in the olfactory system. During respiration, wave packets were objectified by analysis of phase and frequency of simultaneous bursts from numerous cells, and these coherent oscillations were thought to carry information. The olfactory bulb has several recurrent connections with primary olfactory and prepyriform cortex. High covariance of these areas was often noted and the three types of feedback loops were discussed in detail. The key to the model is a non-linear conversion bulbar function which, when stimulated, responds in an oscillatory manner. The state of oscillations increased the internal gain of the bulb which, in turn, initiated its own pattern of activity, eventually resulting in massed oscillatory activation. The oscillations end during expiration, due to inhibitory neurons with the same non-linear gain (Freeman, 1981).

Van Essen, Anderson and Fellman (1992) have developed a non-linear model based on primate cortical function. The basis for their model is a systems engineering perspective, grounded in

basic principles of signal processing constrained by properties of the brain's underlying neural circuitry. The authors described 32 distinct cortical areas based on anatomical, physiological and behavioural information, 25 of which are primarily visual in function. A total of 305 pathways interconnecting the 32 cortical visual areas were identified with modern tracing techniques. According to these authors, there exists a basic distinction in area V1 between simple and complex cells. They suggest that simple cells act as quasilinear filters and complex cells have pronounced spatial non-linearities providing image power within a restricted range of coding properties (Van Essen et al., 1992).

The organization of the visual system discussed thus far hinges on several fundamental principles of cortical organization, common throughout the visual system. The first is convergence, which is evident early in the retino-geniculo-striate pathway and persists through cortical areas of increasingly abstract processing. Convergence is a repetitive anatomical occurrence that may be a necessary component for integration of information over increasing levels of complexity. Similarly, tangential cortical connections are prevalent within and between cortical columns. These connections, like convergence, may share equally in their importance for integration of information across distributed cortical areas. Third, the acknowledgement of the non-linear nature of the olfactory system is one example of how the function of a discrete neural system can be optimally explained with a non-linear model of cellular interaction. With the above conditions of convergence, tangential connections and non-linearity in place, we can now ask, "How are the discrete segments of information that are transduced by the visual system integrated into an actual percept?" One perspective suggests that synchronous oscillations between assemblies of cortical neurons serve as the basis for *linking* sensory information. The oscillations are often reported to be within the gamma range (30 - 110 Hz) (Eckhorn et al., 1988), and are present in cortex and thalamus of several mammalian species.

Stimulus-induced rhythmic oscillations in cat visual cortex have been reported by several researchers. Among the first to discuss this phenomenon were Gray and Singer who liken the

organization of this activity to the studies on olfaction by Freeman and co-workers. In 1989, Gray and Singer recorded local field potential (LFP) and multiunit activity (MUA) to determine whether oscillatory responses could be detected in cat visual cortex during varying conditions of anaesthesia. This permitted a more qualitative analysis of stimulus specificity and temporal properties. The results are interesting in that local groups of neurons within functional columns of cortex were reported to oscillate at a gamma frequency near 40 Hz when presented with a light bar of optimal orientation, in both areas 17 and 18. No comparable responses were observed in thalamus, suggesting that synchronous oscillations are a purely cortical phenomenon. In addition, the oscillatory responses within columns tend to occur preferentially in complex cells (Gray & Singer, 1989).

Subsequent studies (Gray, Konig, Engel and Singer, 1989) show, however, that synchronous gamma band oscillations also extend beyond cortical columns. When recording from neurons with pairs of electrodes in area 17, the authors observed that oscillatory responses in non-adjacent columns were synchronized if their orientation preferences were similar, but showed no fixed phase relationships when orientation preferences differed. A particularly interesting finding was that correlated oscillations were recorded from two sites separated by 7 mm, with no overlap in receptive fields, but with similar orientation preferences. Two different stimuli were used, a long light bar and two short light bars. When the short light bars were moved in a divergent manner over the two receptive fields, there was no evidence of phase locking. When the bars were moved in the same direction, the responses were weakly synchronous and when a long light bar co-stimulated both receptive fields, the responses were enhanced. The results were interpreted to mean that the system of tangential intracortical connections and reciprocal connections from distributed cortical areas may provide an anatomical substrate for synchrony between remote columns (Gray et al., 1989).

Synchronous oscillations were recorded from even greater inter-columnar distances by Engel, Konig, Gray and Singer (1990). The authors recorded LFP and MUA in the 40-60 Hz range from

area 17 of the cat cortex with inter-electrode distances of 4 - 12 mm. For cells with non-overlapping receptive fields that coded for similar line orientations, the oscillations were more synchronous. Conversely, if their receptive fields did overlap, but they responded to different line orientations, they also showed a high incidence of synchrony. For electrode distances up to 12 mm, a high incidence of synchrony was observed between sites with similar orientation preferences. Therefore, oscillatory responses at separate cortical sites can transiently synchronize. The probability and strength of synchronizations are affected by the distance between cells and their orientation preference (Engel et al., 1990).

Differences in the oscillatory nature of simple, standard complex, and special complex cells have also been reported. Standard complex cells responded to their optimal stimuli in an oscillatory mode in 56% of the cells sampled, while simple cells and special complex cells responded at 12% and 11%, respectively. Cells responding in an oscillatory mode were primarily in supragranular and infragranular layers of cortex. Oscillations were enhanced by binocular stimulation and degraded by combined stimulation of light bars. Stimulus velocity and movement were effective in inducing oscillatory responses. The results were interpreted to mean that functional heterogeneity exists among cells within striate cortex based on temporal firing patterns and, that these patterns are influenced by changes in stimulus properties (Gray, Engel, Konig & Singer, 1990). This suggests that as the amount of information converging on a cell increases, so does its need to fire synchronously in order to synthesize information.

Synchronized oscillations have also been recorded by neuronal groups between two different areas of cat visual cortex. Coherence of stimulus evoked resonances was found within vertical columns, between neighbouring hypercolumns and between two different cortical areas. Coherent stimulus evoked resonances between LFPs of areas 17 and 18 were found to extend over two hypercolumns. In addition, oscillations of groups of neurons in area 17 were correlated with LFP oscillations in area 18. The authors interpret the high correlations between visual areas

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to mean that phase locking among assemblies occurs as a process to link features of the visual scene (Eckhorn et al., 1988). In addition, binocular stimulation with a whole field grating evoked large amplitude oscillations of about 45 Hz that were strongly correlated in areas 17 and 18. After the stimulus stopped moving, the oscillatory component vanished and only broad band activity remained. The effects of the stimulus evoked high frequency oscillations among two assemblies in different cortical areas that can be neither explained by far field volume conduction nor by entrainment of the frequency components of the stimulus. Spectral coherence was often high (0.6) during stimulus movement and low (0.1) while stationary (Eckhorn, Reitboeck, Arndt & Dicke, 1989).

Eckhorn and co-workers (Eckhorn, Schanze, Brosch, Salem & Bauer, 1992) have subsequently hypothesized that "synchronization of neural activities forms the basis of a flexible mechanism for feature linking in sensory systems" (Eckhorn et al., 1992, p.47). Further, they reasoned that synchronized activity between discrete neuronal assemblies is responsible for linking proximal and distal regions of visual space in cortex. The basis for their hypothesis is that receptive fields that code similar information will have strong connections compared to those with large inter-field distance and different receptive field properties. In their experiments, correlated gamma band activity was recorded from local cortical columns, between different areas of visual cortex as well as between hemispheres. The authors conclude by stating their belief that oscillations are most probably generated locally (at cortex) and synchronized globally. Additionally, links to higher mental processes such as focal attention may organize independent sense modality activation into a single system of common cortical oscillatory activity (Eckhorn et al., 1992).

Singer (1993) concluded by suggesting that time as a variable received little attention as a dimension for coding sensory information. Similarly, gamma band activity was once considered desynchronized, reflecting temporally incoherent activity of spatially distributed neurons. These distributed neuronal systems occur in parallel at different sites and always involve vast numbers of neurons that, depending on the complexity of the task, may be distributed throughout the

whole cortical sheath. The frequency of these oscillations usually fluctuate over a range of 5-10 Hz, even within a single oscillatory response. If groups of cells with overlapping receptive fields but different orientation preferences are activated with a single moving light bar, they synchronize their responses, even if some of these groups are suboptimally activated. However, if a group is stimulated with two independent stimuli that move in different directions, they no longer form one coherently active assembly but split into two independent synchronously active assemblies, (i.e., those groups join the synchronously active assembly that shows a preference for the same stimulus). Thus the two stimuli become represented by two spatially interleaved but temporally segregated assemblies. Therefore, the coupling between distributed cell groups is dynamic and can change in a stimulus-dependent way (Singer, 1993).

The research completed thus far on cat visual cortex is quite compelling, however, if cat is the only mammalian species capable of generating gamma band activity, there would not be much point in continuing this line of academic pursuit. Reports of gamma oscillations recorded from single units or field potentials have been reported less frequently in primate cortex, and when they are observed, manifest slightly different characteristics. In alert macaque monkeys for instance, synchronized oscillations between spatially separate sites in extrastriate cortex were observed, though they appeared to be more irregular than those observed in the cat (Engel, Konig, Kreiter, Schillen & Singer, 1992). Perceptual feature linking in humans has rarely been addressed, due to the obvious problems of embarking on a research project of this nature at the cellular level. Very recent attempts to investigate feature linking in humans have confronted this issue at the macrocellular level. In an EEG study, Desmedt and Tomberg (1994) recorded 32 channels of EEG during a brief randomly mixed electrical stimulation of the subjects fingers. One finger was designated the target, which the subject was to identify by pressing a button with the right big toe. Oscillations in the 40 Hz range were recorded and filtered using a 35-45 Hz window. The results were interesting in that the sensory input from the target finger elicited contralateral activity first in the primary somatic parietal cortex (P30, P40), then in the posterior parietal cortex (P80, P100), and finally in the dorsolateral prefrontal cortex (N140). The gamma

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waves recorded were not phase locked to the stimuli and therefore any synchrony would have been obliterated by averaging. A clear phase locking of 40 Hz oscillations was observed between contralateral parietal and dorsolateral prefrontal cortex "in spite of their wide separation (about 9 cm)" (Desmedt & Tomberg, 1994, p. 127). The phase locking continued for approximately 125 ms or 5 cycles. Thus transient phase locked oscillations in the gamma range are recordable using macroelectrode recording techniques. The authors bring up the important point that the oscillations were not phase locked to the stimulus, meaning that averaging of repeated trials would nullify any synchronous response. This point raises important methodological concerns, and will be re-addressed at the conclusion of this section.

Research using MEG has also provided some evidence for feature linking in the human brain. In another recent study, 37 channels of MEG data were collected from right hemisphere during the presentation of an auditory stimulus. Subjects were asked to report whether they heard one or two clicks, the double click occurring at varying interclick intervals. The data were averaged using the onset of the first stimulus as the trigger. A power spectral analysis revealed a significant component near 40 Hz. The pattern of response for a two click sequence was that click one triggered a 40 Hz response and the second stimulus induced a similar response only after a specific time interval. The interpretation of the results was that, at interstimulus intervals less than or equal to 14.2 msec, the first stimulus alone is sufficient to elicit a 40 Hz response, while longer intervals allow each stimulus to induce its own 40 Hz activity. The abruptness of the response was considered to be linked to non-linear single cell oscillatory properties. The authors interpreted the results to indicate that 40 Hz oscillatory activity is not restricted to primary sensory processing, but forms part of a binding property that integrates sensory events into a single experience (Joliot, Ribary & Llinas, 1994).

Bursting of 40 Hz oscillations has been reported in the human brain for over a decade, but what the Desmedt article in particular indicates is that the simultaneous oscillations can be transiently phase locked between distributed cortical areas. This serves as evidence for cortical function

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similar to that observed in cat visual cortex. The human studies however, limit their focus to 40 Hz activity, which differs from the perspective of Gray, Singer and Eckhorn's efforts somewhat. Let us then turn to theoretical perspectives of how synchronous cortical systems within the gamma band operate, to develop some testable hypotheses about this organization in humans.

Llinas (1992) has proposed a cellular model for such a system that includes cortical layer IV interneurons, cortex layer VI pyramidal cells, reticular thalamic nuclei, and thalamus. He begins by stating that thalamus may serve a linking function between various cortical sites and this position has been upheld by evidence that thalamic projections have been reported to fire between 30-40 Hz after brainstem cholinergic stimulation. Similarly, cortical interneurons, primarily in layer IV, are capable of subthreshold rhythmic oscillations at frequencies akin to those recorded cortically. Therefore layer IV inhibitory neurons, when depolarised, oscillate at 40 Hz when the optimal stimulus for that cortical column is presented. Inhibitory neurons then produce IPSP's in surrounding cells, including layer V pyramidal cells, in the presence of EPSP's generated in cortex from thalamic sources. Rhythmic inhibition of layer five pyramidal cells oscillate at 40 Hz, which has been clearly demonstrated in IPSP's in visual cortex pyramidal cells (Ferster, 1988). Llinas continues by stating that rhythmic cortical oscillations may communicate 40 Hz excitation to reticular thalamic nuclei establishing a "resonance state in the thalamocortical system via feedback through layer IV neurons" (Llinas, 1992, 278). Cortically recorded 40 Hz rhythms may then constitute both intrinsic rhythms and resonance in the thalamocortical system. Finally, rhythmic firing of pyramidal cells could become synchronous with similarly activated cortical columns and would, via resonance, generate a 40 Hz EPSP-IPSP resonance in thalamus (Llinas, 1992).

Another theoretical perspective, which goes beyond the limitations of a 40 Hz model has been proposed by Edelman (1989). According to Edelman's theory of neuronal group selection (TNGS), reentrant cortical connections are proposed as the basis for processing complex information. Reentry is a process of temporally continuous parallel interactions between

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distributed maps along ordered anatomical pathways (see Figure 1). Reentry is not simply

feedback, but parallel signalling in the time domain between spatially disparate maps of neuronal

groups. Feedback loops differ from the intrinsically parallel nature of reentry, as they usually

involve only a single signal channel or pair of wired connections. Reentrant connections can be

reciprocal or from a geometric range and can be convergent or divergent. Reentry has variable

temporal and spatial properties, similar to a process of correlation between distributed systems.

Activity distributed within and between maps must be correlated temporally and spatially, and for

high order reentrant correlations to be associated with sensory activity, one map must be

topographic. Other maps in the same modality must be reentrantly connected to that topographic

map in order to maintain correlations of properties related to the external world. It is a dynamic

process with a variety of temporal properties: cyclic, intermittent, synchronous, asynchronous.

Therefore, the characteristics of reentry depend upon the various latencies and temporal

properties of neurons and synapses (Edelman, 1989).

Edelman (1989) discusses a specific model of striate and extrastriate cortex to illustrate the

TNGS. Within the visual system, the integration of multiple functionally segregated areas with

potentially conflicting information (i.e., motion, shape, depth, colour) must be combined to form

visual perceptions. The visual cortex of higher animals is functionally segregated (Van Essen,

1992, describes 32 distinct cortical areas based on anatomical, physiological and behavioural

information, 25 of which are primarily visual in function). Edelman makes an important point that

no single dominant integrative area has been located. On the contrary, every visual cortical area

is connected to some subset of other areas. Within a specific cortical area, cells respond

optimally to a particular attribute of the visual scene, and respond at suboptimal rates to others.

The perceptual problem to address in vision is how do distributed mapped regions with varied

cell types integrate their function to produce coherent and unified representations of the visual

scene? The problem is magnified when you consider that this integrated system must respond to

partial, conflicting or ambiguous stimuli, as is demonstrated by visual illusions (Edelman, 1989).
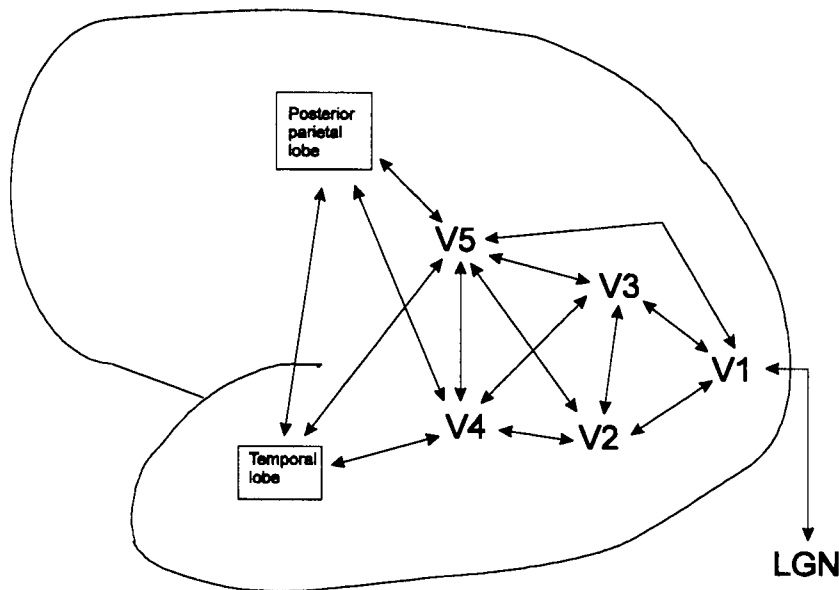
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Figure 1. Schematic overview of reentrant connections between distributed systems in visual cortex. (Adapted from Edelman (1989), p. 71).

Computer models simulating the principles of TNGS have been successful in demonstrating some of these theoretical principles (Finkel & Edelman, 1989). The computer model simulates three interconnected cortical areas in striate and extrastriate cortex of the macaque (simplified V1, V3 and V5). The simulated networks were very complex, containing over 222,000 units and 8.5 million connections. The computer model is able to simulate several of the features of visual integration via reentrant connections such as determining structure from motion. The network also responds in a consistent manner to novel illusions. Three reentrant system types are specified as important to this process: 1) competitive elimination of conflicting responses among segregated neuronal groups, 2) information leaving an area is used optimally by a different area 3) information leaving an area is reentered into that area through lower areas, and can be used iteratively to synthesize responses to complex or illusory stimuli. Removal of reentrant connections however, abolished integrative processes, resulting in a failure of figural synthesis (Finkel & Edelman, 1989).

Edelman also discusses the results of Gray, Singer and Eckhorn's data which, he suggests, all provide support for the TNGS. In fact, Edelman (1993) discusses computer simulations based on cat and monkey cortex showing that reentrant interactions within a single cortical area can give rise to temporal correlations between neighbouring cell groups as well as distant groups with a near zero phase lag. In addition, he discusses another simulation where neuronal groups oscillated in much the same manner in response to moving bars as did cat cortex in Gray and Singer's experiments. Similar to the previously described simulation, the correlations of neuronal activity depended critically on reentry, and disappeared when the underlying connectivity was disrupted (Edelman, 1993).

In a review of his TNGS and reentrant processes, Edelman (1993) makes an excellent point that can be extended throughout neuroscience. He suggests that "what is needed to connect the growing body of evidence in biology and psychology is a theoretical framework sufficiently broad to connect biology and psychology in a fashion consistent with developmental and evolutionary systems" (Edelman, 1993, p. 115). In his words, to be useful a global brain theory should accomplish at least two things. The first is that it should help to predict fundamental structure and function of the CNS. Second, it should provide a basis for recording and understanding morphological, physiological and behavioural observations generated by the multitude of research options available in neuroscience today. As was previously discussed, the theory does not invoke coded signals acting in precisely defined linear circuits, but instead emphasises spatial and temporal correlations occurring within volumes of tissue. This statement implies at least two things. The first is that some connections between neuronal groups are inherently non-linear. The second is that correlations of neuronal groups operating within a distributed system should be present during information processing. The two points are testable using EEG and MEG methodologies and should serve as a suitable initial test of Edelman's TNGS.

The remainder of this thesis will focus on the cortical correlates of Necker cube reversals, recorded with EEG and MEG. The EEG phase will serve as the preliminary phase where two

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methodologies will be used to test the TNGS. The MEG phase will serve the purposes of replication and extension of optimal strategies found during the EEG phase. An ambiguous figure, like the Necker cube will be a useful tool to elicit the features of sensory feature linking, since newly formed percepts are constantly being produced. However, several studies that attempted to address the question of how the brain functions during reversals of ambiguous figures, modified the stimulus, therefore altering the phenomenon that occurs continually during perception. In order for spontaneous brain responses that occur during continuous perceptual reorganisation of the cube to be recorded, the stimulus will be presented in its standard form, with no alterations. This sentiment is echoed by Freeman (1981) who states:

> "if by assumption a main function of the brain is to construct representations, then the key studies must be done as those representations are made, that is, by making observations within the normal brain as it performs this function" (Freeman, 1981, p. 566).

The first hypothesis to be tested is that non-linear patterns of cortical activity will exist during perception of Necker cube reversals. When compared to processing of a two-dimensional figure using a generalised regression neural network (GRNN). The GRNN is a non-linear classifier, developed by Specht (1991), and discussed by Wasserman (1993). In general terms, the GRNN, like the back-propagation neural network, is able to approximate any functional relationship between input and output. The GRNN performs a bayesian classification, and will, in fact, approach an optimum Bayesian classifier given a large enough number of training exemplars (Wasserman, 1993). A complete description of the GRNN can be found in Appendix A.

Hypothesis two is that increased correlations of neuronal groups operating within distributed systems should be present during Necker cube reversals, and correlations should be somewhat lower during processing of the two-dimensional figure. The model of correlations of EEG and MEG data will be similar to those observed in Edelman (1989, p. 71), where reentrant connections are described between visual areas of primate cortex. The reentrant connections

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between areas of visual processing will be replaced by correlations between EEG electrode positions and MEG sensor sites over parieto-temporo-occipital cortex.

Method

EEG

Subjects and Recording Conditions

Five (5) adult right handed subjects, three males and two females, participated in the EEG

phase. Subjects were between 18 - 34 years of age, with a mean age of 26.6 years. The data

from one subject (male) was excluded due to an equipment malfunction during data collection.

Twenty-two silver-silver chloride electrodes were applied according to the international 10-20

system (Jasper, 1958). Linked ear references and an Fpz ground were used. One electrode,

placed at the nasion and referenced to Cz was used to trigger EEG data collection when subjects

closed their eyes. Electrode impedances were maintained below 5 kOhms. Subjects were

seated in a comfortable chair in a natural laboratory environment (not a soundproof room). The

illumination in the room was natural light (to reduce 60 Hz noise) for all subjects and was

measured to be 0.493 ft L. The EEG amplifiers were Nihon-Kohden model EEG-4217 linked to a

software interface via a National Instruments model ATMI064-F analog to digital board. The

software[1] was specifically designed to record single EEG trials. Single trial recording epochs

occurred between -1000 to 0 milliseconds, encapsulating a one second period prior to the trigger,

digitised at 1024 points per second. Each single trial was triggered externally by an electrical

potential generated from the nasion electrode referenced to Cz. The sensitivity for the trigger

was 7 uV/mm, with the time constant at 0.03 and the high filter at 70 Hz[2]. The sensitivity for the

EEG amplifiers was 20 uV/mm with time constant of 5, the high filter set to 70 Hz and the notch

filter IN.

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[1]   Brainwave V1.1 © Procet Engineering 1993, Nanaimo, B.C., Canada.

[2]   During experimental preparation for each subject, the first attempt to trigger EEG trials
was always with sensitivity set to 7 uV/cm. Depending on the strength of electrical potential
elicited from the eyes, the sensitivity setting was increased or decreased to allow for optimal
triggering with as few "false triggers" as possible.

Visual stimuli consisted of two geometric figures, each presented on an 8 1/2 x 11" piece of white paper (both of which are presented in Appendix C). One figure was a square with side lengths of 15.5 cm. The second figure was a Necker cube, first described by Necker (1832), with a vertical side length 10.8 cm and a diagonal length of 6.5 cm. The line thickness for the experimental and control figures was 2.8 mm. The 2-D square served as the control stimulus, while the Necker cube was used to elicit two perceptual effects. The first effect was designated to be when the Necker cube was perceived to shift "up", so that the upper left-most corner of the *cube face* was in the upper left-most quadrant of the figure. The second perceptual effect (down) was designated to be the opposite in direction of shift from the previous effect. The two figures and their perceptual effects are shown in Figure 2.

Procedure

The experimental (shift up or down) and control effects were recorded in random order, each for a period of time that allowed a minimum of 20 single trials to be collected[3]. During all single trial recordings, the electrical potential generated from an eye closure was used to trigger EEG data collection During perception of the control stimulus, the subject was instructed to spontaneously close the eyes while focusing on the stimulus to trigger data collection. During perception of the experimental effects, data collection occurred as a result of eye closure immediately after a reversal occurred in the correct direction.   While focusing on the Necker cube, subjects were instructed to close their eyes only when a "clear" reversal had occurred and were told to ignore those occurring incompletely or in rapid succession. Therefore, single EEG trials did not include all reversals, but a subset of reversals that were of a subjective "high quality". Subjects were also instructed to allow perceptions of the cube to reverse spontaneously without attempting to change the perception by moving the eyes. The data for the three effects were collected until 20 - 30 single trials were available for analysis. To ensure that eye closure and not eye movement artifact was triggering data collection, all subjects were video monitored during the experiment. If

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[3]   During the EEG phase, it was first thought that early Necker cube reversals may be more easily classified due to the brain's response to a novel stimuli. Therefore, an arbitrary number of a minimum of 20 single trials was chosen in an attempt to obtain a homogeneous data set that contained novel responses.

a) Necker cube perception
   shifts up

b) Necker cube perception
   shifts down
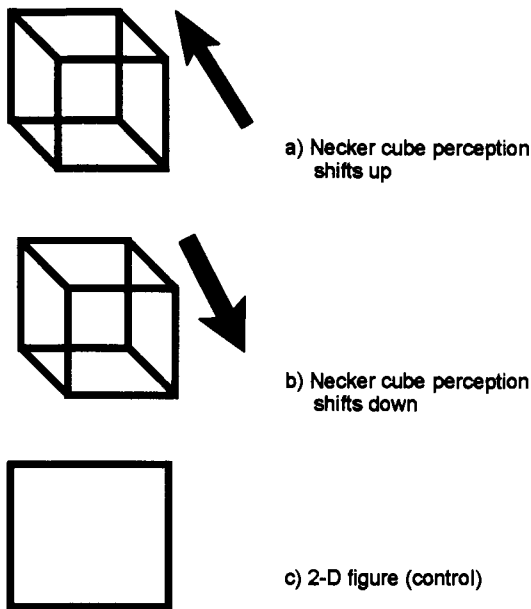

c) 2-D figure (control)

Figure 2. The perceptual effects of experimental stimuli used during recording of single trials: a) perception of the Necker cube shifting "up". b) perception of the Necker cube shifting "down". c) the 2-D control figure.

data collection occurred while the subject was viewed to have their eyes open, completely or incompletely, that trial was manually rejected.

Preprocessing. All EEG single trials were pre-processed prior to neural network analysis. Since the EEG phase served as the preliminary phase for the second (MEG) phase, several different preprocessing attempts were made before one method was selected (a full description of all processing and analytical techniques attempted is described in Appendix B). Although the original single trials consisted of 19 electrodes of 1024 points, a reduced number of electrode positions were eventually selected since increased signal to noise is believed to be important for neural network classifications. This subset included central, temporal, parietal and occipital positions (T3, C3, C4, T4, T5, P3, P4, T6, O1 and O2). Correlation matrices were calculated for this subset of electrode positions, resulting in a 10 x 10 matrix for each of the single trials. Since redundant information exists in the upper and lower quadrant of each matrix, these values were removed. Additionally, the diagonal of each correlation matrix was removed since all values equal one. The lower quadrants were then transformed into one row vectors (1 x 45).

The first step toward creation of network training matrixes was to "stack" the vectors from each experimental condition and for each subject separately. For instance, if 20 single trial vectors from Subject 1, condition 1 were combined, a 20 x 45 matrix would be the result. Matrixes from

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two categories were then combined (i.e., experimental condition and control condition for each subject) to form a *training matrix*. An additional column (column 46) was added to each training matrix, containing dummy codes for vector category membership; 0 for control vectors and 1 for experimental vectors. Therefore two training matrixes were created for every subject, for a total of eight training matrixes. A visual description of training matrix construction for EEG single trials is shown in Figure 3.

Network Analysis. The purpose of the network analysis was to determine whether the single EEG trials could be classified as representing either the Necker cube reversal or the 2-D control condition, on the basis of correlation matrix vectors. The network used for analysis was the generalised regression neural network (GRNN) developed by Specht (1991), and discussed by Wasserman (1993). In the present case, the input to the GRNN consisted of individual exemplar row vectors from the network training matrix. The corresponding output of the GRNN was the probability that the input vector belonged to a category. The smoothing parameter chosen for all EEG classifications was set to 0.25.

Because of the limited number of exemplars, a jack-knifing procedure was adopted and was carried out as follows. From the network training matrix, a single exemplar vector was removed. The network was trained on the remaining exemplars in the network training matrix. The network was then tested by presenting the single withheld exemplar. The result was a number indicating the probability of the single exemplar belonging to its imputed category, given the exemplars remaining in the training matrix. The GRNN is thus performing a Bayesian classification, and will, in fact, approach an optimum Bayesian classifier given a large enough number of training exemplars (Wasserman, 1993). A graphical representation of the GRNN is shown in Figure 4. A complete description of the GRNN procedure and algorithm can be found in Appendix A.
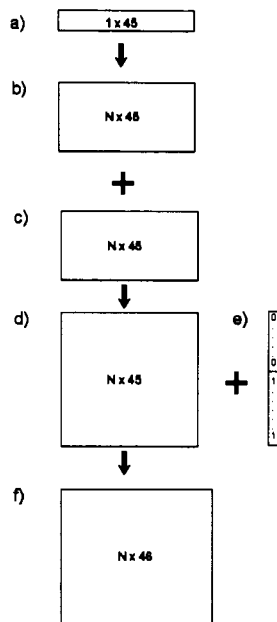
Figure 3. Training matrix construction. a) Correlation matrixes were calculated for a subset of the total electrode positions. Non redundant values were chosen from the matrix and were transformed into a 1 x 45 vector for each single trial. b & c) Vectors were stacked to form n x 45 training matrixes (where n = the number of single trials included for each condition). d) The stacked experimental and control vectors were then combined. e) Dummy codes (0 = control; 1 = experimental effect) were added as the 46th column. f) The complete training matrix.

EEG Hypothesis 1: The GRNN jack-knife classifications resulted in a number representing the probability that each single trial vector (either a 0 = control vector, or 1 = experimental vector) was similar to those in the experimental group. The probabilities were then grouped into control and experimental vectors within subject for statistical analyses (i.e., for each subject, two comparisons of probabilities were generated, experimental condition 1 vs. control and experimental condition 2 vs. control). Two statistical analyses, one tailed equal variance t-tests[4] and the Kendall's Tau procedure (one tailed) were used (significance p.< 0.05).

EEG Hypothesis 2: EEG single trials were analyzed to determine whether, as Edelman's theory predicts, higher correlations between distributed cortical systems exist during visual information processing. An a priori model was developed (see Figure 5a) based on Edelman's description of reentrant pathways in primate visual cortex made up of the scalp positions used in the GRNN analysis. These included electrode pairings over occipital cortex, parietal association cortex and posterior temporal cortex. The subset of correlations chosen (12 of 45) were intended to represent occipito-occipital connections both within and between hemispheres, occipito-parietal association cortex connections, occipto-posterior temporal connections and posterior temporal lobe connection via the corpus callosum. Average correlations were calculated across single

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[4] It was found after a preliminary descriptive analysis that EEG single trial variance was remarkably similar for experimental and control conditions and thus, equal variance t-tests were used in the analysis. A one tailed test was chosen because the direction of prediction was known.
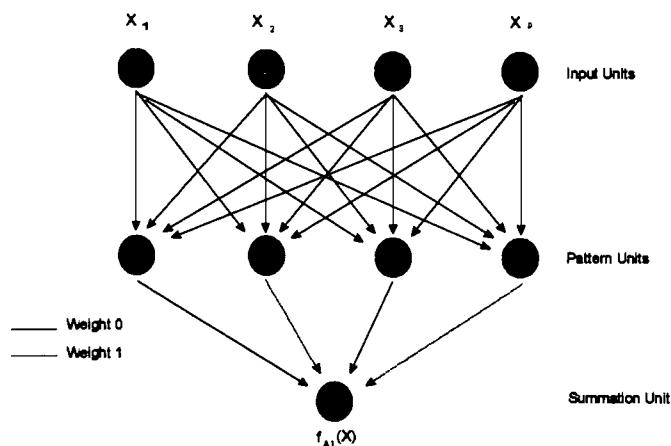
$$f_{A1}(X) = \sum_{i=1}^{m} \exp \left[\frac{(X - X_{Ai})^t (X - X_{Ai})}{2\sigma^2} \right]$$

Where: $f_{A1}(X)$ = the PDF estimate
i = the pattern number
m = the total number of training patterns
X_{Ai} = i th training pattern from category θ_A
σ = "smoothing parameter"

Figure 4. The Generalised Regression Neural Network (GRNN) from Simulnet (Copyright 1993-1994).

trials, within subject and experimental condition, and were subsequently summed. The summed averages were then analyzed using the stepwise Bonferroni procedure for multiple comparisons, with an overall significance level of $p. < 0.05$. An overview of this analysis procedure is shown in Figure 6.

MEG

Subjects and Recording Conditions

An additional five (5) adult right handed subjects, three males and two females participated in the second (MEG) phase. Subjects were between 18 - 32 years of age, with a mean age of 26.4 years. A 64 channel MEG system[5] was used for data collection. Subjects were seated in a pneumatically adjustable chair that raised and lowered the subject into and out of the MEG dewar. The MEG system is located in a natural laboratory environment (not a soundproof room) and the illumination in the room was natural lighting for all subjects. The luminance in the room was measured at 7.472 ft L. The visual stimuli in experimental and control conditions were identical to those described in the EEG methodology.

Procedure

The experimental and control conditions were presented in random order. Data were recorded during 15 trials that were each 15 seconds in duration. There were two experimental trials for

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[5]   64 Channel MEG System © CTF Systems Inc. 1993, Port Coquitlam, B.C., Canada.
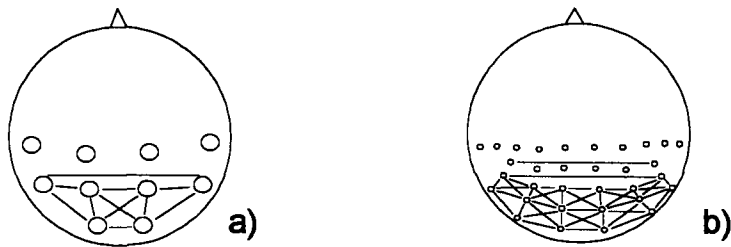
Figure 5. The lines represent correlations between electrode/sensors that were included in the respective subsets. a) EEG subset of correlations used in paired t-tests. b) MEG sensor subset of correlations used in paired t-tests.

each direction of reversal (i.e., 2 x up + 2 x down = 4 experimental conditions) and one control condition[6]. The sampling rate was 250 points per second. During the control condition, the subject was instructed to spontaneously close the eyes at approximately 2 second intervals while focusing on the subjective centre of the control stimulus. In the experimental conditions, subjects were instructed to close their eyes for approximately 0.5 - 1.0 second immediately after a reversal occurred in the appropriate direction. While focusing on the Necker cube, subjects were instructed to close their eyes only when a "clear" reversal had occurred and were told to ignore those occurring incompletely or in rapid succession. Therefore, single MEG trials did not

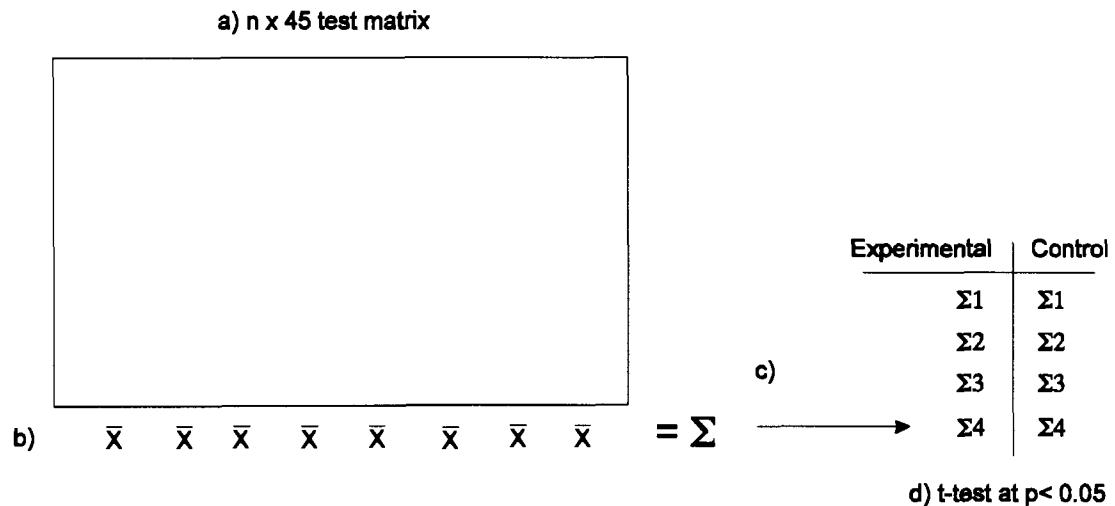Figure 6. The subset of correlation averages calculated based on the models in Figure 5. a) An n x 45 matrix consisting of *either* experimental or control data. b) Averages were calculated across single trial vectors for correlations represented as lines between electrode/sensors in Figure 5. c) Summed averages are entered into columns for analysis. d) Paired t-tests are calculated on the summed averages.

include all reversals, but a subset of reversals that were of a subjective "high quality". To ensure that subjects were closing their eyes at the appropriate times, they were instructed to "blink repeatedly" if they needed to blink, or if a spontaneous eye closure had occurred.

Preprocessing. Each 15 second MEG trials was subjected to a visual analysis before single trials were extracted. Two frontal sensor locations (SL 31 and SR 31) were used to observe eye closures in each trial. A one second data segment of 250 points was extracted from the entire record, only if an unambiguous eye closure (which resembled a square wave) ensued. For the -1000 - 0 millisecond epoch, the 0 point was objectively defined as the first data point where the deflection of an eye closure was evident. Unlike the first phase of the experiment, the actual number of single trials was determined by the number of reversals a subject experienced within the time frame of the experiment.

A subset of the original 64 MEG sensors was selected to replicate those chosen in the EEG pilot phase. This subset included central, temporal, parietal and occipital positions. This subset is shown in Figure 4b. Correlation matrices were calculated for this subset of sensor positions, resulting in a 32 x 32 matrix for each of the single trials. Since redundant information exists in the upper and lower quadrant of each matrix, these values were removed. Additionally, the diagonal of each correlation matrix was removed since all values equal one. The lower quadrants were then transformed into one row vectors (1 x 496). MEG network training matrixes were created in a similar manner as described in the EEG phase (see Figure 2) with the exception that 1 x 496 value vectors were used instead of the 1 x 45 value EEG vectors.

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[6]   It was expected that the spontaneous eye closures in the control condition would outweigh the number in a single experimental condition of the same length. Therefore, both experimental conditions were repeated twice to ensure a sufficient number of single trials for experimental conditions.

Network Analysis. The network analysis for the MEG phase was identical to that described in the EEG methodology, with the exception that several smoothing values were used during GRNN analysis (0.1, 0.25, 0.5, 1, 2, 4).

MEG Data Analysis (1): The GRNN jack-knife classifications resulted in a number representing the probability that each single trial vector (either a 0 = control vector, or 1 = experimental vector) was similar to those in the experimental group (1). The probabilities were then grouped into control and experimental vectors within subject for statistical analyses. Two analyses, one tailed equal variance t-tests and the Kendall's Tau procedure (one tailed) were used with significance levels of $p < 0.05$. The stepwise Bonferroni procedure for multiple comparisons was used with an overall probability of $p < 0.05$ per experimental vs. control group comparison. A table of all comparisons and p values is shown in the Results section.

MEG Data Analysis (2): MEG single trials were analyzed in an attempt to partially replicate the EEG results of higher correlations between a subset of sensors locations. An a priori model was developed (see Figure 4b) that included the sensor positions used in the GRNN analysis. These included sensors over occipital cortex, parietal association cortex and posterior temporal cortex. The subset of correlations chosen (95 of 496) were intended to represent spatially similar connections to those in Edelman's model. Averages across all single trials, within subject and experimental condition were calculated and summed. The summed averages were then analyzed using the stepwise Bonferroni procedure for multiple comparisons, with an overall significance level of $p < 0.05$. This stage of the analysis is identical to the analytical procedure shown in Figure 5 for EEG, with the exception of 95 summed averages for MEG, instead of 12 for EEG.

Results

EEG

Hypothesis 1: GRNN Classification Analysis

Significant classifications were observed for each of the four subjects. As shown in Table 1.,

both one tailed equal variance t-tests and the one tailed Kendall's Tau procedure resulted in

significant classifications of GRNN generated probabilities. For two subjects, experimental effect

1 vs. control and experimental effect 2 vs. control classified significantly based on GRNN

probabilities, while for the remaining two subjects, only one of the two comparisons classified

significantly. No dominant direction for reversal was observed based on the classifications and

appeared to be variable across subject.

		Kendall's Tau	One Tailed T-test
Subject 1	Up vs control	0.091815	0.124415
	Down vs control	0.001055*	0.0144*
Subject 2	Up vs control	0.024745*	0.01289*
	Down vs control	0.48075	0.46063
Subject 3	Up vs control	0.000005*	0.000035*
	Down vs control	0.028315*	0.042055*
Subject 4	Up vs control	8.35e-10*	5.8e-9*
	Down vs control	0.00015*	0.00867*

Table 1. P values for one tailed t-tests and the Kendall's Tau procedure for all subjects and training matrixes (smoothing value set to 0.25). The "up" effect is a perceived shift of the cube face to the upper left quadrant of the Necker cube. "Down" was a perceived shift in the opposite direction. An asterisk (*) is used to indicate p values significant at the 0.05 level.

Hypothesis 2: Correlation Subset Analysis

The summed averages analyzed using the stepwise Bonferroni t-test for multiple comparisons

are shown in Table 2. Since the overall p value was 0.05, each of the two comparisons were

tested at the 0.025 level on the first iteration. The p value for the control vs. the upward shift

effect was $p = 0.019205$. The p value for the control vs. the downward shift effect was $p =$

0.02926. Since the control vs upward shift comparison was significant at the $p. < 0.025$ level, it

was removed from the next iteration, and the remaining p value was significant at the $p. < 0.05$

level.   Since the correlation subset was chosen a priori, no further corrections were deemed

necessary.

	Control sum	Shift up sum	Shift down sum
Subject 1	7.04475	7.213921	7.379134
Subject 2	8.034971	8.32044	8.307196
Subject 3	8.579889	9.167189	9.190951
Subject 4	7.533373	7.626054	8.202462

Table 2. The summed averages from the subsets of correlations used in the stepwise Bonferroni procedure for EEG.

MEG

Hypothesis 1: GRNN Classification Analysis

Significant classifications were observed for each of the five subjects. As shown in Tables 3a

and 3b., both one tailed equal variance t-tests (Table 3a) and the one tailed Kendall's Tau

procedure (Table 3b) resulted in significant classifications of probabilities. For all subjects,

experimental effect 1 vs. control and experimental effect 2 vs. control classified significantly

based on GRNN probabilities. No dominant direction for reversal was observed based on the

classifications and appeared to be variable across subject.

		Smoothing Parameter Values					
		0.1	0.25	0.5	1	2	4
Subject 1	up vs cntrl	2.59 e-15	4.35 e-15	8.28 e-17	1.47 e-20	5.12 e-19	3.06 e-15
	down vs cntrl	0.00007	0.00002	4.2 e-6	3.03 e-8	2.3 e-10	2.04 e-8
Subject 2	up vs cntrl	2.8 e-45	7.01 e-45	2.8 e-44	0	5.69 e-40	5.97 e-34
	down vs cntrl	1.42 e-15	1.11 e-16	3.38 e-18	6.35 e-23	2.55 e-19	7.23 e-15
Subject 3	up vs cntrl	0.001	0.00008	0.00001	6.96 e-9	2.48 e-13	2.16 e-7
	down vs cntrl	0.00013	0.00007	0.00003	2.09 e-6	2.4 e-8	0.00004
Subject 4	up vs cntrl	3.12 e-10	2.79 e-10	5.79 e-11	5.84 e-14	8.67 e-12	5.3 e-8
	down vs cntrl	0	0	0	0	9.81 e-44	1.76 e-37
Subject 5	up vs cntrl	0.00005	0.00002	5.86 e-6	1.02 e-8	1.44 e-14	4.47 e-12
	down vs cntrl	0.00003	0.00004	0.00011	0.00002	7.29 e-10	5.92 e-9

Table 3a.   P values for one tailed t-tests for all subjects and training matrixes.   The "up" effect is
a perceived shift of the cube face to the upper left quadrant of the Necker cube. "Down" was a
perceived shift in the opposite direction. All comparisons are significant at the p. < 0.05 level
after a Bonferroni correction (p = 0.05 / 60 comparisons equals p = 0.00083 for each
comparison).

		Smoothing Parameter Values					
		0.1	0.25	0.5	1	2	4
Subject 1	up vs cntrl	2.2 e-21	1.35 e-22	5.67 e-18	3.66 e-18	7.67 e-20	1.76 e-16
	down vs cntrl	1.47 e-9	3.04 e-7	2.13 e-7	1.16 e-9	1.52 e-13	7.95 e-11
Subject 2	up vs cntrl	0	0	5.91 e-34	6.06 e-31	4.95 e-31	2.47 e-30
	down vs cntrl	1.47 e-27	3.03 e-26	3.13 e-22	6.07 e-24	2.33 e-26	2.74 e-24
Subject 3	up vs cntrl	6.14 e-9	1.63 e-8	1.31 e-9	4.79 e-10	6.85 e-15	2.37 e-10
	down vs cntrl	5.02 e-8	2.63 e-9	9.94 e-9	6.49 e-9	7.85 e-10	1.3 e-6
Subject 4	up vs cntrl	3.53 e-16	5.63 e-15	2.02 e-14	4.15 e-14	2.3 e-14	8.07 e-8
	down vs cntrl	6.92 e-42	4.07 e-41	8.31 e-35	1.58 e-21	1.68 e-21	7.14 e-22
Subject 5	up vs cntrl	9.53 e-10	5.38 e-9	3.03 e-10	2.77 e-11	3.56 e-15	1.43 e-13
	down vs cntrl	4.08 e-8	2.46 e-6	7.94 e-6	2.97 e-7	3.44 e-12	8.95 e-11

Table 3b.   P values for one tailed Kendall's Tau for all subjects and training matrixes. "Up" is a perceived shift of the cube face to the upper left quadrant of the Necker cube. "Down" was a perceived shift in the opposite direction. All comparisons are significant at the p. < 0.05 level after a Bonferroni correction (p = 0.05 / 60 comparisons equals p = 0.00083 for each comparison).

Hypothesis 2: Correlation Subset Analysis

The summed averages analyzed using the stepwise Bonferroni t-test for multiple comparisons are shown in Table 4. Since the overall p value was 0.05, each of the two comparisons were tested at the 0.025 level on the first iteration. The p value for the control vs. the upward shift effect was p = 0.039891. The p value for the control vs. the downward shift effect was p = 0.016712. Since the control vs downward shift comparison was significant at the p. < 0.025 level, it was removed from the next iteration, and the remaining p value was significant at the p.< 0.05 level.   Since the correlation subset was chosen a priori, no further corrections were deemed necessary.

	Control sum	Shift up sum	Shift down sum
Subject 1	39.99959	42.09368	41.84251
Subject 2	42.08386	43.46183	44.03807
Subject 3	44.62125	44.09061	45.31322
Subject 4	41.41223	42.12664	41.39542
Subject 5	44.01119	46.10864	45.49712

Table 4. The summed averages from the subset of correlations used in the stepwise Bonferroni procedure for MEG.

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Discussion

Implicit in Edelman's theory of neuronal group selection (TNGS) (1989) is the idea that distributed groups of neurons operating within a system will display complex patterns of activity that will be correlated. The purpose of the present thesis was to test two aspects of this theory, 1) that non-linear patterns of activity will be present between distributed neuronal groups during a visual information processing task, and 2) that increased patterns of correlations will be observed between distributed neuronal groups during a complex processing task, consistent with reentrant pathways in the cortex.

For both EEG and MEG phases, evidence in support of hypotheses one and two was obtained. The GRNN classifications for hypothesis one were able to find non-linear patterns in the experimental effects that were different than those observed in the control effect. The EEG single trial classifications were somewhat weaker than the MEG classifications however, in that only six of eight experimental effects were classified differently than control effects at the $p. < 0.05$ level. MEG single trials on the other hand were classified in 10 of 10 attempts. The magnitude of classifications for MEG was considerably larger as evidenced by the high t-test and Kendall's Tau values shown in Tables 3a and 3b.

At least three possible reasons for this difference in classification significance levels will be discussed. Firstly, the MEG has far better spatial resolution of the underlying cortical sources. The subset chosen to represent visual information processing areas contained 32 sensors while the EEG subset covering a comparable area contained a mere 10. Therefore, the GRNN had more spatial information to process for MEG classifications compared to the EEG. This may have increased the signal to noise ratio somewhat, as more signal behaving as correlations between sensor locations would be available in the MEG phase compared to the EEG signal which had fewer correlations and a degraded original signal due to attenuation from

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cerebrospinal fluid, bone, skin etc.   Second, the MEG phase consisted of more single trials which is important, because with enough information, the GRNN "is guaranteed to converge to a Bayesian classifier (the usual definition of optimality) despite an arbitrary and complex relationship between the training vectors and the classification" (Wasserman, 1993, p.35). Finally, MEG is primarily sensitive to tangentially oriented sources while EEG is more sensitive to radially oriented sources.   Gilbert and Wiesel (1983) discuss tangentially oriented collaterals of extraordinary richness and extent, extending over considerable areas of cortex, forming a number of distinct repeating clusters.   These   horizontal cortical connections may extend beyond wide cortical columns and, in fact, extended beyond hypercolumns (Gilbert, 1985).   Consistency of cortical connections is one of the focal tenets discussed by Zeki and Shipp (1988) and probably involve intercommunication between specialized systems. Tangential interconnections between distributed neuronal groups are presumably important components of cortico-cortical non-linear networks active during complex visual information processing. Therefore non-linear relationships between neuronal groups have an anatomical basis in the tangential network of collaterals that MEG is most sensitive to detecting.

It is important to emphasise at this point the role the GRNN classifications had in the selection of the transformation type and subset of electrode positions used in the EEG phase that eventually led to the methodology for the entire thesis. As is discussed in Appendix B, correlation and covariance transformations were used in order to discover which of the two transformations would contain enough information for GRNN classifications. The optimal transformation used for non-linear analysis is essential as this type of classifier (the GRNN as well as other neural network algorithms) is extremely sensitive to the signal to noise characteristics of the data. Similarly, the number and location of electrode positions that were optimal for GRNN classifications were not known at the outset of the project, and only after several different combinations of transformation and electrode array did the optimal combination surface. In retrospect, correlation transform data over the parieto-temporo-occipital cortex seems to be the obvious choice, especially when Edelman's position is taken into account. However, initially it

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was not known what contribution frontal lobe would have, or how variance in non-linear systems would affect the GRNN's ability to classify the data. The point is that GRNN analysis was not only an important index of non-linearity of neuronal groups active during processing of the Necker cube. It was an important indicator of the nature of neuronal activity and the spatial distribution of importance in this non-linear system. Consequently, consideration of GRNN analysis should not be limited to classification of non-linear systems, but should also be included as a method to parse salient information about a non-linear system from the universe of possible alternatives.

Hypothesis two was also supported by both the EEG and MEG phases of the thesis. According to Edelman's TNGS, reentry "varies statistically or regularly in time and space and, therefore, has components that relate it more to a process of correlation than signal control" (Edelman, 1989, p. 68). Therefore, one would expect correlations between proximal and distal electrode/sensor sites to be an appropriate index of this type of system. Significantly increased correlations between a subset of a priori selected electrode/sensor positions were observed for all paired comparisons. This is consistent with Edelman's process of reentry between distributed systems active during visual information processing.

In this instance however, no difference in magnitude of significance levels for EEG or MEG was observed, indicating that EEG and MEG are equally suited for this type of analysis. It is possible that radially oriented sources are affected equally, compared to tangentially oriented sources, in terms of their reentrant connections. The only difference may be that radial sources may connect to a higher proportion of subcortical neuronal groups, while tangential sources may contain more cortico-cortical projections. A more plausible explanation might be the optimal subset of correlations was not chosen in the initial a priori selection. As a result, the most appropriate subset of correlations could be drawn from the total number available to be more representative of the areas involved in processing information. In fact, there are probably numerous subsets that operate optimally at variable locations in time and space and that an a

priori, equally distributed subset that encapsulates the entire epoch only captures a fraction of the activity available for analysis. Due to the apparent non-linear nature of this process, the optimal subset of correlations that represent a reentrant process may not even be attainable with this simplistic mode of analysis. The initial results of this thesis then, look to be in agreement with the most elementary tenets of Edelman's theory. A non-linear pattern of activation is present in both of the reversal conditions that is classified differently than processing of a two dimensional figure. This complex pattern of activation results in higher correlations between electrode or sensor sites, and can be considered consistent with the process of reentry.

Certain experimental design issues should be addressed as they may be partially responsible for the results obtained. The first issue is the choice of the control stimulus. It has been rightly brought to the attention of the author that the simplistic two-dimensional figure (a square with side lengths of 15.5 cm contained in Appendix C) may not have been of sufficient complexity to serve as the control figure for the Necker cube reversal condition. Unfortunately the problem with selection of an appropriate control figure for the Necker cube condition is that a non-reversing figure is required. This limits the selection to a number of simple two-dimensional figures, as most figures that have a three-dimensional quality, also exhibit the property of perceptual reversal. Bergum and Flamm (1979) discuss and demonstrate the perceptual qualities of very simple figures, all of which have the quality of perceptual reversal to greater of lesser degrees. What may be responsible for even simple figures having this quality are what Kawabata (1986) called vertices, or intersections of three lines at a single point. Vertices were described in the introduction as important features for Necker cube reversals, and must also be considered important for a variety of other figures.

Since vertices appear to be responsible for perceptual reversals of several figures, using a two-dimensional figure such as a square is somewhat more justifiable. Nonetheless, a two-dimensional square is probably not *the* optimal control figure. A possible alternative would be to reorganise the lines and orientation of the Necker cube to remove all vertices. A

two-dimensional control figure of this nature would maintain the content of the Necker cube without the properties of perceptual reversal. This would ensure that processing of line orientation of the control figure would not be confused with processing of figure-ground and depth of the Necker cube.

Another design issue to be considered is the use of single trials instead of an average time locked to the stimulus or an event in the record. Investigations of Necker cube reversal have been performed using averaged evoked potentials. O'Donnell, Hendler and Squires, (1988) investigated the effects of changes in perceived orientation of the Necker cube in visual evoked potentials (VEPs). VEPs were recorded to a Necker cube and to two non-reversing stimuli. The non-reversing figures were described as perceptually invariant cubes shown in two different orientations at 180 degrees intended to be analogous to the two orientations of the Necker cube. All stimuli were projected for 700 msec on a translucent screen with a 3.3 second ISI. VEPs were recorded from Fz, Cz, and Pz and EOG was recorded from an electrode below the infraorbital ridge. Reversal trials were added to the average only after not reversing for the previous three trials.

Both the Necker cube and non-reversing figures produced VEP changes. A late positive component appeared to both the Necker cube and non-reversing stimuli. The late positive component was largest over Cz and peaked at 550 msec for non-reversing figures. The Necker cube on the other hand peaked positively at 625 msec frontally and did not appear at Oz and did not return to baseline within the 700 msec recording epoch. The authors conclude that attentional and cognitive processes are integral to figure reversals (O'Donnell, Hendler, Squires, 1988).

The central methodological issue with the type described above is that in avoiding the problems associated with time locking the response to the stimulus, the study also avoided the most interesting question, that being "What is the brain doing to create the perception of a reversing

cube when the actual stimulus remains constant?". This issue harkens back to Freeman (1981) who generally states that important results will come from studies that observe the brain as it performs the function of interest. The most interesting thing about the Necker cube as a perceptual tool is that even though the stimulus remains constant, the perception of the stimulus is progressively changing. Therefore, while averaging responses to a stimulus momentarily flashed on a screen offers the promise of a concise response, it also strays from the response of interest - the brain's activity that causes the spontaneous reversal of the Necker cube.

If the purpose of a research endeavour is to monitor brain function during spontaneous perceptual reversals, averaged responses are not a realistic option since no phase locked events are likely to occur. Even when an event is phase locked to a stimulus, other responses that are not phase-locked to the stimulus, such as transient synchronous oscillations would be blurred or lost during averaging (Desmedt & Tomberg, 1994). As for the current study, there was no guarantee that the patterns of correlations occurring prior to a reversal were related on a trial by trial basis. In fact, one should almost expect that over a number of successive trials, variability in the duration and intensity of the response will occur if the system is dynamic and non-linear. Therefore single trial EEG and MEG responses appear to be an effective index of non-linear cortical activity *provided the noise floor is sufficiently low.* This point especially salient with MEG as a variety of environmental magnetic fields can contaminate records in unshielded environments.

A final design issue to be discussed is the use of bandpass filtering as a method of enhancement of synchronous signals. Appendix B (analysis 3) describes the band pass filtering attempted on the EEG single trials based primarily on the literature that suggests increased 40 Hz activity present during information processing can be enhanced using this procedure. Considerable effort was expended to arbitrarily divide each EEG single trial into four 256 point quadrants (0-256; 257-512; 513-768; 769-1024) with the intention of locating the section of the single trials with the highest mean difference in 40 Hz (35-45 Hz) activity. Each single trial was subjected to

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band pass filtering for each 256 point quadrant within subject. No obvious difference in 40 Hz activity was observed in the single trial records between experimental and control conditions for any of the subjects.

Others have shown beneficial results from band pass filtering as a method of enhancing 40 Hz activity. Desmedt and Tomberg (1994) used two limited frequency windows (35 - 45 Hz) while Joliot et al., (1994) employed a wider window (20 - 50 Hz) to obtain images of gamma oscillations in the 40 Hz range. Consequently, band pass filtering appears to benefit researchers who are interested in parsing out activity within a narrow frequency band, however, there are at least two points to consider when using this method. The first is a technical consideration. Issues concerning narrow band pass filtering have been discussed by Bullock (1992), who cautions against their use in certain situations. Wide-band activity in short epochs or where activity is transient in frequency, damps out, or is not time locked to the event. An example he gives is that even when a sudden burst of noise containing a variety of frequencies is passed through a fairly broad band pass filter, burst of spindles in the gamma band can be artificially produced (Bullock, 1992).

The second is an anatomical reason. Singer (1993) describes variability in synchronous oscillations fluctuating between 30 and 60 Hz. Further, he states that the "frequency of these oscillations usually fluctuates over a range of 5 to 10 Hz even within a single oscillatory response" (Singer, 1993, p. 356). Constant frequencies are reported to be stable for 100 - 300 msec and reoccur several times while responding to a stimulus (Singer, 1993). More importantly, oscillations in primate cortex are reportedly more irregular than those observed in the cat (Engel et al., 1992). Therefore a narrow band pass filter may not be the optimal method of analysis especially for dynamic systems for several reasons. When used improperly, narrow band pass filtering could generate artifacts that resemble real oscillations in the 40 Hz range. More importantly, there is evidence that suggests synchronous activity is transient in nature and fluctuates dynamically within the gamma range. This point appears to be more salient when

discussing primate cortex. For a variety of reasons then, band pass filtering may not be the optimal analytical tool for monitoring gamma activity in cortex. In the current thesis, it failed to provide an indication of synchronous activity in the 40 Hz range, even though complex patterns of correlations were classified by the GRNN. It is possible that synchronous oscillations in other frequency bands such as alpha and beta were responsible for the majority of synchrony observed during reversals although that position would contradict most of the data presented thus far on gamma band synchrony in cortex during information processing. A more plausible explanation is that to analyze a dynamic system requires a dynamic method, such as neural network analysis which bypasses these shortcomings, especially when accompanied by appropriate transformations.

Therefore, future endeavours should capitalise on the use of neural network and correlation analysis to extend the results of the present thesis along the lines of Edelman's TNGS. The next logical step for research using ambiguous figures should be to detail the temporal sequence of events in visual cortex that occur immediately prior to perceived reversals, since it is unlikely that processing related to reversals occurs throughout the entire one second epoch prior to their occurrence. One way to accomplish this would be to use MEG single trial data similar to that collected for this thesis. If MEG single trials were scrutinised for increased correlation patterns over the 1000 msec epoch, on an individual basis, relationships between sensor locations represented by increased correlations should surface. A sliding window of 150 Hz for example could be used to gain information about increased correlations in that epoch, within one single trial. The window could then be moved by a predetermined value (e.g., 50 msec), and the processes of calculating which sensor sites had the maximal correlations could be repeated. Eventually, one could make comparisons between subjects as to which sensor locations shared the highest correlations, and most importantly, the temporal sequence in which the correlation patterns occurred. Of course, this would be a lengthy process, but the eventual possibility of answering the question of how temporal activity in visual cortex occurs during processing of a complex figure may outweigh the costs of lengthy periods of analysis time.

To conclude, as a preliminary test of Edelman's TNGS, neural network classifications coupled with correlation matrix transformations were successful in demonstrating the presence of non-linear patterns of activity during reversals of the Necker cube as different than processing of a two-dimensional figure. Significantly higher correlations in the experimental conditions were interpreted to be consistent with reentrant processes between distributed neuronal groups. The results provide evidence that although consistent with Edelman's TNGS, do not provide information about the temporal characteristic of information processing during reversals. Future research will focus on a detailed analysis in the time domain of each epoch prior to reversals, to further elucidate the nature of cortical activity during visual information processing. Increased use of neural network algorithms are advocated as methods for the detection of non-linear biological systems. Furthermore, neural network analysis should not be limited to classification of non-linear systems, but should also be included as a method to delineate meaningful information about a non-linear system, from the universe of possible alternatives.

Probabilistic Networks

The operation of the Probabilistic Network function in Simulnet is based on the principles of the generalised regression neural network (GRNN) developed by Don Specht (Specht, 1991), and discussed by Wasserman (1993). In general terms, the GRNN, like the back-propagation neural network, is able to approximate any functional relationship between input and output. The following description will be based on a GRNN being used as a classifier; that is, to learn to place test exemplars into one of two or more categories. The GRNN can, however, also function as an associator, learning the association between the values of one or more predictor variables, with the values of one or more criterion variables.

Structurally, the GRNN resembles the back-propagation neural network. The GRNN has a number of inputs equal to the number of predictor values in the training or testing exemplars. The input nodes of the GRNN, like those of a back-propagation network, are merely connection points to which the elements of the test exemplars are applied, one at a time. The GRNN has a number of hidden units equal to the number of training exemplars. There is one hidden unit for each training exemplar. Unlike the back-propagation network then, the GRNN does not require an estimate of the number of hidden units to be made before training can begin. Finally, the GRNN has a number of outputs equal to, if the GRNN is used as a classifier, the number of categories being discriminated, or more generally, the number of criterion variables being predicted.

Functionally, however, the GRNN differs from the back-propagation neural network. First, there is no counterpart to the iterated back-propagation network training phase. Instead, the entire training matrix is installed in the GRNN, as the weights between the input and hidden layers. In more detail, the weights between the input nodes and each hidden node represent a single

training exemplar. Thus, the weights between the input layer and hidden node 1 are the components of the predictor part of training exemplar 1 (remember that each exemplar, whether in the training matrix or the testing matrix, consists of two parts: the first part consists of the predictor values representing the values of the variables being used to predict some outcome, while the second part consists of the criterion values representing the values of the variables being predicted). The equivalent of training the GRNN thus takes no more time than is required to load the contents of the training file into working (RAM) memory. This scheme is in direct contrast with back-propagation networks which iteratively apply a heuristic, such as the method of steepest descent, to adjust the values of the input node to hidden node weights.

The testing phase of the GRNN similarly differs significantly from that of the back-propagation network. In order to describe the GRNN testing phase, it is useful first to state what the outputs of the GRNN represent (again, when the GRNN is used as a classifier). The outputs of the GRNN are the probabilities that the test exemplars belong to the categories being discriminated. The GRNN implements a procedure for estimating the probability of a test exemplar vector given a set of training exemplars, based on the principle of bayesian classification. The GRNN will, in fact, approach an optimum Bayesian classifier, given a large enough number of training exemplars (Wasserman, 1993). The algorithm used for GRNN testing may be described as follows.

The testing phase begins with a testing exemplar being applied to the input nodes. Each hidden node will thus receive the product, and more precisely the vector dot-product, of the testing exemplar and the training exemplar corresponding to that hidden node. This vector dot-product is a direct measure of the collinearity, or in general terms the similarity, between the test vector and a training vector. Other similarity measures can also be used. The algorithm used in Simulnet uses the sum of squares of the difference between the test and training vectors.

Each hidden node then performs a non-linear transformation on this dot-product. While in the back-propagation network the transformation generally involves the sigmoidal function, in the case of the GRNN the corresponding transformation involves the exponential function. The meaning of this transformed dot-product is that it represents the probability of obtaining the testing exemplar, given a probability density function with a mean equal to the training exemplar, and standard deviation defined by a parameter referred to as smoothing (generally, smoothing is the only parameter than needs to be selected when using the GRNN). Straightforwardly, the GRNN computes at each hidden node the probability of the current test exemplar, given the existence of the training exemplar corresponding to that hidden node. In sum, the more similar or collinear the testing and training exemplars are, the greater the probability of that testing exemplar belonging to the training exemplar category will be.

These individual probabilities need to be combined in order to generate the desired output of the GRNN. That is, the probability of the test exemplar, given all of the training exemplars. This combining is performed in the hidden to output section of the GRNN. The transformed output of each hidden node is connected to each output node. As in the back-propagation network, these connections between the hidden and output nodes contain weights. However, and again in contrast with the back-propagation network, these weights in the GRNN are not trained, but rather are assigned values. These values are dummy codes representing the category of each of the hidden nodes. Remember that each hidden node represents one training exemplar, and that that exemplar belongs to one of the categories being discriminated. The dummy codes between a hidden node and all the output nodes are 1 for the output node which represents the same category as the training node, and 0 for all other output nodes. As an example, if there are two categories, A and B, being discriminated, the GRNN will have 2 output nodes, node A and node B.

Let us assume that hidden node 1, representing training exemplar 1, belongs to category A. The weight between hidden node 1 and output node A will be 1, and the weight between hidden node

1 and output node B will be 0. The effect of this coding is to connect only hidden and output nodes of the same category, with the result that an output node of a particular category will receive inputs only from hidden nodes of the same category. The output node then simply sums these individual inputs. While each of these inputs represents the probability of the current test exemplar given a particular training exemplar, this sum represents the probability of the current testing exemplar given all of the training exemplars in one category. Finally, in order to generate an output which represents the actual probability, the value at each output node is normalised by dividing by the sum of all hidden node outputs.

Thus, for the 2 category example, the value generated by the network at output node 1 is the probability that the currently-applied test exemplar belongs to category A. The value at output 2 is the probability that the testing exemplar belongs to category B.

This technique of combining the probability density functions of individual exemplars of a category to approximate the probability density function of the category is due to Parzen (1962). Parzen showed that with a sufficient number of exemplars of a class, the result will approach the true probability density function of the category.

An advantage that the probabilistic network has over the neural network and the genetic network is the single pass nature of the algorithm. Training and testing can typically be several orders of magnitude faster for the probabilistic network than for the neural or genetic networks. A potential limitation is that, since all training examples are stored in working memory (RAM), the size of the training data set is limited by the amount of available memory. With 4 Mb of extended memory, a training file can consist of up to roughly several thousand examples with several hundred variables in each example.

Algorithm:

The following algorithm describes the testing phase of the GRNN.

For each test exemplar x_i

For each training exemplar u_j

Compute an estimate of the probability of x_i given the probability density function of u_j:
   $h_j = \exp[-(x_i - u_j)T(x_i - u_j) / (2s^2)]$ (where s is smoothing)

Compute the sum over the probabilities for all training exemplars: Sum (h_j)
For each output (category) c_k

Compute the sum of the probabilities h_j for training exemplars from category k.
   $c_k = \text{Sum } (h_j = k)$
Convert this sum to a probability by dividing c_k by the sum over all h_j:
   $c_k = [\text{Sum } (h_j = k)] / [\text{Sum } (h_j)]$
c_k now represents an estimate of the probability of test exemplar x_i given all training exemplars h_j from category k.

References

Parzen, E. (1962) On estimation of a probability density function and mode. Annals of Mathematical Statistics, 33, 1065-1076.

Specht, D. F. (1991) A general regression neural network. IEEE Transaction on Neural Networks, 2(6), 568-576.

Wasserman, P. D. (1993) Advanced Methods in Neural Computing. New York: Van Nostrand Reinhold.

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Appendix B

The following is a step by step procedural description of the EEG phase of this project. Several analytical attempts were made in this phase, and it is hoped that a review of these attempts may help the reader understand how the final methodology was developed. The data discussed in this review are EEG data only, since the EEG phase was intended to be the exploratory phase of the project.

Analysis 1. As stated, the original EEG single trials consisted of 19 electrodes, each with 1024 points. Early in the analysis procedure, it was found that single trials would classify based on the small eye movements present during Necker cube reversals. To avoid this confound, Fp1 and Fp2 were removed from the analysis, leaving 17 electrode positions for analysis. From this point, four different processing conditions were carried out. For each single trial, covariance and correlation matrices were calculated, resulting in two 17 x 17 matrixes. Since reductions of signal to noise were believed to be important for neural network classifications, a reduced number of electrode positions were also selected from areas of cortex thought to be involved in this type of processing. This subset included central, temporal, parietal and occipital positions (T3, C3, C4, T4, T5, P3, P4, T6, O1 and O2). Covariance and correlation matrices were calculated for this subset of electrode positions, resulting in two 10 x 10 matrixes. Therefore, four matrix types were processed for each of the single trials.

Each of the four matrix types were analyzed using one-tailed equal variance t-tests and the one-tailed Kendall's Tau procedure. Two classification attempts were made per matrix (experimental condition 1 vs. control; experimental condition 2 vs. control) for a total of 8 classification attempts. Clearly, the 10 x 10 correlation matrix classified significantly more often than did any other matrix. In order of classifiability, the four matrixes, from best to worst were as follows:

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1. 10 x 10 correlation matrix   (6 of 8)

2. 17 x 17 correlation matrix   (4 of 8)

3. 10 x 10 covariance matrix   (3 of 8)

4. 17 x 17 covariance matrix   (3 of 8)

As shown above, covariance matrixes did not classify as well in comparison. In general, the 17 x 17 matrixes mimicked the 10 x 10 matrix classifications, correlation matrixes resulting in significantly more classifications per subject. Therefore, the decision to use the 10 x 10 correlation matrix data was obvious, as it appeared to hold more important information than did any of the others.

Analysis 2. To ensure that high correlation subsets of were not restricted to posterior locations, a subset of correlations between frontal (F7, F3, Fz, F4, F8) and parietal, posterior temporal and occipital (T5, P3, Pz, P4, T6, O1 O2) electrode positions were analyzed for mean and variance differences between experimental and control groups. No consistent differences were observed between the conditions, and intersubject variability was high. Interestingly, a consistent pattern found across all subjects and conditions was low mean values for correlations between electrode positions over left fronto-temporal cortex. Specifically, drastically low or even negative correlations were observed when any posterior electrode was compared to either F7 or T3. No low correlations were found in the homologous electrode positions, suggesting that this area of cortex may be involved in processing different from posterior cortex or right hemisphere.

Analysis 3. Band pass filtering was also attempted, primarily based on the literature that suggests increased 40 Hz activity may be present during complex visual information processing. Considerable effort was expended to arbitrarily divide each EEG single trial into four 256 point quadrants (0-256; 257-512; 513-768; 769-1024) with the intention of locating the section of the single trials with the highest mean difference in 40 Hz (35-45 Hz) activity. Each single trial was subjected to band pass filtering [7] for each 256 point quadrant within subject. No obvious difference was observed in the single trial records between experimental and control conditions

for any of the subjects. A discussion as to the appropriateness of band pass filtering for complex cortical activity can be found in the discussion section.

Analysis 4. Preliminary attempts were made to observe slow shifts in the data. A limited number of single trial (5 per condition/subject) were plotted and scrutinised for consistent slow shifts at a point in time related to eye closure. The data appeared heterogeneous in nature, especially between subjects, and no further frequency analysis of slow wave activity was undertaken.

Analysis 5. Other neural network algorithms were used in attempts to determine the best non-linear classifier. A back-propagation neural network and a genetic algorithm from SIMULNET were employed to classify data that had been successfully classified using the GRNN network. Neither the back-propagation or genetic algorithm classified any of the training-testing files, and subsequently they were not used in any further analyses.

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[7]   The software used during the frequency analysis was developed by a member of the Brain Behaviour Laboratory (KJ Jantzen).
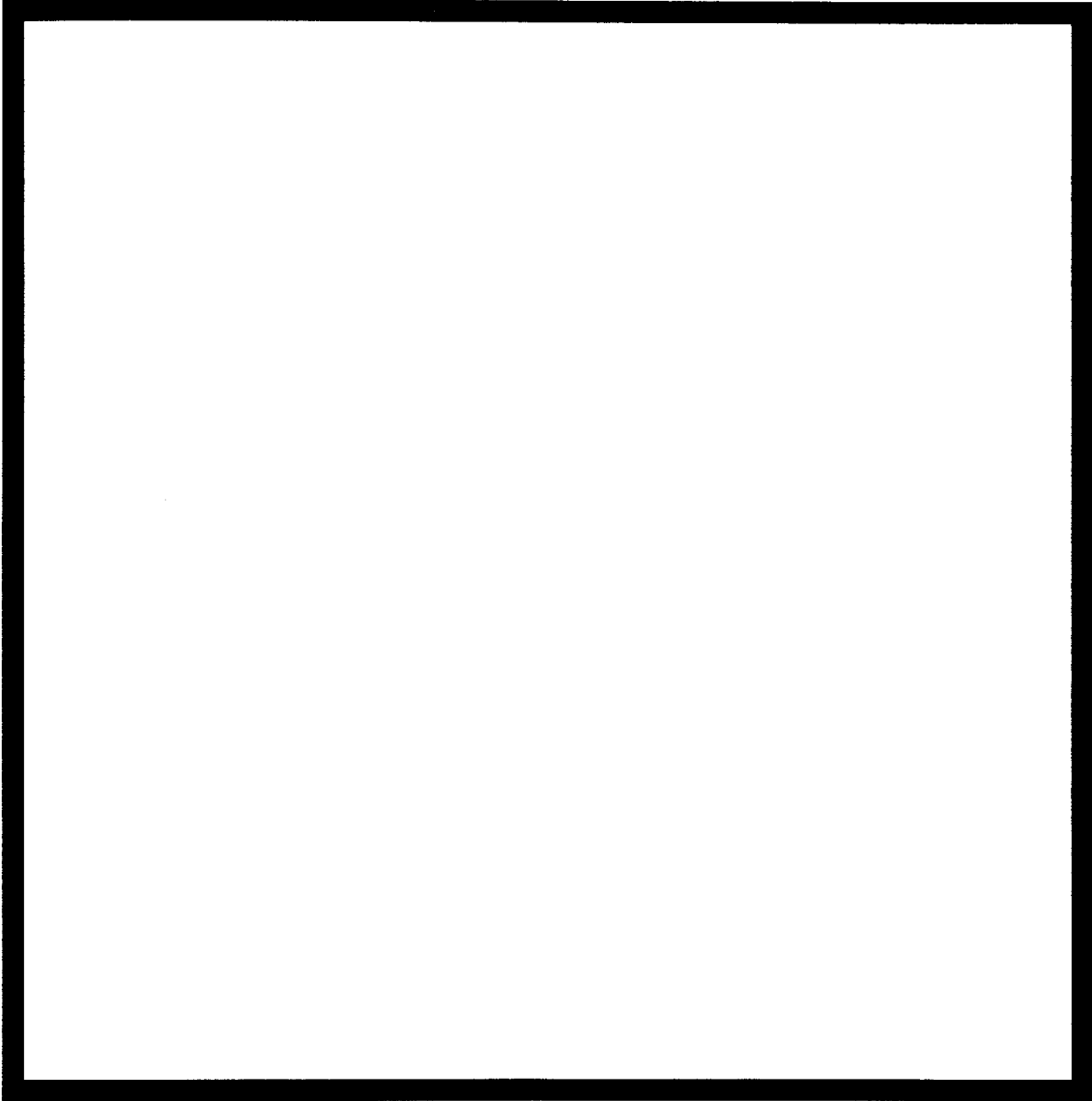
The Necker Cube
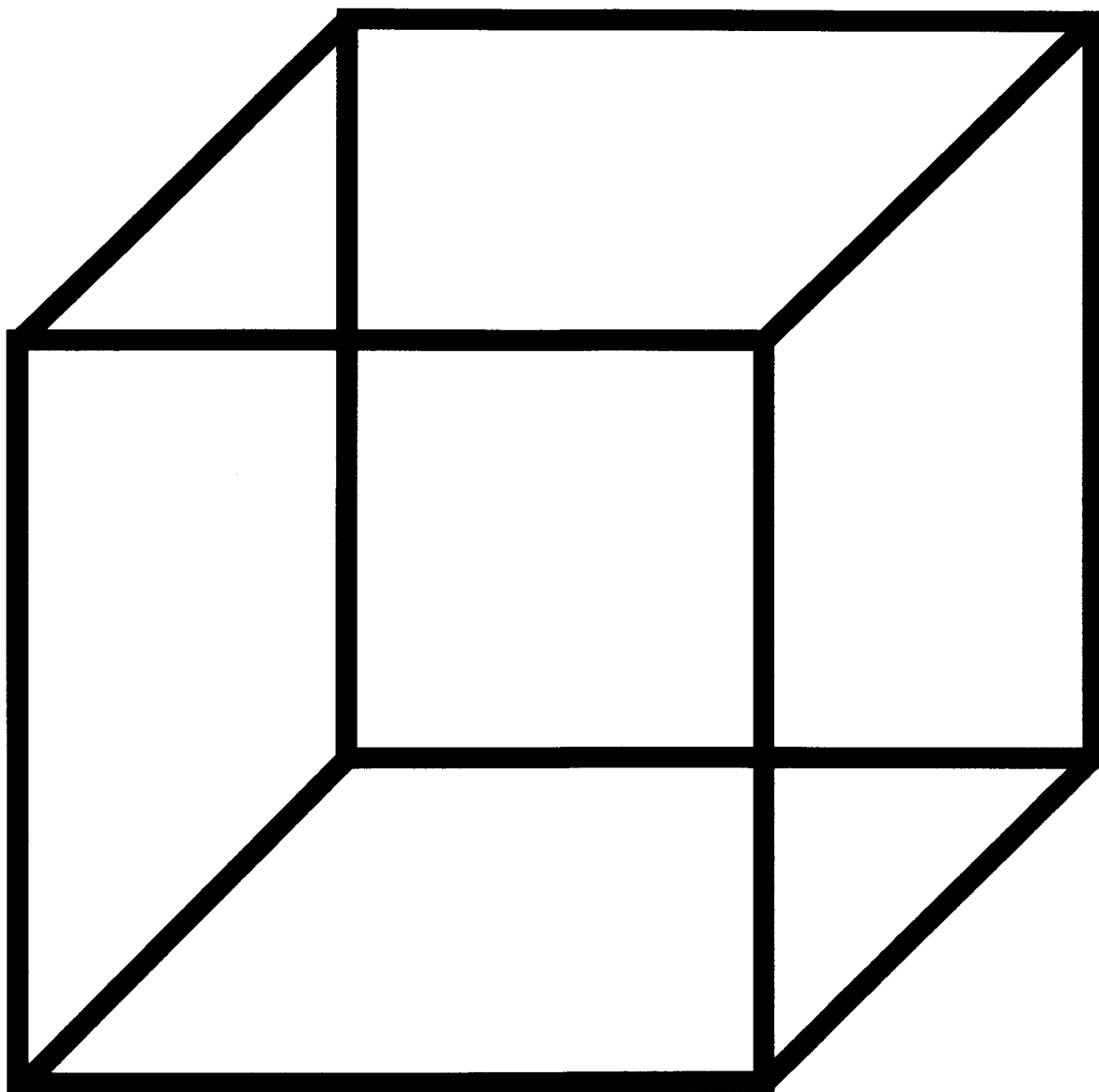
Appendix C cont.

The 2-D control figure

References

Babich, S., & Standing, L. (1981). Satiation effects with reversible figures. Perceptual and Motor Skills, 52, 203-210.

Bullock, T. (1992). Stimulus-specific synchronizations in cat visual cortex: Multiple microelectrode and correlation studies from several cortical areas. In E. Basar & T.H. Bullock (eds.), Induced Rhythms in the Brain (pp. 1-26). Boston: Birkhauser.

Camp, C., Markley, R., & Danielson, J. (1982). Necker cube reversals in young, middle-aged, and elderly females. Perceptual and Motor Skills, 54, 1215-1218.

Cohen, L. (1959). Perception of reversible figures after brain injury. A.M.A. Archives of Neurology and Psychiatry, 81, 765-775.

Desmedt, J., & Tomberg, C. (1994). Transient phase-locking of 40 Hz electrical oscillations in prefrontal and parietal human cortex reflects the process of conscious somatic perception. Neuroscience Letters, 168, 126-129.

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., & Reitboeck, H. (1988). Coherent oscillations: A mechanism of feature linking in the cat visual cortex? Biological Cybernetics, 60, 121-130.

Eckhorn, R., Reitboeck, H., Arndt, M., & Dicke, P. (1989). A neural network for feature linking via synchronous activity: Results form cat visual cortex and from simulations. In R.M.J. Cotterill, (ed.), Models of Brain Function (pp. 225-272). Cambridge: Cambridge University Press.

Eckhorn, R., Schanze, T., Brosch, M., Salem, W., & Bauer, R. (1992). Stimulus-specific synchronizations in cat visual cortex: Multiple microelectrode and correlation studies from several cortical areas. In E. Basar & T.H. Bullock (eds.), Induced Rhythms in the Brain (pp. 47-80). Boston: Birkhauser.

Edelman, G. (1989). The Remembered Present. New York: Basic Books.

Edelman, G. (1993). Neural Darwinism: Selection and reentrant signalling in higher brain function. Neuron, 10, 115-125.

Ellis, S., & Stark, L. (1978). Eye movements during the viewing of Necker cubes. Perception, 7, 575-581.

Engel, A., Konig, P., Kreiter, A., Schillen, T., & Singer, W. (1992). Temporal coding in the visual cortex: New vistas on integration in the nervous system. Trends in Neuroscience, 15, 218-226.

Ferster, D. (1988). Spatially opponent excitation and inhibition in simple cells of the cat visual cortex. Journal of Neuroscience, 8, 1172-1180.

Finkel, L.H. & Edelman, G.M. (1989). Integration of distributed cortical systems by reentry: A computer simulation of interactive functionally segregated visual areas. Journal of Neuroscience, 9 (9), 3188-3208.

Freeman, W. (1979). Non-linear dynamics of paleocortex manifested in olfactory EEG. Biological Cybernetics, 35, 21-37.

Freeman, W. (1981). A physiological hypothesis of perception. In: Perspectives in Biology and Medicine. Chicago: University of Chicago Press, 561-592.

Gilbert, C. (1985). Horizontal integration in the neocortex. Trends in Neuroscience, 8, 160-165.

Gilbert, C., & Wiesel, T. (1983). Clustered intrinsic connections in cat visual cortex. The Journal of Neuroscience, 3, 1116-1133.

Girgus, J., Rock, I., & Egatz, R. (1977). The effect of knowledge of reversibility on the reversibility of ambiguous figures. Perception and Psychophysics, 22, 550-556.

Gray, C., Konig, P., Engel, A., & Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature, 338, 334-337.

Gray, C., Engel, A., Konig, P., & Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: Receptive field properties and feature dependence. European Journal of Neuroscience, 2, 607-619.

Gray, C., Engel, A., Konig, P., & Singer, W. (1992). Mechanisms underlying the generation of neuronal oscillations in cat visual cortex. In E. Basar & T.H. Bullock (Eds.), Induced Rhythms in the Brain (pp. 29-46). Boston: Birkhauser.

Gray, C., & Singer, W. (1989). Stimulus specific neuronal oscillations in orientation columns of cat visual cortex. Proceedings of the National Academy of Science, 86, 1698-1702.

Gray, C., & Singer, W. (1990). Stimulus-dependent neuronal oscillations in cat visual cortex: Inter-columnar interaction as determined by cross-correlation analysis. European Journal of Neuroscience, 2, 588-606.

Hubel, D., & Wiesel, T. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. Journal of Physiology (London), 160, 106-154.

Jasper, H.H. (1958). The ten-twenty electrode system of the International Federation. Electroencephalography and Clinical Neurophysiology, 20, 371-375.

Joliot, M., Ribary, U., & Llinas, R. (1994) Human oscillatory brain activity near 40 Hz coexists with cognitive temporal binding. Proceedings of the National Academy of Science, 91, 11748-11751.

Kawabata, N. (1986). Attention and depth perception. Perception, 15, 563-572.

Lezak, M. (1976). Neuropsychological Assessment. New York: Oxford University Press.

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

Llinas, R., (1992). Oscillations in the CNS neurons: A possible role for cortical interneurons in the generation of 40 Hz oscillations. In E. Basar & T.H. Bullock (Eds.), Induced Rhythms in the Brain (pp. 29-46). Boston: Birkhauser.

Long, G., Toppino, T., & Kostenbauder, J. (1983). As the cube turns: Evidence for two processes in the perception of a dynamical reversible figure. Perception and Psychophysics, 34, 29-38.

Necker, L. (1832). "Observations on some remarkable phenomenon seen in Switzerland: and an optical phenomenon which occurs on viewing a figure of a crystal or geometrical solid". Philosophical Magazine and Journal of Science, 1, Third Series, 329-337.

O'Donnell, B.F., Hendler, T., & Squires, N.K. (1988). Visual evoked potentials to illusory reversals of the Necker cube. Psychophysiology, 25, 137-143.

Reisberg, D., & O'Shaughnessy, M. (1984). Diverting subjects' concentration slows figure reversals. Perception, 13, 461-468.

Riani, M., Olivia, G., Selis, G., Ciurlo, G., & Rossi, P. (1984). Effect of luminance on perceptual alternation of ambiguous patterns. Perceptual and Motor Skills, 58, 267-274.

Schellinger, T., & Beer, J. (1993). Passive viewing of the Necker cube during massed and distributed practice. Perceptual and Motor Skills, 76, 31-34.

Schulman, G. (1993). Attentional effects on Necker cube adaptation. Canadian Journal of Experimental Psychology, 47, 540-547.

Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. Annual Review of Physiology, 55, 349-374.

Specht, D.F. (1991) A general regression neural network. IEEE Transactions on Neural Networks, 2(6), 568-576.

Ta'eed, L., Ta'eed, O., & Wright, J. (1988). Determinants involved in the perception of the Necker cube: An application of catastrophe theory. Behavioral Science, 33, 97-115.

Toppino, T., & Long, G. (1987). Selective adaptation with reversible figures: Don't change that channel. Perception and Psychophysics, 42, 37-48.

Van Essen, D., Anderson, C., & Felleman, D. (1992). Information processing in the primate visual system: An integrated systems perspective. Science, 225, 419-422.

Wasserman, P. (1993) Advanced Methods in Neural Computing. New York: Van Nostrand Reinhold.

Zeki, S., & Shipp, S. (1988). The functional logic of cortical connections. Nature, 335, 311-317.