VISUAL PROCESSING OF PICTORIAL AND FACIAL IMAGES IN HUMAN AND MONKEY

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VISUAL PROCESSING OF PICTORIAL AND FACIAL IMAGES IN HUMAN AND MONKEY

BY

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PhD. thesis submitted to the University of St. Andrews.
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FOR MY FATHER AND MOTHER

(a) I..SHARON THOMAS hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfillment of any other degree of professional qualification.

Signed..
Date..............17./6./92......................

(b) I was admitted to the Faculty of Science of the University of St. Andrews under Ordinance General No. 12 on ...1st Oct....1988...and as a candidate for the degree of Ph.D. on....1st Oct..1988..........

Signed..
Date............17./6./92....................

(c) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the degree of Ph.D.

Signature of Supervisor................................. Date.........17/6/92........................

Maybe my mind didn't snap. Maybe
it was just trying to stretch:
itself
into a new shape:
The cerebral cortex trying to grow a thumb
of sorts:

It might seem like I got delusions of grandeur on
top of: everything else,
but maybe I didn't have a:
breakdown - maybe I had a break*through*.
Maybe: evolution's using my mind
in some kind of scientific
experiment.

Sure feels like it.
But look, if I can be of service to
humankind's progress, the:
loss of my mind is a small price to pay.
I just think I should have been consulted.

Jane Wagner:
"The Search For Intelligent Life In The Universe"

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CONTENTS

CHAPTER EIGHT.

EVENT-RELATED POTENTIAL STUDY IN A NON-HUMAN PRIMATE SUBJECT USING FACE AND OBJECT STIMULI: REPETITION EFFECTS AND STIMULUS SPECIFICITY.

CHAPTER NINE.

HUMAN BEHAVIOURAL STUDY OF REPETITION EFFECTS WITH FAMILIAR AND UNFAMILIAR FACES.

ABSTRACT

Over the last two decades, the study of 'repetition effects' in behavioural and Event Related Potential (E.R.P) research has originated and added to theories of memory organisation. In this series of experiments, behavioural and E.R.P correlates of human and monkey visual memory were investigated, using the repetition effect as the main index of processing, and manipulating the semantic content of the experimental stimuli. The research has a large founding in established results from lexical studies. The use of pictorial material in this series of experiments extends these results to more general visual memory functions.

E.R.P recordings were taken from two monkeys trained extensively to perform a matching-to-sample picture recognition task. The waveforms generated by novel instances of highly familiar pictures were compared to those elicited by repeats. In a further study with unfamiliar pictures the repetition of items had an effect on the evoked potentials for only one of the two subjects. Two further studies were made with one monkey viewing unfamiliar and familiar face pictures. In both these studies, an early potential emerged which was more positive in response to faces than to objects.

In order to investigate the importance of the semantic content of stimulus items for memory processes, human E.R.Ps generated by novel and repeated presentations of 'meaningful' and 'meaningless' pictorial images were recorded. Repetition of the meaningful (but not meaningless) pictures attenuated the N400 component associated with the first presentation of a stimulus.

CHAPTER ONE

HUMAN MEMORY SYSTEMS: THEORETICAL FRAMEWORK

Repetition effects were also investigated in humans at the behavioural level using famous and unknown facial stimuli. Subjects could recognize pictures of both famous and unfamiliar faces after a 20min delay. However, only exposure to famous faces resulted in a facilitation of subsequent reaction time in a famous/non famous decision task. The results indicate that long term repetition effects require access to existing semantic memory processes.

CHAPTER ONE

HUMAN MEMORY SYSTEMS: THEORETICAL FRAMEWORK

1.1 INTRODUCTION

This chapter consists of a review of the current state of research into encoding and retrieval processes in human memory, with particular emphasis on verbal and facial memory. Attention will mainly be focused on research investigating priming phenomena in which the manipulation of task and stimulus material has led to associated theories of memory organisation.

1.2 TYPES OF MEMORY

Distinctions are frequently made in research between types of memory. One such distinction which has promoted a great deal of interest and research is that proposed by Tulving (1972). He distinguishes between *semantic* and *episodic* memory. Semantic memory is thought to contain general knowledge about the world and language. It allows the individual to make both concrete and abstract mental models of the world. Episodic memory is the system which allows individuals to remember personal happenings in the past. It stores information about events in terms of the time and place of occurrence. Tulving revised his theory (1983, 1984) suggesting that episodic memory is a part of semantic memory rather than an independent system. He also proposed two additional memory systems independent from either semantic or episodic memory. These he termed "procedural" and "lexical" memory. Procedural memory stores learned connections between stimuli and responses.

The distinction between semantic and episodic memory has been called into question by a number of researchers (eg. Baddeley 1984, Hinzman 1984, McKoon et al 1986, Roediger 1984) and some experimental findings have blurred their independence

(McKoon and Ratcliff 1979, McKoon et al 1985). These theorists explain the phenomena associated with a distinction in memory by reference to a framework of *unitary* memory. Results which imply a distinction in memory are explained with reference to the type of investigative task used at retrieval.

Other functional distinctions have been made in memory theory which broadly correspond to semantic and episodic memory. Schacter and Graf (1986) distinguish between "implicit" and "explicit" memory. Explicit memory is similar to episodic memory, while implicit memory is akin to semantic (and procedural) memory. Memory with and without "awareness" has also been proposed (Jacoby and Witherspoon 1982). Such distinctions are closely related to "two-process" models of encoding and retrieval. These are discussed in detail below.

Of particular interest in studies investigating the relative contributions of semantic and episodic memory to encoding and retrieval, is the widely studied "repetition effect". This refers to the effect whereby a previously experienced stimulus will be recognised more quickly and more accurately minutes, hours or days later than a stimulus that has not received the same pre-exposure. The phenomenon was first reported for word recognition and has been demonstrated in a variety of tasks, eg. word identification (Jacoby and Dallas 1981, Jacoby 1983, Jacoby and Witherspoon 1982, Morton 1979, Murrell and Morton 1974) and also in tasks employing lexical decisions (Scarborough et al 1977, Scarborough et al 1979).

Much research has centered on the question of whether these repetition effects are functions of semantic/lexical memory or episodic memory. The former is proposed as the locus of the repetition effect by Morton (1969, 1979).Within the framework proposed by Morton, repetition effects result from the temporary modification of abstract pre-existing memory representations. The abstract representations for words are termed "logogens" which are "word detectors" with thresholds that must be exceeded before the logogen "fires" and the word is recognised. Following each firing, the threshold is lowered slightly such that a word recognised recently will be recognised again slightly faster than a word not so primed. Thresholds of logogens may be lowered directly following presentation of the word itself (repetition priming or identity priming). Also, a semantically related item can prime recognition of a target - this has been termed 'Associative' or 'Semantic' priming. For example, if the word "salt" is identified once, it will be identified faster on a later occasion. The word "pepper" will also be identified more quickly because of its association with the word "salt", than an unrelated stimulus word from another category. Both repetition and semantic priming have been explained in terms of a recognition unit framework, with repetition priming resulting from the direct lowering of the recognition unit and semantic priming resulting from a "spreading activation" throughout the system. The response facilitation is accounted for by assuming that activation spreads from the prime to the target, so that when a target is presented, its activation level has already been raised, and therefore a faster and more accurate response can be made to the target stimulus.

The word recognition model proposed by McClelland and Rumelhart (1981) appealed to an instance-based account of repetition effect phenomena while still retaining abstractive word detector units within the model. The model was proposed to be made up of two levels of feature detectors and word detectors operating in "cascade" - that is, before analysis has been completed at the feature detector level, analysis has already begun at the word detector level. The feature and word detector levels could both facilitate and inhibit one another. More recently, McClelland and Rumelhart (1985) have discarded abstractive units from their model and have accounted for abstractive properties in terms of the summation of particular instances. These abstractive properties are seen to emerge from a parallel distributed memory network which retains all previous instances of a concept, while still preserving recent instances. The units within the network are interconnected and may represent particular features, but features may also be represented as patterns of activities within the networks. The units all send signals at different strengths modulated by a corresponding set of weights. Instances themselves are not stored. It is the change in weights between the different connections, resulting from the particular instance which is stored. Memory patterns can then be recreated with partial activation of the network. This "module" or pattern of interconnections, will respond strongly to a prototype pattern, but it will also show strong response to particular recent instances of the pattern.

Alternative to these spreading activation accounts of how priming works, it has been proposed that the facilitation occurs not from any modification to the target in long-term memory, but rather the prime and target together are matched against long-term memory. This has been termed "compound cue" theory (Ratcliff and McKoon 1988). That is, upon presentation of a target, it is matched in recent memory with the prime and these together form a compound cue to be matched against long-term memory. The greater the association between prime and target in long-term memory, the greater the facilitation in response to the target.

An alternative account of word repetition effects has been proposed which postulates that they depend on purely episodic memory processes (eg. Jacoby 1983, Feustel et al 1983). The repetition effects are seen to result from the formation and subsequent retrieval of a *specific* memory about an item's prior presentation. The fact that non-words exhibit repetition effects is often emphasized in episodic accounts, as they presumably do not possess any prior representations in memory (Feustel et al 1983, Salasoo et al 1985). These nonword repetition effects however, last for a much shorter period of time than those observed with real words (Monsell 1985) and there have also been other explanations as to why such effects could occur without abandoning a recognition unit explanation, such as that suggested by Feustel et al (1983). They suggest that the semantic store *is* contacted on presentation of nonword stimuli because of the automatic nature of spread of activation through the network. The representations of words that are similar to nonwords are thus partially activated. It has been demonstrated by Rugg and Nagy (1987) in an experiment using event related potentials, that there were significant differences in priming effects depending on whether the nonword was 'orthographically legal' or not. They suggest that the orthographically legal parts of nonwords (letter strings which are found in real words) could partially activate established recognition units and this manifests itself as a repetition effect.

The assertion that the repetition effect is tapping semantic rather than episodic memory is supported by the finding that repeating an item has a much different effect on recognition memory, an episodic task, than on semantic tasks. The repetition effect may persist essentially without change for days in a semantic task, while recognition performance for the same materials deteriorates over comparatively short periods of time (Jacoby and Dallas 1981, Jacoby and Witherspoon 1982, Scarborough et al 1977, Scarborough et al 1979, Tulving et al 1982). The implication that this independence reflects different memory systems has been questioned by Feustel et al (1983). They posit that a word must be identified before a recognition judgement can be made. Thus, the identification process is completely embedded in the recognition processes, with recognition requiring a further additional decision stage. They conclude that the independence observed between recognition responses and identification facilitation bears on the type of processing necessary for performing the two tasks. This does not reflect the working of two different memory systems. Jacoby (1983) has also suggested that the identification process is intimately involved in recognition memory performance. Feustel et al (1983) thus do not necessarily posit the distinction between the two memory systems and are open to the idea that semantic knowledge is an emergent property of amalgamations of individual episodic traces. Alternatively, they suggest that the identification response could result from a 'race' between episodic and semantic traces or from some synergistic interaction between the two. They emphasise however, that a sharp distinction is posited between one characteristic of semantic codes for words (logogens) and another characteristic of episodic codes for nonwords: the presence or absence of a "unitized response". Word/nonword differences may be due to an automatic generation of a unitized code for words that is not available for (unfamiliar) nonwords. They suggest that it is this availability of a unitized code that appears largely independent of the factors producing repetition effects. The presence of an episodic image for a word speeds the identification process more or less uniformly, whereas the fact that an item is a word tends to increase the ease with which it is encoded into a form more resistant to decay. The levels in the "analytic path" in the Feustel et al model make contact with the episodic traces that are consistent with the activations within these levels. To the extent that an episodic image is consistent with the activations at any given level, it will itself become active. The analytic process also interacts with the preexperimental traces, including codes like "logogens" and lexical codes in the case of words. These contain unitized representations that are responsible for automatically producing a phonological code and/or name code when appropriate. The most important point is that both semantic and episodic memory components are accessed during the identification of words and nonwords - what is important is the manner in which an identification response is produced for word and nonword stimuli - a unitized code being available for words, whereas for nonwords, an additional phonological construction process is required to produce a response.

1.3 ENCODING PROCESSES

The type of processing performed on an item to be remembered may influence how well the item is stored in memory. This is the corner stone to the 'levels of processing' theory proposed by Craik and Lockhart (1972). They suggest two types of analysis which are carried out on stimulus items; 'shallow' and 'deep'. Shallow analysis is concerned with the physical attributes of the stimulus, whilst deep analysis is concerned with meaning and associative relationships between the stimulus and other stimuli. Factors such as the semantic content of the stimuli, attention and the task involved determine the depth of encoding. In support of this, some studies (eg. Hyde and Jenkins 1973, Schulman 1974) have demonstrated that when subjects attention is drawn to the meaning of a word (ie. a semantic task) rather than its physical attributes (eg. phonemic structure), it leads to greater recall. While this initial tenet of the levels of processing approach has been substantiated in many studies, the concept of depth of processing has been called into question by a number of researchers (eg. Baddeley 1978, Eysenck 1977). The concept of 'elaboration' has been suggested in order to define more fully the levels of processing approach (Craik and Tulving 1975, Lockhart et al 1976, Anderson and Reder 1979). Also proposed is the concept of 'distinctiveness' (Bransford et al 1979, Craik and Jacoby 1979, Jacoby and Craik 1979, Nelson 1979, Eysenck 1979). These researchers suggest that semantically processed traces are more distinct from each other than traces processed with regard to their surface properties. They therefore predict that more distinctive traces will be recalled more efficiently. The studies which have been reported directly investigating this proposition have in the main manipulated the task requirements. For example, Jacoby et al (1979) varied the difficulty of semantic judgements at stimulus presentation. They found that more difficult decisions led to better retention. They conclude that more difficult initial processing promotes elaborative or extensive analysis and this results in a more distinctive memory of the event. This is then retrieved with greater ease than a trace for items which have not undergone such extensive processing.

The concept of the 'effort' involved in the processing of stimulus items has also been important in the discussion of levels of processing. This has been used to explain the 'generation effect' (Jacoby 1978, Slamenka and Graf 1978). Slamenka and Graf presented subjects with related word pairs which were either complete (eg. rapid-fast, ruby-diamond) or incomplete word pairs (eg. rapid-f , ruby-d). Words which were generated were recalled and recognised more efficiently than non-generated words. Jacoby (1978) suggested that it is the involvement of consciousness and heightened arousal that is responsible for superior performance with generated words.

The extent to which the initial processing of an item will influence future processing is not absolutely clarified, but there is little doubt that the type of task required when a stimulus is first encountered in a particular context can be a powerful determinant of performance on future tests. The next section deals with direct and indirect tests of memory after encoding stages.

1.4 RETRIEVAL PROCESSES:DIRECT AND INDIRECT TESTS OF MEMORY

Comparisons of performance on direct and indirect tests of memory are important in order to gain some insight into how memory for an event is influenced by prior knowledge. An indirect test of memory for instance can be a stem completion task. In this case, subjects are not asked directly to report on memory for a prior event but may be presented with a word stem (eg.com-) and are asked to complete the stem with the first word which comes to mind (eg.comic). The finding that there is an increased tendency to generate a word which has been presented earlier (eg.Graf and Mandler 1984), is indirect evidence of memory for the previous presentation. Recall and recognition tests are, on the other hand, direct tests of memory for events in the past.

Jacoby et al (1981) have proposed two bases for recognition memory. The first of these is termed 'perceptual fluency' which is effected or incremented by prior presentations and emphasises intra-item encoding. The second is 'retrieval of study context'. Jacoby suggests that recognition depends on both perceptual fluency and retrieval of study context, but that recall depends on retrieval of study context alone. In 1981, Jacoby and Dallas showed a dissociation of the effects of encoding upon perceptual identification and recognition. Task manipulation affected recognition memory but not perceptual identification while varying the number of repetitions affected both recognition memory and perceptual identification.

Jacoby (1983) has suggested that perceptual fluency may underlie all repetition effects eg. word-fragment completion, lexical decision, solving tasks. Jacoby and colleagues (Johnston et al 1985) have provided evidence for this theory. They suggested that if perceptual fluency is the basis for recognition memory, then words which are fluently perceived (quickly identified) would tend to be judged 'old' regardless of their actual old/new status. This was found to be the case. This was also found to be true when non-words were used as stimuli. Jacoby and colleagues conclude that perceptual fluency is the basis for feelings of familiarity, and that "a feeling of familiarity is the essence of remembering" (Whittlesea et al 1990). Familiarity is defined as a conscious feeling that accompanies retrieval of memory for past experience. Therefore, having and using a memory trace is necessary for a feeling of familiarity to arise. This assertion is tempered with the consideration that the use of memory does not always give rise to feelings of familiarity (eg. unintentional plagiarism). Illusions of memory may also exist as the phenomenon of 'deja vu'. Thus feelings of familiarity do not directly reflect the use of memory. Jacoby and others have attempted to induce illusions of familiarity in a variety of tasks (Witherspoon and Allan 1985, Mandler et al 1987, Jacoby and Whitehouse 1989, Whittlesea et al 1990). Jacoby suggests that these cognitive and perceptual illusions can be explained as resulting from an influence of prior experience on the fluency of perception and thinking (Jacoby and Whitehouse 1989). Effects of past experience on perceptual and cognitive fluency can be experienced as a change in the quality of current processing and therefore are misattributed to a source in the present. Following on from this line of thinking, Jacoby and colleagues suggest that it should be possible to produce an illusion of familiarity by manipulating the physical characteristics of a stimulus item in a way that influences perceptual fluency without affecting prior experience of that item. Whittlesea et al (1990) tested this possibility in a word recognition task. In the first experiment reported, 58 subjects were presented with a list of seven high-frequency four letter words at a rapid rate. The reason for rapid presentation was to preclude the possibility that subjects would engage in any mnemonic strategies. They were then immediately presented with an eighth word as a recognition test item. On half the trials, this test word was repeated from the original list ('old' word) and subjects were informed of this fact. Subjects were asked to pronounce the test word and also to state whether it was old or new. The fluency of processing this test word was also manipulated by masking varying from 20% occlusion to 40% occlusion. The authors predicted that both old and new words would be more likely to be called 'old' when they were presented in light rather than heavy masking, ie. the ease of fluency would be misattributed to prior experience.

Post-experimental questioning of the subjects revealed that 8 of them had been aware of the mask manipulation and their data was thus discarded from the major analysis. Subjects also reported that they had relied on recall or feelings of familiarity as the basis for their decisions. Subjects were found to pronounce the test words more quickly when the mask was light rather than heavy, confirming that perceptual fluency had been manipulated. Pronunciation was also faster when the test word had been seen before.

Subjects were also twice as likely to report a word as old if it had appeared earlier than if it had not, but they were also more likely to report the word as old if it had been presented in light rather than heavy mask. The authors concluded that fluency of perception was the basis for the recognition judgements. In order to examine whether perceptual fluency is also important for modality as well as recognition judgements, the experiment was repeated, this time manipulating typeface. The prediction was that the manipulation of mask would again influence judgement as to whether the test word was in the same case as it was when earlier presented. In this case, the test word was always a repetition of one previously presented word. It was found that subjects were faster at pronouncing the test word when it was lightly rather than heavily masked. It was also found that subjects were more likely to report 'same case' when this was true of the test item. There was no main effect of mask level on same-case different-case decisions. There was however an interaction between mask level and match of case from which the authors concluded that for case, as for word identity, manipulation of perceptual fluency influences same/different decisions. The question was then asked as to whether these false familiarity effects were an attribute of fluency, or an attribution based on fluency. A further experiment was carried out in order to clarify this point. The experimental design was identical to the previous two experiments, but this time, subjects were informed about mask-level manipulation. If familiarity is an attribute of fluency, then it is proposed that informing subjects of mask manipulation should not allow them to escape its influence. If on the other hand, familiarity is an attribution of the source of fluency, then knowledge of mask level manipulation may prevent a feeling of familiarity. Subjects were again faster at pronouncing the test word when it had appeared earlier, and also when the mask level was light rather than heavy. There was however, no effect of mask level on recognition decisions. Thus when sources of fluency differences are known to be in the present, there appears to be no misattribution of familiarity feelings to prior experience. In fact, subjects made more errors of rejection when the mask was light, suggesting that they attributed genuine familiarity feelings to current sources. The authors conclude that when no current source of fluency is available, as in the first two experiments, then fluency feels like familiarity. When awareness exists about a current basis for fluency differences, then fluency may feel like perceptual clarity. If this is the case, then it should be possible to cause subjects to attribute fluency to current perceptual characteristics rather than any familiarity feelings.

A final experiment sought to establish this reverse illusion. The experimental set-up was broadly similar to the previous experiments, except that one word in the presentation list was masked at a constant level. When the test word was a repeat, then the same word was masked in the list. When the test word was new, the masked list word was chosen at random. The subjects task was to pronounce the test word and also to state whether the mask level was the same for the test word as for the masked word in the previous list. The mask level for the test word varied from 20% to 30% occlusion. Subjects were faster at pronouncing the test word when the mask was light rather than heavy, and were also faster when the word was a repeat. Word repetition was also found to have an effect on mask density decisions. Repeated words were rated as less noisy than non-repeated words. Thus prior exposure to a stimulus item gave rise to a feeling of clarity rather than familiarity. The results of this experiment in conjunction with those previously reported lead the authors to conclude that feelings of familiarity and perceptual clarity are attributions of fluency to some source which is currently evident. A false sense of familiarity can be created in the absence of a memory trace. This research has distinct implications for Jacoby's proposal for two types of memory "with and without awareness" (Jacoby and Witherspoon 1982). Jacoby and Whitehouse (1989) had subjects make recognition judgements as to whether test stimuli were 'old' or 'new' relative to a prior inspection task. There also appeared a 'context stimulus' which was a match to the test stimulus, a different word, or a nonword. This context stimulus appeared in conjunction with the test stimulus at either long (200 or 600 msecs) or short (50 or 16 msecs) durations. They found that the frequency of false 'old' judgements was greater when the context stimulus was a mismatch rather than when it was a match, in the long exposure condition. The reverse was true in the short duration exposure condition. The authors concluded that when stimuli matched in the short duration condition, this induced false recognition for new test stimuli. This was attributed to differences between conscious and unconscious processing, and the authors used the terms 'aware' and 'unaware' to describe their long and short duration conditions and referred to subliminal perception in explanation of their results.

The nature of the subliminal processes referred to by Jacoby and Whitehouse has been called into question by Bernstein and Welch (1991). They refer to an experiment (Bernstein et al 1989) which demonstrated that stimulus identification thresholds were lowered when presented in the context of clearly visible semantically related material. They therefore sought to clarify the 'Jacoby-Whitehouse' effect, by ridding the effect of "the unnecessary baggage of the subliminal" (Bernstein and Welch 1991). They presented subjects with a study list of 95 words and informed them that memory for the words would later be tested. In the test phase, subjects in the long duration condition were presented with a context stimulus for 600 msecs, followed by a 500 msec mask. There then followed after a 300 msec gap, a test stimulus. Subjects were instructed to say the test words aloud, or to say 'nonword' if the context word was a nonword. They then made old/new recognition judgements. In the short duration condition, subjects were not informed that there would be a context stimulus. They were told that a 500 msec mask would appear followed after a gap of 300 msecs by a test stimulus. they then made old/new recognition judgements of the test word. In this condition, the mask was in reality preceded by a 16 msec context stimulus. In a third experimental condition (perception condition), subjects were told about the short duration context stimulus and were asked to judge whether the test word was the same as the context stimulus, different from the context stimulus or a nonword. In a final experimental condition (dual condition), subjects were given the same instructions as for the perception condition, but were additionally required to make an old/new recognition judgement about the test word.

Results from the long duration context condition revealed that matching context and test stimuli produced fewer 'old' responses than mismatching stimuli. This was in accordance with the results obtained by Jacoby and Whitehouse (1989). However, it was also found that different test words led to more 'old' responses about the context stimulus than nonwords did. They also found that the effect of the context stimulus on the memory judgements were independent of the test stimulus. In the short duration condition, results indicated that matching context stimuli evoked more 'old' responses than nonmatching stimuli. This was also true of the dual judgement condition. An important finding was that comparison of judgements in the perception and dual conditions were different, which refutes the assertion that the context stimuli were subliminal. The authors therefore conclude that they are in agreement with the Jacoby-Whitehouse results that briefly presented matching context stimuli increase the tendency to report test stimuli as 'old', while longer duration has the opposite effect. they also agree that context stimuli affect both old and new stimuli implying contingent biases rather than perceptual effects. Their main contention is that briefly presented stimuli need not be subliminal or 'unconscious' to produce the results obtained by Jacoby and Whitehouse. They further describe the briefly presented context stimuli as 'incidental' or 'subtle' rather than subliminal.

It is suggested (Jacoby and Hollingshead 1990) that performance on indirect tests of memory reflects influences of memory on reconstructive or generative processes, while direct tests of memory include additional reproductive or recognition processes. They further propose a generate/recognise model of recall which has its basis in an episodic view of memory processes. This is in contrast to models which propose the locus of generative effects as activation of abstract representations (eg.logogens) or activation of a fixed associative network (eg. Anderson and Bower 1972). Jacoby and Hollingshead (1990) seek to demonstrate that effects on generation processes are specific to memory for prior episodes rather than being more general effects which could arise from activation of abstract representations. In support of this stance, Allen and Jacoby (1990) present the finding that in a word recognition test, there was an advantage in perceptual identification for words presented earlier in their normal form over those presented as anagrams to be solved. (The perceptual identification task involved the presentation of words for a duration of 17-50 msecs. The subject then attempted to report the presented word.) There was however an advantage in recognition performance for those words presented as anagrams. It is suggested that for the perceptual identification test, the matching of visual characteristics of an item along with match in perceptual processing is important for performance. Activation accounts, which hold that effects of prior experience are mediated by abstract general representations, would predict that memory should not be restricted by the details of prior presentation. The advantage in recognition memory for the solved anagram words over normally presented words is suggested as evidence that recognition memory benefits from more extensive or elaborative processing.

The generate /recognise model of recall proposed by Jacoby and Hollingshead (1990) was tested by comparison of performance on three tasks; stem-completion, cued recall and generate/recognise. 24 subjects participated in each of the test conditions (cued recall, stem-completion and generate/recognise). A stimulus set of 100 five letter word stems was constructed. 50 of these could be completed with 4 or 5 different five letter words, while the other 50 stems could only be completed with one five letter word (eg.oas-, oasis). The words were also selected so as to have one anagram. In the first phase of the experiment, subjects were presented with normal words or anagrams to be solved. They reported the words as soon as they were identified/solved. In the test phase, subjects were presented with word stems. In the stem completion task, subjects were asked to report the first five letter word that came to mind. In the generate/recognise condition, subjects were additionally required to report whether the generated word had been presented earlier. In the cued recall condition, subjects were asked to use the word stems as cues for recall of words read or solved in the presentation phase. The most important finding was significant interactions between test conditions and factors which have differential effects on generation and recognition processes. The interactions show that the test conditions differed in their dependence on recognition memory processes. The performance on tests of cued-recall are proposed to be a 'mix' of performance in the other two test categories. The main impetus for the work was to re-establish the validity of a generate/recognise model of recall. This had been previously dismissed by Tulving and Thomson (1973) as they found recognition failure for recallable words. This was also found by Jacoby and Hollingshead (1990) but they also found false recall of words which were correctly rejected on a test of recognition. The authors reason that if the generation of a word is sufficiently fluent,then it is not subjected to a recognition check before being output as recalled.

Jacoby's stance can best be summarised by the assertion that different study conditions and task requirements result in various types of processing. Performance at test will depend on the overlap between the processing at encoding and that at test. Jacoby (1983) suggests that reading a word without context involves bottom-up, data-driven processing. Generating a word on the other hand (eg. black-???) requires top-down, conceptually driven processing. Recognition memory is seen to depend on conceptually driven processing, while perceptual identification is seen to require data-driven processing.

Jacoby and others (Roediger and Blaxton 1987) explain interactions among study and test conditions in terms of the kind of processing required at each phase.

The existence of separate memory systems is not necessary for differences between performance on direct and indirect tests of memory to be observed. This interpretation, emphasising the importance of interactions between encoding and retrieval processes has emerged as an important aspect of recent research. It is best addressed within the context of 'two process' theories which are discussed below.

1.5 TWO-PROCESS THEORY: NO NEED FOR DISTINCTION

The distinction between episodic and semantic memory has also been addressed in dual process theory (Mandler et al 1990). There is no suggestion of separate memory systems, but rather two different processes operating on the same underlying memory representations. The theory postulates two processes that address the representation of an event:intra-event activation and integration which affects the relations among the features of an event and inter-event elaboration which reflects relations between the event representation and other mental contents. Activation/integration is automatic, and occurs whenever the representation of an event is accessed. Activation boosts the level of activation of all the constituent features of the event. Integration occurs automatically, as the previously established connections among the features lead to further selective activation of the specific features of the item and thus 'integrate' and isolate the specific event that is activated. Integration occurs automatically for an existing representation that is activated and activation/integration is therefore considered to be a single process. The process of elaboration on the other hand, establishes connections to other mental contents, and allows access to memory representations through search and retrieval processes.

Contrary to the claim that word recognition and word priming are dissociated phenomena generated by different memory systems (eg. Tulving 1982, Squire et al 1985), dual process theory includes the assertion that activation processes have similar and parallel effects in word priming and recognition. Mandler (1980) suggested that activation affects the 'familiarity phenomenon' in recognition as well as word priming in the stem completion task. In cases of recognition, both activation and elaboration determine judgements. The subjective sense of familiarity can be experienced in the absence of semantic/search processes. To further identify what exactly the event is, or the time and place of the previous encounter, prior elaboration is necessary. This then allows retrieval of the identification of the event.

Mandler et al (1990) present further experiments to investigate the proposal that activation processes have similar and parallel effects in word priming and recognition. A study is reported which examined prior direct and indirect activation using reaction time as the dependant variable in stem completion and recognition tasks. The reaction time measure examined those items for which there was a previously presented item that was either identical (direct) or phonologically or semantically (indirect) related to them. It was suggested that the direct target items should show the greatest degree of activation, followed by the phonologically related items, followed by the semantically related items. Semantically related items should show the slowest RT because they are dependent on complex spreading of activation and conceptual mediation. In experiment one, subjects were presented with either a block of five semantically related words (eg. coat, jacket, blouse, pants, skirt) or a block of five rhyming words (eg. coat, moat, gloat, bloat, oat). In both cases the word 'coat' is the direct target. Words like 'sweater' and 'throat' are designated indirect semantic and indirect rhyming targets. The words were presented one at a time on a computer screen. Eight filler words were presented before the stimulus set and eight afterwards to reduce primacy and recency effects. Subjects were required to rate each word according to how much they 'liked' it on a scale of 1 to 7, as quickly as possible. After the rating task, one group of subjects did a stem completion task, followed by a recognition task. The other group of subjects completed a recognition task before the stem completion task.

This initial investigation revealed that subjects were faster at the recognition task than the stem completion task. This was interpreted as being due to an imbalance in response requirements, so a modified version of the experiment was also carried out. In the recognition test, words were presented with a space separating the first three letters from the rest. Subjects were required to type the last group of letters if they recognised the word or a hyphen if they did not recognise the word.

Experiment two was identical to experiment one except that the task at presentation required the subjects to count the number of vowels in each word as quickly as possible. This was again followed by recognition and stem completion tasks.

Another experiment was designed as a control for experiment two. The reason for the experiment was to show the differential effects of semantic and non-semantic processing on word recall. The procedure was similar to that of experiments one and two, except that one group of subjects counted vowels at presentation and the other group rated the words according to how much they liked them, as well as being told that the experiment was investigation memory for words. All subjects were then given a recall test. The first part of the recall test required the subjects to write down as many of the presented words as they could remember. They were then asked to read over these words and write down any others of which they were reminded. Finally, subjects were asked to write down any words which they thought were related to the words already recalled. They then underlined any of these generated words that they thought occurred in the original stimulus set.

The resultant accuracy data from the series of experiments showed that only when subjects engaged in initial semantic processing did they show any effect of overall priming on semantically related target items. Non-semantic priming produced only direct and perceptual (phonological) overall priming effects. The reaction time data showed parallel and comparable effects of activation (in either semantic or non-semantic processing) for both recognition and stem completion tasks. Thus 'activation' is proposed as a preferable description of the phenomena underlying word priming than the effects of prior experience.

In summary, the dual process theory proposed by Mandler et al (ibid), proposes that activation and elaboration are the two processes which operate on memory representations.

Roediger and colleagues (eg. Roediger and Blaxton 1987) also argue against the idea of separate memory systems. Instead a more process-oriented framework is proposed. This view emphasises the mental operations engaged in during tasks and the information required to accomplish these. The type of processing engaged in upon presentation of a series of stimuli affect the information which is encoded from this experience. For example, subjects may or may not know about later tests of recall or recognition, they may be required to make judgements on surface characteristics alone or to engage in imagery etc. The coding at presentation will subsequently influence performance on a task at test. The critical determinant of performance will be the degree of similarity between the processes engaged in at presentation and test, or to use Jacoby's terminology (1983) how matched the tasks are in data-driven or conceptually driven processing.

Support for an abstract memory system source of repetition effects comes from findings that effects of repetition are independent of surface characteristics of the stimuli. These findings have been refuted by other researchers (see Kolers and Roediger 1984 for review). These contrary findings in the main came from different task specifications - recall and recognition being the dependent variables in the tests that found no effect of surface characteristics, while later results came from tests which required less conscious recollection. This discrepancy would indicate that the type of test employed is critical as to the effect of surface characteristic manipulations. Roediger and Blaxton (1987) tested this proposition in a variety of memory tests. They varied modality (visual/auditory), typography (handwriting/typing, upper/lower case), language (Spanish/English), and form of referent (word/picture). The tests employed were free recall, recognition and word-fragment completion. The authors predicted that the variables which would have an effect on tests of free recall would have no effect on tests of fragment completion. This prediction was based on the theory of 'transfer appropriate processing' (Morris et al 1977). Within this framework, performance will improve to the extent to which types of processing at test correspond to those required at presentation.

The results indicated that the task of fragment completion is highly sensitive to modality and typography manipulations between study and test. This was true of testing some minutes after the initial presentation and also one week later, though performance had declined. Recognition was less sensitive to the manipulation of typography and modality. The authors propose that the effects of typography manipulation provided some evidence towards specificity of visual features in priming.

In the language manipulation paradigm, bi-lingual subjects were presented with a list of words which they either read twice in Spanish, twice in English or once in each language.

At test, some subjects engaged in a recognition task (circling recognised words in a list). The test words were all English, but subjects were required to circle concepts they remembered from previously presented Spanish words. Another set of subjects engaged in a fragment completion task, again with English words, while the remaining subjects were instructed to recall as many of the previously presented words as possible in either language.

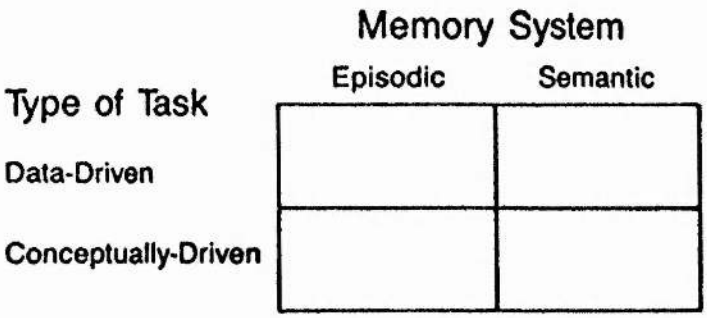
Recall was superior in the cases where subjects read words in both Spanish and English at presentation. This is interpreted as support for Jacoby's suggestion that free recall is a conceptually driven task. Results from the word fragment completion task showed that when subjects studied a word twice in Spanish, no reliable priming effects emerged. However, reading a word in English, or in both English and Spanish produced effects of priming. This is interpreted as evidence that the word fragment completion task is a data-driven task. In summary of these findings, the authors conclude that free recall is a conceptually driven task, while word fragment completion is a data driven task. recognition memory is seen to be a mixture of the two types of processing. This is quoted as further support for Jacoby's proposal (1983).

Another experiment reported by Weldon and Roediger (1987) compared priming effects with words and pictures. The study arose out of previous findings that pictures are recalled and recognised better than their verbal labels (Paivio 1971). Advantage is greater at test when the original stimulus is presented in picture form, even when tested with a word stimulus. These findings have been interpreted in terms of pictures being encoded into a richer or more elaborate representation in memory than words. Roediger and Blaxton (1987) proposed that given the assumption that fragment completion is a data driven task, then medium of presentation should have a bigger influence on this task performance than it would on recognition or recall. The authors found that pictures were recalled better than words, but this was reversed in the fragment completion task. This again supports the proposition that word fragment completion is a data driven process, which is facilitated by a match between the study and test phase tasks.

The results can be summarised thus. If some of the same underlying cognitive processes are used at study and at test, there will be transfer between the two phases. If the two phases have no processes in common, there will be no transfer. This 'transfer appropriate' procedures model suggested by Roediger and colleagues thus provides alternative explanations of results which have been previously attributed to the existence of separate memory systems. Support for the model derives from findings that dissociations can exist within episodic memory. For example, high-frequency words are better recalled than low-frequency words, but low frequency words are better recognised than high-frequency words (Balota and Neely 1980). Recall and recognition are both considered to be episodic tasks, yet such dissociations exist. Weldon and Roediger (1987) suggest that transfer appropriate procedures account for this in that high frequency words are more richly or elaborately processed, while low frequency words are more distinctive and receive more data-driven processing.

In clarifying the nature of previous investigations which have appealed to a distinction in memory systems, Roediger et al (1987) provide a useful representation (See Fig. 1.1). They point out that only two 'cells' in the diagram have been explored; episodic tasks have been conceptually driven (recognition, recall) while semantic tasks have been data-driven (word-fragment completion, perceptual identification). In order to broaden the picture, Blaxton (1985) devised four tasks which explored more combinations of types of task and memory systems. At presentation, subjects studied items with no context (eg. xxxx-COPPER), with a semantic associate (eg. tin-COPPER) or they generated the item (eg. tin-C-----). The four different tests given are shown in Fig. 1.2. A data-driven

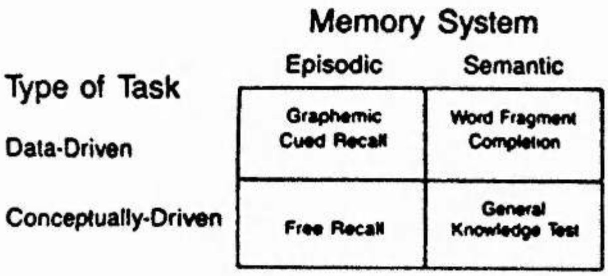
FIGURE 1.1. Crossing of two memory systems with types of processing.Most studies have investigated only the lower left and upper right cell combinations. From Roediger and Blaxton 1987.



Type of Task	Memory System Episodic	 Semantic
Data-Driven		
Conceptually-Driven		

Crossing of two memory systems with types of processing. Most previous experiments have involved a comparison of conceptually driven episodic memory tests with data-driven semantic memory tests, the lower left and upper right cells.

FIGURE 1.2. Test conditions used in Blaxton (1985, experiment one).



Type of Task	Memory System Episodic	 Semantic
Data-Driven	Graphemic Cued Recall	Word Fragment Completion
Conceptually-Driven	Free Recall	General Knowledge Test

1. Graphemic Cued Recall: CHOPPER
2. Free Recall: No cues given
3. Word Fragment Completion: C __ P__ E__
4. General Knowledge Test: What makes up 10% of yellow gold?

episodic task was devised which involved cued recall with words which looked like the target word (eg. CHOPPER for COPPER). The conceptually driven semantic task was a test of general knowledge (eg. What metal makes up 10% of yellow gold?). Free recall and fragment completion tasks were also included to test conceptually driven episodic memory and data-driven semantic memory respectively. The author predicted that if distinct memory systems exist, then the two episodic tasks should produce similar performance, different from that in the two semantic tasks. What actually transpired was a similarity between data-driven tasks, different from conceptually driven tasks. This is interpreted as support for the transfer appropriate model.

Related experiments have been reported by Hamann (1990). The starting point for the experiments is the prediction that a conceptually driven implicit (semantic) task will be affected by level of processing. Previous studies of the effect of levels of processing have demonstrated that it has a large effect on explicit tasks but no effect on implicit tasks (eg. Graf and Mandler 1984, Jacoby and Dallas 1981). Hamann (1990) chose two conceptually driven implicit tasks; the first was a general knowledge retrieval task and the second a category exemplar generation task. Level of processing was also manipulated at study phase. In the general knowledge task, subjects in the study phase were presented with 40 of the 60 answer words for the subsequent questions and were asked to rate them for 'likability'. Another set of subjects made vowel count comparisons between words. At test, subjects answered 60 general knowledge questions with a single word or generated exemplars of specific categories. It was predicted that the tasks at test would benefit more from semantic rather than physical processing at study as they were both conceptually driven.

The results showed that there was more general knowledge priming following semantic study conditions than physical study conditions. There was also more priming in the category exemplar generation task after semantic study conditions. The results were thus consistent with the predictions from a processing framework.

A second experiment reported by Hamann (1990) examined the time course of priming in conceptually driven implicit tasks. The level of processing was again manipulated at study, either being semantic or physical. The task at test was category exemplar generation. After study, subjects engaged in a distractor task for ten minutes and were then instructed to generate exemplars for nine different categories. Subjects then engaged in another distractor task until 30 minutes had elapsed since the study phase. They then generated more exemplars from another set of categories. This was again repeated after 90 minutes had elapsed.

The results showed a decline in performance as delay increased for both the semantic and physical processing conditions. However, priming from the physical processing condition was first to reach baseline. This was explained by the fact that it started at a lower level than the semantic condition.

Although almost all of the research which has contributed to theories of memory organisation has dealt with lexical processing, the results have been used as a starting point for explanations of how other classes of stimuli are processed. In particular, models of face recognition have incorporated many of the features described in lexical memory research. As this thesis is concerned to some degree with processing facial stimuli, it is appropriate to review the more influential models of face recognition.

1.6 MODELS OF FACE MEMORY

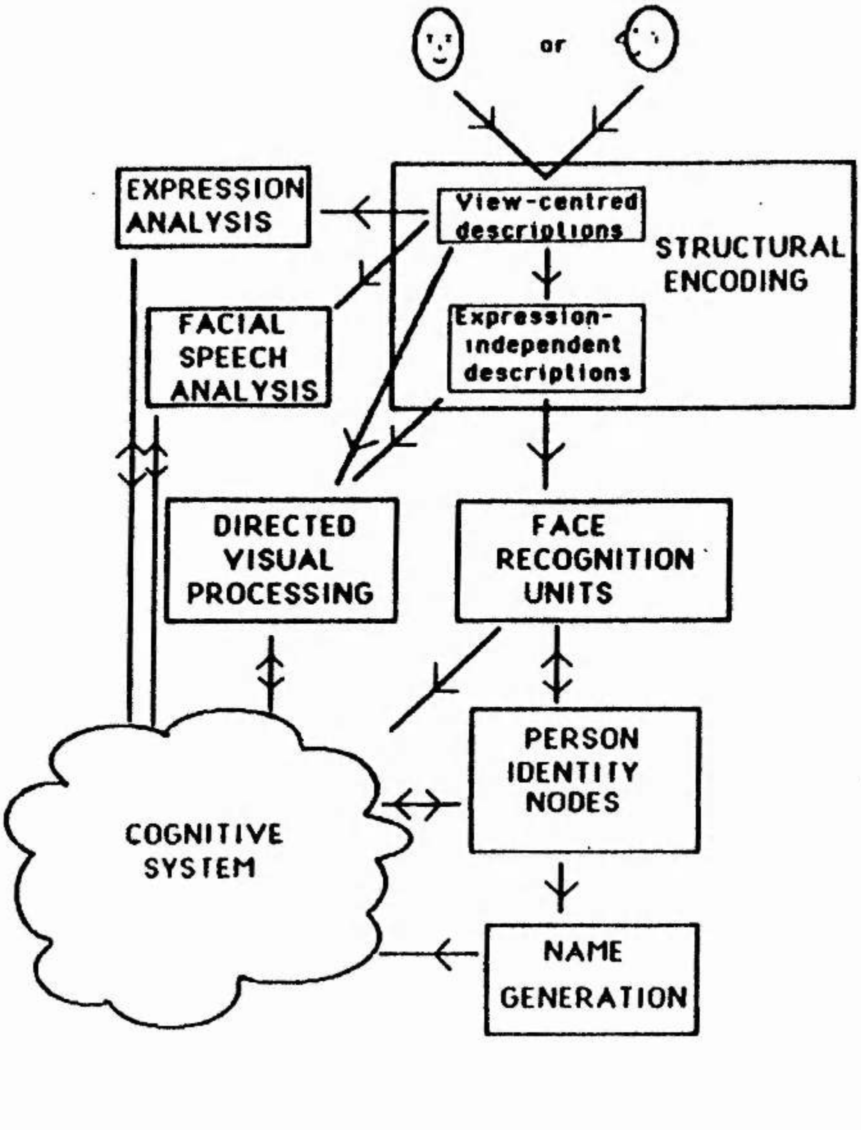
The aim of experiments investigating face perception and memory is to develop a theoretical model for understanding how we recognise familiar faces; a model which can accommodate the various phenomena associated with face perception and recognition and has some explanatory power when considering how an unfamiliar face becomes familiar and recognisable in time. Current models of face recognition have a large founding in theories of word recognition and consequently the semantic/episodic distinction in memory research which has already been outlined will also be addressed in this review.

A model of face recognition which has promoted much research is that proposed by Hay and Young (1982). This model was later modified to that shown in Fig. 1.3. (Bruce and Young 1986) and further modified by Ellis et al (1988).

Proceeding through the model, the first stage is that of "structural encoding" or "representational processes". These processes are said to somehow furnish visual descriptions suitable for recognition purposes, which can be matched with similar descriptions contained within the 'face recognition units'. The structural encoding is of an abstract nature specifying individual facial identity independent of pose, expression, lighting or other conditions of view. These descriptions match similarly abstract representations contained in the face recognition units, just as logogens are proposed to contain graphemic/phonological codes to specify lexical identity at a level more abstract than that of a particular typeface or handwriting (Clarke and Morton 1983, Scarborough et al 1977, Warren and Morton 1982).

The independent position of expression analysis in the model has gained support from a number of studies showing that such characteristics can be identified without the explicit identification of the face in question. Young et al (1986) found that expressions were

FIGURE 1.3. Bruce and Young's (1986) functional model for face recognition.



matched no more easily if the faces viewed were familiar, than if they were unfamiliar. Also, Bruce (1986a) found that decisions about facial expressions were not made any more quickly to familiar than unfamiliar faces. The only evidence to back the separate route in the model for "facial speech codes" comes from clinical observations (Campbell, Landis and Regard 1986) who found a patient who could judge which phonemes were being mouthed in facial speech, without being able to recognise faces or judge their expressions. Also reported is a patient who could make judgements about expression and identity of faces without being able to make phonemic judgements. Thus the abilities to interpret expression and facial speech have been afforded separate routes in the Bruce and Young model to that of facial identification, emphasizing the abstract nature of the face recognition units.

Ellis Young and Flude (1988) followed up these experiments in order to establish that face recognition units are not involved in determining the sex or emotional expression of a face. In their first experiment, classifying familiar faces by occupation facilitated subsequent responses to the same faces in a familiarity decision task, but not in an expression judgement task or a sex decision task. In a second experiment, familiar faces showed repetition priming in a familiarity decision task, regardless of whether a familiarity judgement or an expression judgement had been asked for on first presenting the face. Again, expression judgements to familiar faces failed to show repetition priming. A third experiment demonstrated that familiar faces showed repetition priming in a familiarity decision task regardless of whether a familiarity judgement or a sex decision had been asked for when the faces were first encountered. Sex decisions to familiar faces again failed to show repetition priming. These results are presented as evidence then for the assertion that the systems which mediate expression and sex decisions do not contain person-specific representations and hence do not show repetition priming. These results are also proposed as evidence to demonstrate the "mandatory and unstoppable" activation of face recognition units for familiar faces, even when the priming task does not require the explicit recognition of a face.

Support for the hypothesis of face recognition units was first derived from experiments on associative or semantic priming. Bruce (1983) developed the familiarity decision task in order that the decision could be instant and did not involve the explicit naming of a face. Using this basic task Bruce (1983) found that the familiarity decisions were made more quickly to faces preceded by close associates than to faces preceded by unrelated familiar faces. For example, subjects were quicker to decide that the face of Princess Diana was familiar in the test series if it had been preceded by the face of Prince Charles than by an unrelated face. These effects were convincingly large, in the order of 126 msecs. It is worth noting however that Bruce (1986b) showed that identity priming and semantic priming do not have similar decay rates. Semantic priming effects are observed only at the shortest lags, where the prime item immediately preceded the target. This same result was found in a lexical decision task by Dannenberg and Briand (1982). The observation of semantic priming when even a very short interval (250 msecs) separates the prime and the target (Bruce and Valentine 1986) is consistent with an automatic spreading activation effect within the system.

In an effort to clarify further the sequence of events which take place when a familiar face is recognised, Bruce and Valentine (1985) carried out a series of experiments investigating subjects' recognition thresholds to faces where earlier they had been exposed to either (a) the names corresponding to these faces (b) different pictures of the same people, or (c) the same pictures of the same people. The thresholds in these three conditions were then compared with those obtained in a control condition where no prior exposure had occurred. What the experimenters found was that familiarity decisions were made more quickly to familiar faces which had earlier been presented either in the same or a different picture, compared with the control condition. As well as this main result, the authors pointed out that the identical photograph used as both prime and target resulted in the most facilitation. This result, at first consideration, seems to argue against the abstract nature of face recognition units and seems to imply an episodic component in face priming. Bruce (1982,1983, Bruce and Young 1986) have interpreted this in terms of a separate "pictorial code" which are resemblances of particular pictures of faces. Every different picture of a face gives rise to a different pictorial code but should give rise to the same structural codes. Thus, visual similarity effects when they occur are a property of episodic memory, and not the recognition units. The other main result in this study was that no facilitation was observed at target when earlier exposure had been to the name corresponding to the face. This result was similar to that obtained by Warren and Morton (1982) who found no priming from names to pictures of familiar objects. Bruce's result suggested that the locus of identity priming from an earlier view of the face is at a stage earlier than that to which names have access - the face recognition units being the obvious possibility.

The position of name generation in the Bruce and Young model is one which has received support from various studies and examples from everyday life also go some way towards justifying the position of the name generator (Young et al 1985). A familiar feeling is one of "knowing" a face without being able to explicitly generate a name. The converse situation of knowing a name without being able to access a face never occurs.

The "person identity nodes" in the model contain all the semantic information about a person which we have gathered as they become more familiar; information about clothing, gait, posture, occupation etc. Again, this stage of identification is very frequently reached before a name can be generated. Even in two tasks where the same word served either as a name or an occupation (eg. Butler, Baker) the time taken to name the faces was significantly greater than that taken to name the occupation (for review see Bruce 1988, Young and Bruce 1991).

The further justification for the separation of naming, identification and person-information in the Bruce and Young model comes from a number of studies examining the influence of name or face distractors on the processing of simultaneously presented names and faces. The basic paradigm for these investigations involves the presentation of a face with a printed name alongside it. Subjects are then asked to make a response either to the face (ignoring the name) or to the name (ignoring the face). Results from studies conducted by Young, Ellis et al 1987 demonstrate that distractor names interfere with face naming but have little effect on face categorisation (is this a politician or a pop-singer ?). On the other hand, distractor faces interfere with name categorisation but have no effect on naming tasks.

The same threshold mechanism is used to explain facilitation in both repetition and semantic priming. In identity priming the threshold reduction results directly from prior exposure while in semantic priming it should result indirectly from activity within the semantic system. If both semantic and identity effects are explicable in terms of reduced thresholds in recognition units, then we might expect the effects to decay in similar ways over time, yet we have already seen that Bruce (1986) found this not to be the case in that semantic priming of familiar faces does not persist beyond 5 seconds s.o.a (stimulus onset asynchrony), whereas repetition effects are robust and persistent. One way in which to accommodate the apparently different effects of semantic and identity priming is to propose that they stem from different components of the face recognition system with identity priming seen as a face recognition unit effect and semantic priming requiring a post access explanation. This would mean abandoning the original Hay and Young position that decisions about face familiarity can be made purely on the basis of activity within the face recognition units. Recently Young et al (1988) have suggested that face recognition units be seen not as threshold devices but as devices which signal the degree of resemblance between their input and the representation they hold. Experiments explicitly addressing this question have been reported by Ellis, Young Hay et al (1988). A replication of Bruce and Valentine's 1985 study is reported determining whether the speed of recognising a famous face is primed by earlier exposure to either the face or the name. The results showed again that latencies in the face priming condition were faster than in either the name priming condition or the unprimed condition. Thus far the results were compatible with the results obtained by Bruce and Valentine and the account of repetition priming in terms of effects within face recognition units. The second experiment was designed to address the question "do we possess recognition units that respond to faces alone or are they person recognition units?". Subjects were required to identify familiar people from full length photographs with the head blocked out, then identified faces as in experiment one as familiar or unfamiliar. If face recognition forms only part of a highly integrated person recognition system, then priming should occur with the faces of those people whose headless bodies had been identified. Results in fact showed that latencies in the face priming condition were faster than in either the body priming condition or the unprimed condition. Thus what is emerging is a system with a set of separate recognition units for face, body, voice, clothes etc. of an individual.

A third important experiment reported in this paper arose out of the alternative accounts of priming (other than recognition units) - the difference between recognition unit accounts and others being that recognition unit models are of an abstractive nature and indifferent to pose or expression of a familiar face. Instance - based models, such as that proposed by McClelland and Rumelhart (1985) represent a stimulus as a pattern of activation expressed over the network of processing elements and each stimulus. The study reported by Ellis et al (1988) found that priming with identical, similar and dissimilar views resulted in graded repetition effects, with an identical stimulus at target producing the greatest facilitation, a similar photograph producing less facilitation and a dissimilar photograph producing least of all. The proposed abstract nature of recognition units makes the explanation of the differences between similar and dissimilar stimulus facilitation problematic. In favouring such a theory, the authors would have predicted equal priming in the similar and dissimilar conditions because of the abstract nature of recognition units. The observed graded facilitation was quoted as support for an episodic or instance-based account of priming effects. It could be argued however, that in the similar and dissimilar conditions, identity is held constant through activation of the recognition unit and the graded result could be an indication of some sort of overlap in the pictorial code or episodic trace for the stimulus held constant through activation of the recognition unit. The graded result could be an indication of some sort of overlap in the pictorial code for the stimulus.

The implication that a purely abstractive account of face recognition is inadequate directly parallels similar accounts of word recognition. Instance-based accounts are potentially more explanatory, as they allow for episodic and semantic phenomena within the same conceptual framework (cf. Jacoby 1983). However, there may be aspects of facial recognition which are not as 'easily' integrated into an instance-based account as words may be. For example, the fact that faces can never be named in the absence of prior access to identity specific semantic information is problematic. One suggestion (Bruce 1988, Rumelhart and McClelland 1985) is that distributed memory models may describe the 'microstructure' of cognition, while the 'macrostructure' of processing modules contribute to complex information processing tasks. This echoes the suggestion that an episodic memory system may be embedded in a semantic system or, more broadly, the unitary framework of memory which has emerged in recent research.

Lexical and face research has often gained from reports of human neurological impairments. There is a vast amount of literature which addresses the insights gained from such studies. There follows a brief review of the research which has directly contributed to the issue of distinct memory systems.

1.7 NEUROLOGICAL IMPAIRMENTS: EVIDENCE FOR SEPARATE SYSTEMS?

Dissociations observed as a consequence of brain damage have been put forward as evidence for the existence of different 'kinds' of memory. The reasoning implies that these kinds of memory are subserved by different neural mechanisms which can be selectively impaired. In this section, the evidence from impairments in word and face recognition will be reported and briefly assessed.

A distinction between episodic and semantic memory finds much support from neurological evidence. Amnesics may be specifically impaired in the encoding and retrieval of episodic information while semantic memory remains intact (Kinsbourne and Wood 1975, Cermak and O'Connor 1983, Tulving 1983). Accounts of retrograde amnesia are especially open to interpretation in the framework of an episodic/semantic distinction.

Contrary to studies implying that dissociations infer different memory systems, is the suggestion that the things amnesics can and cannot do are due to different types of retrieval from a single memory store (eg. Jacoby 1984). Dissociations in this context arise from the degree to which retrieval is dependant on conscious voluntary processes rather than automatic processes. It was demonstrated by Graf et al (1984) in a word-completion task that amnesic patients showed improved performance from cues only when they were encouraged to guess rather than attempt any conscious recall. This was suggested as evidence for two different types of retrieval for the same memory, only one of these being available to the amnesics. In a further study, Graf and Schacter (1985) employed a paired association learning task. In this case, the patients were presented with lists of word pairs for learning (eg. house-chair). At test,they were presented word pairs in which the second word was incomplete (eg. cha?). These incomplete words were paired with either their original associate or with a new word. It was found that patients performed better when the original associate was presented in conjunction with the incomplete word. This was interpreted as evidence that the patients could form new associative memories, and that this was only evident in an indirect test of memory. Like many other studies in this research, these results were not true for all subjects but only for those with a 'mild to moderate' memory impairment (Schacter and Graf 1986).

Overall, evidence for the distinction between implicit and explicit memory (or episodic/semantic) in memory impairments seems less strong than evidence that the nature of retrieval task is critical.

1.8 CONCLUSIONS AND IMPLICATIONS

Although the distinction between episodic and semantic memory has gained wide acceptance and promoted much research, an alternative explanation of the dissociations found in memory tasks has emerged. There appears to be a consensus among researchers that the kind of processes engaged in at encoding stages largely determine retention. In addition, the type of processing engendered at test will determine ease of retrieval. Recent explanations, modelled within a processing framework, are not diametrically opposed to a distinction between implicit and explicit memory tasks, but rather make the distinction along different dimensions. The emphasis is on the extent to which the processing at memory test overlaps the processing at encoding stages. The types of processing are seen as either data-driven or conceptually driven. There is no strict dichotomy between these processes, but they are rather considered along a continuum.

Different encoding and retrieval processes, either due to task or stimulus manipulation may give rise to different patterns of electrical activity in the brain. This is the basis of electrophysiological research, and in particular, the study of event Related Potentials. The contributions of studies using E.R.Ps as the investigative tool to memory research will be the subject of the next chapter.

CHAPTER TWO

EVENT RELATED POTENTIALS AND MEMORY

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EVENT RELATED POTENTIALS AND MEMORY

2.1 INTRODUCTION

It is possible to record, non-invasively, the brain's electrical activity from the scalp of subjects performing psychological tasks. The activity recorded in this way can be used in addition to behavioural measures to investigate the processes underlying encoding and retrieval. This chapter reviews the relation between scalp recorded electrical activity and memory processes. First, it is appropriate to review the manner in which these scalp recordings are made.

2.2 RECORDING EVENT RELATED POTENTIALS

The electro-chemical signals which function as the communication between neurons may cause external currents to flow between upper and lower layers of brain tissue. The summed activity of these currents constitutes the human encephalogram (E.E.G.) and can be recorded on the scalp. Changes in the E.E.G. can be correlated with changes in brain state. The E.E.G. also contains phasic brain potentials which are elicited by cognitive, sensory and motor events. These "event related potentials" can be identified by enhancing the signal-to-noise ratio to the ongoing E.E.G., most commonly by means of the "averaging" process. This process involves the recording of the electrical activity following each repetition of a particular event. The digital values of the resultant waveforms are averaged. The random background activity will tend towards a similar mean value at each point in time. As averaging proceeds, it will deviate less and less from the mean. The E.R.P correlated with the eliciting event will remain constant and thus become increasingly distinguishable from the background E.E.G.

Within each averaged waveform, there will be a number of positive and negative deflections in the voltage. These are termed "components" and are correlated with neural activity during information processing stages. The components are usually named with respect to their polarity (N or P) and the common latency in milliseconds at which they occur (eg. N400, P100). A distinction is often made between components which are sensitive to the physical characteristics of a stimulus (exogenous) and later components which are sensitive to the cognitive and perceptual processes carried out on the stimuli (endogenous).

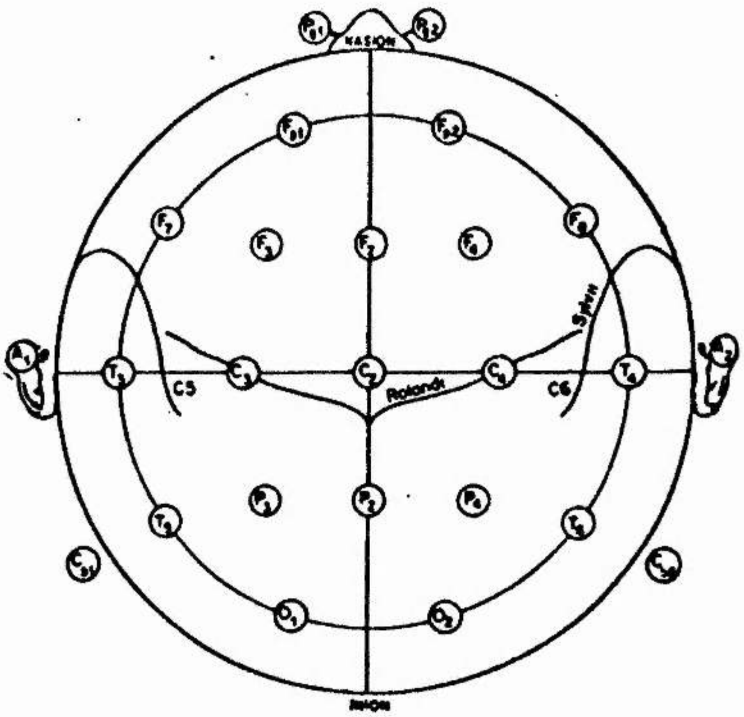
The purpose of E.R.P research is to correlate changes in the latency and amplitude of these components with changes in experimental variables. In this way, the sensory and cognitive processes responsible for each component may be identified.

E.E.G. activity is recorded by means of attaching electrodes to the scalp. It is usual to record from a number of sites to aid component identification (see Fig. 2.1 for example of standard electrode sites). The scalp electrodes are referred to one or more electrodes at sites such as the earlobe or the mastoid bones. It is also common to record ongoing eye-movements (EOG) during recording. Should this activity contaminate the recordings from scalp electrodes, it can then be eliminated from analysis.

2.3 E.R.Ps AND MEMORY

The non-invasive nature of E.R.P recording makes it a useful tool in determining the neural substrates of cognitive processes. Their use in examining memory is superior to behavioural measures in that a real-time index of encoding and response processes can be examined. Used in conjunction with behavioural measures, like reaction time, stimulus evaluation and response processes may be clarified.

FIGURE 2.1. Figure showing all standard positions of the ten-twenty electrode placement system. The figure represents the head drawn in one plane seen from above. The location of the Rolandic and Sylvian fissures are indicated. The outer circle was drawn to the level of the nasion and inion. The inner circle represents the temporal line of all electrodes. From Picton (1978)



There are many components which have been studied with respect to memory processes in particular. The majority of research investigating these components has been conducted using lexical tasks. For the purposes of this review, one main component is of interest - the 'N400', which is a negative going deflection which peaks at around 400msecs post-stimulus.

This component was originally reported by Kutas and Hillyard (1980) to be generated by incongruent words in an otherwise meaningful sentence eg. " I drink coffee and dogs". The word "dogs" elicited a negative component peaking near 400ms. Words which were physically anomalous did not evoke this negativity. The N400 is also evoked in the case of congruent but less probable sentence endings (Kutas and Hillyard 1984). In this case the amplitude of N400 is inversely related to the CLOZE probability of the final word, i.e the lower the expectancy, the greater the N400 amplitude. In this context, the N400 can be interpreted as reflecting the violation of a semantic "prime" set up by the preceding words. The maximum for N400 is found at centro-parietal sites and is slightly larger over the right side of the scalp (Kutas and Hillyard 1982). The amplitude of the N400 does not depend on the overall truth value of a sentence, but rather it reflects the semantic relationship between the content words. Similar components are found in tasks where words are presented in series without a sentence structure, so long as the critical word is semantically unrelated to the preceding words.

Some studies have reported late negativities which occur in the same latency range as the N400 but which are not equated with the N400. Neville et al (1982) have recorded an 'N410' component elicited by the visual presentation of words which was larger in amplitude over the left hemisphere than the right. Bentin et al (1985) have recorded an N400-like negativity elicited by stimuli in a semantic priming paradigm. It was found that potentials generated by words which had been semantically primed were more negative at 400 msec than those elicited either by primes or non-related items. They hesitated to identify this component with the N400 as described by Kutas and Hillyard, maintaining that it could be the result of an increased positivity generated by non-target words. Rugg (1985) has reported a similar negativity generated by attended words. Rugg and colleagues (Rugg 1984, 1985, Rugg and Barrett 1987) have also described a negative component which peaks at around 450 msecs after stimulus onset. This component is associated with orthographic or phonological mismatches in a word-pair rhyme detection task. The effect was found to be larger on the right side of the scalp.

The question of what exactly the N400 component reflects is dependent on the relationship of the N400 to these other late negativities. It has also been suggested that it is a late manifestation of the 'N200' component (Polich 1985). Polich found that in a study where subjects did a series of matching tasks, the presence of N400 negativities corresponded to increased response latency. He suggested that the difficulty of making semantic judgements about words led to a delayed N200 negativity. He concluded that the N400 is one manifestation of a single system involved in comprehending similarities and relationships among stimulus items, also reflected in the N200 component. These negativities may not be related to the same cognitive processes and the finer discriminations between them are important.

It has been found by other researchers (Kutas and Van Petten 1987, Rugg and Barrett 1987) that the amplitude of N400-like negativities is inversely related to the amount of contextual pre-activation of the memory item under processing. Stuss et al (1986) have suggested that N400 amplitude is an index of the amount of search in long-term memory. More recently, Stuss et al (1988) have proposed that the N400 is associated with post-lexical evaluation rather than lexical access. This possibility was addressed by Rugg

(1990) in a study examining E.R.P repetition effects using high and low frequency words. It was found that E.R.Ps evoked by unrepeated words were more negative going than those evoked by high frequency items. This was interpreted as a modulation of the N400 component, which was particularly prominent in waveforms evoked by unrepeated low frequency items. It is suggested that the N400 reflects postlexical processes, correlated with the extent to which the stimulus and context form an unfamiliar or unexpected conjunction. Because high frequency words have been experienced in a wider range of contexts than low frequency words, they form a less unfamiliar conjunction with the experimental context.

The exact nature of the processes associated with N400 is not definitely resolved but it has emerged as an important component for examining processes in long-term memory. It has also emerged as an important component with regard to stimulus repetition effects.

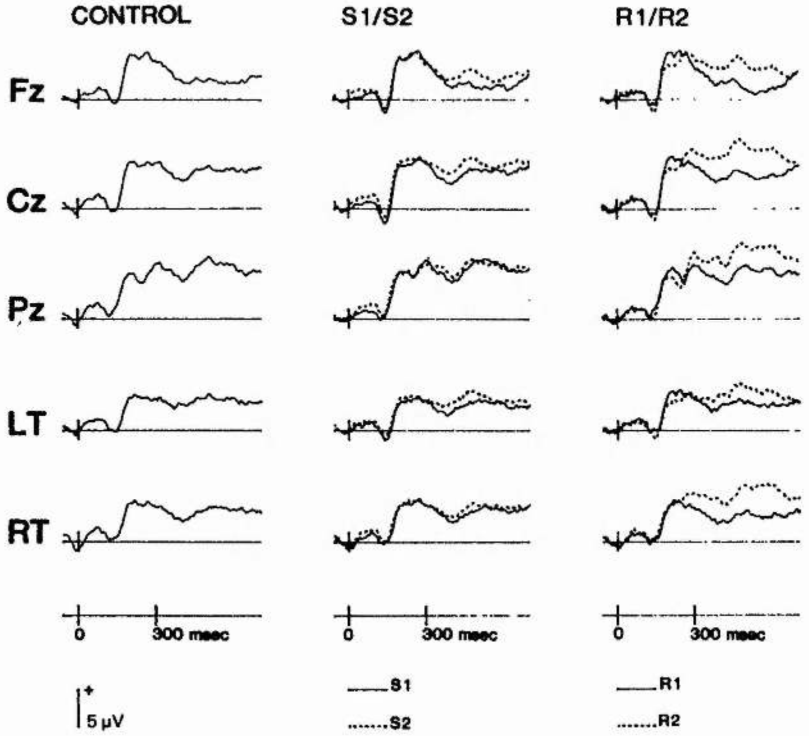
2.4 E.R.Ps AND REPETITION EFFECTS

As well as with behavioural indices, effects of word repetition have been reported with the use of scalp-recorded event-related potentials eg.(Rugg 1985,1987; Rugg and Nagy 1987, Bentin and Peled 1990). While effects of repetition have been observed with the use of E.R.Ps, it should be pointed out that dissociations have been found between these effects and those observed using behavioural measures as the dependent variable. For example, Bentin and Peled (1990) found an absence of long-lasting repetition effects in a recognition memory task as compared to a decision-making task. It has been previously shown that task-related decisions are not a necessary condition for obtaining long-lasting behavioural repetition effects (eg.Jacoby 1983). However, such dissociations do not preclude the fact that repetition does have substantial effects on E.R.Ps, even if these effects reflect only some of the processes involved.

In experiment one, reported by Rugg (1987) subjects counted occasional non-words (eg. FICT) against a background of words, some of which were either repeated or were semantically related to their immediate predecessors. The resultant E.R.Ps to repeated items showed a widespread large, positive-going shift (See Fig 2.2.). A smaller effect, most prominent at frontal and central sites was seen with the semantically associated stimuli. In the second experiment reported, subjects counted words against a background of non-words, some of which repeated. The E.R.Ps to repeated non-words again showed a positive-going shift but it was smaller and less sustained than that obtained with repeated words. These results were interpreted as evidence that repetition effects differ according to whether or not the item has a pre-existing representation in memory. It is also possible that the differences were due to the availability of a unitized code for the words.

As mentioned previously, behavioural repetition effects have occasionally been found using non-words as stimuli (Feustel et al 1983; Salasoo et al 1985). Such findings were interpreted as evidence that repetition effects are due more to episodic rather than semantic processing. In order to clarify further the nature of these non-word repetition effects using E.R.Ps, Rugg and Nagy (1987) compiled a stimulus set of orthographically *legal* and *illegal* non-words. Legal words were pronounceable letter strings derived from words by altering only one or two letters (eg. GARL). Illegal items are unpronounceable letter strings, whose constituent segments are seldom encountered in English (eg.FRKL). The reasoning behind this stimulus construction was that if repetition effects with non-words result from the formation of episodic memories, then repeated legal and illegal items should modulate E.R.Ps to the same extent. Alternatively, should the legal items result in greater effects, an interpretation involving something other than purely episodic memory would have to be invoked.

FIGURE 2.2. From Rugg (1987). Effects of repetition on evoked potentials.



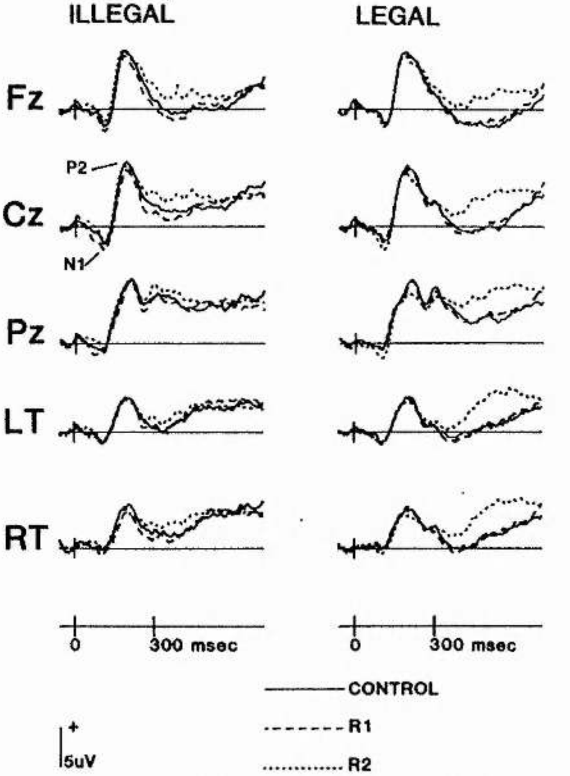
Grand average waveforms from Experiment 1, elicited by control items, and first and second items of semantically associated (S1 and S2) and repeated (R1 and R2) pairs of words.

The results demonstrated that E.R.Ps were modulated to a greater extent by repeated legal rather than illegal items. (See Fig 2.3). This suggested that the interpretation of repetition effects would have to involve some reference to semantic/lexical processing - either in terms of a logogen model or the activation of a unitized code for the orthographically legal nonwords.

In order to assess whether these differences in repetition effects were due to differential processing of the *initial* presentation of an item or the repeated items, Rugg et al (1988) devised an experiment which contrasted lexical and non-lexical processing of words. Three tasks were employed; in one task, target/non-target discriminations were made on the basis of physical features of the stimulus (upper or lower case letters). In the other two tasks, a lexical (word/non-word discrimination) or a semantic decision (animal/non-animal) was required.

Repetition effects were prominent in the lexical and semantic discrimination tasks, where the repeated item showed a large, sustained positive-going shift. The onset of this effect was around 200-300ms and lasted for some 400ms. In contrast, the repeated items in the case discrimination task elicited only slightly more positive E.R.Ps than non-repeated items. Rugg et al (1988) interpreted this as being consistent with the idea that the manifestation of sustained repetition effects requires that attention is drawn to the identity of a stimulus, which is thus processed to a greater depth than a stimulus which has been processed using superficial features only. A further finding was that the initial presentation of an item in the case task was found to elicit more positive-going waveforms than in either the non-word or semantic tasks. Thus the repetition effect seemed to be primarily due to an increased negativity in the E.R.Ps to the initial presentation of an item in the case decision task, rather than an increased positivity to a repeated instance.

FIGURE 2.3. From Rugg and Nagy (1987). Waveforms elicited by legal and illegal non-words.



Grand average waveforms from Experiment 1, elicited by control, R1, and R2 orthographically illegal and legal nonwords. Fz, Cz, and Pz refer to frontal, central, and parietal midline electrodes. LT and RT signify left and right temporal electrodes. N1 and P2 components are indicated.

Rugg et al (ibid) suggest that the negativity observed for initial presentations is an example of the 'N400' component. The E.R.P. repetition effect can be interpreted in two ways; The negative wave evoked by first presentations is attenuated on repetition either because repeated items are easier to integrate with their context, or because they are integrated less fully when they are initially presented. With the former interpretation, the repetition effects would be caused by the initiation of a range of processes to integrate various attributes of the item upon its first presentation. These processes are associated with a negativity in the E.R.P. On repetition of the item, this integration may be more rapid or occur to a lesser extent and therefore results in a more positive-going E.R.P. Alternatively, when presented with items in a task such as upper/lower case discrimination, subjects do not need to engage in lexical memory integration processes on the first presentation and there is little associated negativity.

2.5 E.R.Ps AND PICTORIAL REPETITION EFFECTS

Most of the studies investigating repetition effects in E.R.Ps have been conducted using words as stimuli. The question arises as to whether the resultant insights into memory organisation can be extended to more general visual memory functions. Negativities around 400 msec have been reported by some researchers using pictorial stimuli. A study comparing E.R.P. recordings from adults and children was reported by Friedman et al (1988). The stimuli consisted of a set of standardised pictures developed by Snodgrass and Vanderwart (1980). The task was a modification of Posner's letter-matching paradigm (1978) in which subjects were required to decide whether two sequentially presented pictures were the same or different. There were three bases on which to make this decision: whether the pictures were physically identical, shared the same name or belonged to the same semantic category (eg. body parts, animals, vehicles etc.). Recordings were taken from 22 children (6-8 years) and 25 adults (20-38 years) with electrodes located at FPz, Fz, Cz, Pz and Oz all referred to a nosetip electrode. Subjects began the sequence by pressing two buttons. After 1550 msecs, a prestimulus E.R.P. recording period of 300 msec was initiated after which the first stimulus was presented (S1) for a further 300 msecs. This was followed 2000 msecs later by the second stimulus (S2) for another 300 msecs. Subjects made delayed response 1650 msecs after the onset of S2. The S1 waveforms for adult recordings were characterised by a positive peak at around 400 msecs followed by a negative going potential which reached peak latency at around 450 msecs. This was followed by a late positivity peaking at around 500 msecs, maximal at Pz. The adult occipital waveform consisted of a P120-N200 complex which was followed by a positivity peaking at around 180 msecs. The children waveforms showed a large-amplitude negative component at about 400 msecs, maximal at frontal and central sites. This was followed by a positivity at 700 msecs, maximal at the parietal site. The children occipital waveform was characterized by a large-amplitude positive component at around 150 msecs, followed by a positive component peaking between 300 and 500 msecs. The adult S2 waveforms were characterised by two late positive components at 400 and 500 msecs, both maximal at Pz. the children waveforms show a large-amplitude late positivity at 700 msecs, maximal at Pz. In the case of the 'different' waveforms (where subjects decided that the second stimulus was different from the first) there was a negativity peaking at about 400 msecs at frontal and central electrodes. In order to clarify the differences between 'same' and 'different' waveforms, subtraction waveforms were calculated which showed a negative potential at the same latency and topography in the two age groups, although the amplitude of the children waveform was about twice as large as the adults. The main difference of interest here is that in the case of the children, both S1 and S2 'different' waveforms were characterised by a negativity at 400 msecs. This was seen in the S1 data of the adults and only in the S2 waveforms when subtraction waveforms were calculated.

Other investigators working with children have recorded similar components. Symmes and Eisengart (1971) recorded a late negative wave to colourful depictions of familiar scenes and household objects. Neville (1977) recorded a late negative wave peaking at 400 msecs to a variety of line-drawn objects. Courchesne (1978,1973) recorded a 'Nc' component to novel stimuli peaking at 400 msecs which was largest and most distinct in the two youngest age groups tested. Some functional correlates for these late negativities have been suggested, including further processing of stimuli with attention getting characteristics (Courchesne 1978), the perception of meaningful stimuli (Symmes and Eisengart 1971) and the processing of non-verbal information (Neville 1977).

Whether the negativities observed in waveforms resulting from the viewing of lexical and other stimuli are indices of the same memory processes is not definitely resolved. There is no doubt, however, that such research can lead to valuable insights into memory organisation. As well as the effects that repeating stimuli can have on evoked potentials, recent research has proposed the existence of components which occur in response to specific stimulus classes. This research is reviewed in the following chapter, with particular emphasis being given to the proposed existence of 'face-specific' potentials.

CHAPTER THREE

STIMULUS SPECIFICITY IN VISUAL PROCESSING

CHAPTER THREE

STIMULUS SPECIFICITY IN VISUAL PROCESSING

3.1 INTRODUCTION

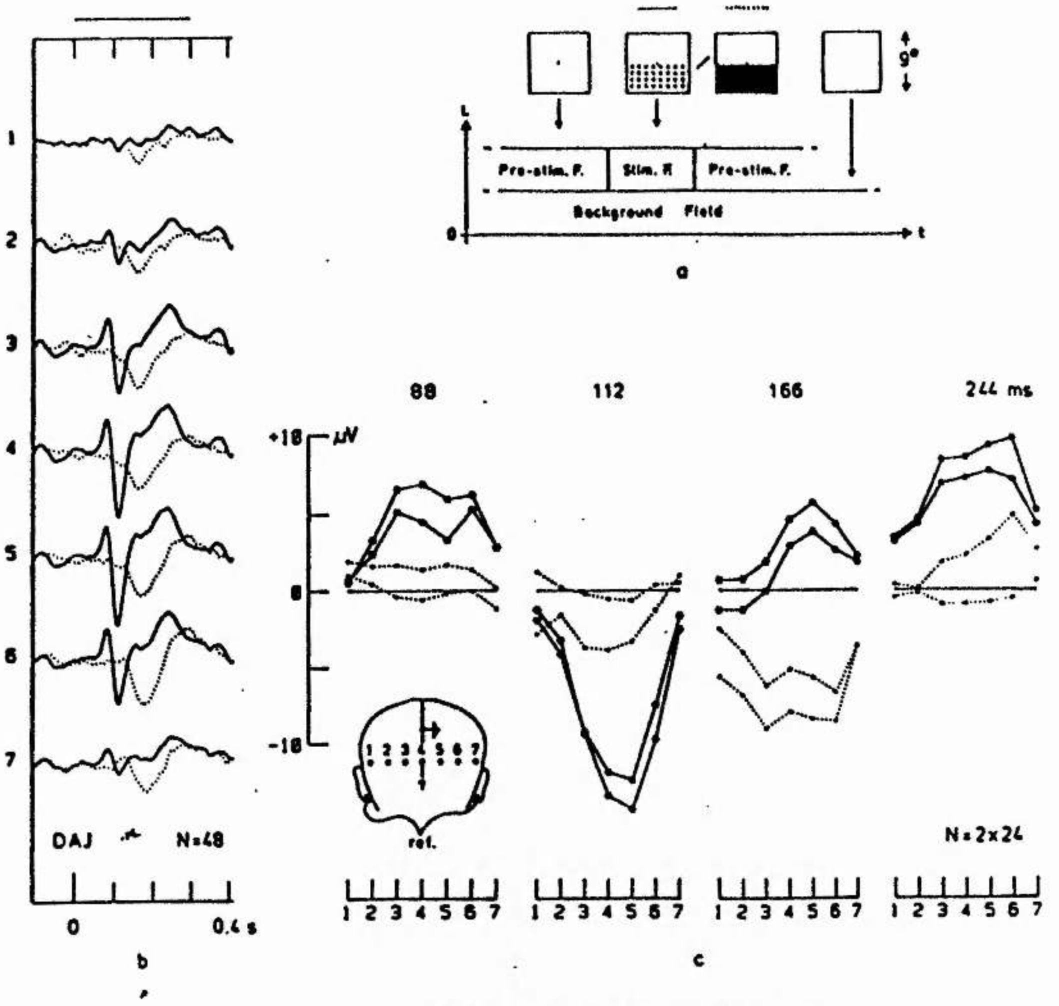
This chapter considers electrophysiological evidence for neural mechanisms specialized for processing particular types of visual stimuli, with particular emphasis on facial stimuli. Evidence is reviewed from three sources with a primary focus on E.R.P measures of selectivity.

3.2 STIMULUS SPECIFICITY IN EARLY EVENT RELATED POTENTIALS

In order to discuss in full the possibility of evoked potentials specific to stimulus categories, it is necessary to have an understanding of how simple elements of visual stimuli (lines, contours, colour) affect the electroencephalogram. Jeffreys (1989) has reviewed investigations into recorded responses which are specific to pattern related information processing in the visual cortex. The main aims of these studies have been to identify any components which correspond to pattern-onset, and also to determine where in the visual cortex these components are generated. The scalp distributions of the components is important in this respect, in that they can be used to predict the likely source locations of the EP components (Vaughan 1982). It is important to note however, that the precise source of origin cannot be determined from surface recordings alone.

In most experiments, Jeffreys (1989) reported visual evoked potentials (V.E.Ps) to tachistoscopically presented achromatic pattern (See Fig. 3.1). Responses were recorded from a transverse row of seven or five electrodes, with the central midline electrode at Oz, to a linked earlobe common reference.

FIGURE 3.1. Typical experimental set-up for study of pattern-onset V.E.Ps. From Jeffreys (1989).



Experimental set-up for study of pattern-onset VEPs. a) Stimulus presented by alternately switching from an unpatterned (pre-stimulus) to a patterned (stimulus) tachistoscope field. with a 3rd (background) field continuously illuminated and unpatterned. Stimulus field size 9 x 9 deg; pattern contrast 0.5.; luminance level 200 cd/m^2.

b) Averaged VEPs recorded from transverse row of 7 electrodes to patterned (0.4 deg isolated-squares) and unpatterned (luminance change) stimuli in the bottom half-field. shown by the full and dotted traces, respectively. Central midline electrode (Oz) 3-4 cm above inion; electrode separation 3 cm; linked-earlobes reference. Mean cycle period 1.2s; stimulus duration 0.3s (indicated by horizontal line over top time-scale).

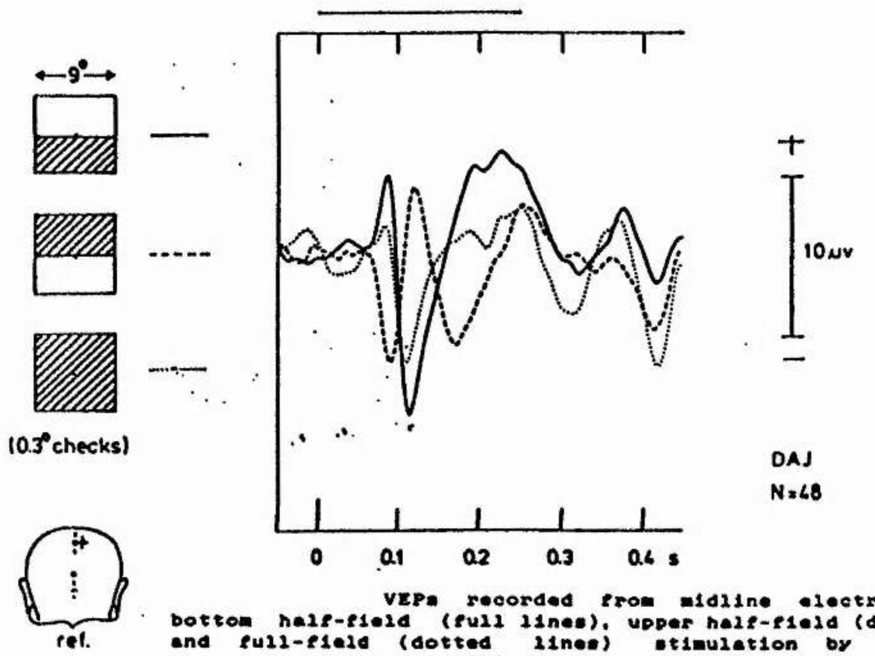
c) Response amplitude distributions across electrodes, at post-stimulus delays of 88ms, 112ms, 166ms and 244ms, the peak latencies of the 4 major deflections in the pattern VEPs in (b).

A typical VEP to a stationary stimulus pattern consisted of initial short duration positive and negative peaks, followed by a more prolonged double-peaked positivity. Studies conducted earlier (Jeffreys and Axford, 1972) on the initial bi-phasic part of the VEP showed that changes in the site of stimulation influenced the polarity and form of the scalp distribution of both the first and second peaks. Most notably, separate stimulation of the lower and upper half-fields evoked peaks of similar latency but reversed polarity in most subjects. Also, the response to a full-field pattern was found to be approximately the sum of the half-field responses. That is, each half (and quadrant) of the visual field contributed independently to the pattern visual evoked potential (See Fig. 3.2).

The first and second VEP peaks had distinct amplitude distributions and were taken to reflect two different components, C1 and C2. These were seen as originating from separate cortical areas. C1 and C2 were also influenced by site stimulation and were therefore suggested to be generated in visuotopic cortex. In comparison, a late negative peak in the VEP to the unpatterned stimulus had a consistent polarity and distribution which was not affected by varying stimulus location. It is suggested that this component has its origin in some non-visuotopic cortical region.

The main stimulus-related properties of C1 and C2 can be briefly summarized. C2 is mostly responsive to well-defined stationary contours in the central visual field. The largest response in terms of the amplitude of C2 are found to be evoked by stimulus patterns with many contour discontinuities, and the smallest amplitudes by continuous straight line contours. The amplitude of C2 is also found to vary according to the subjective appearance of the stimulus contours, and is maximal only if the pattern element boundaries are clearly visible. Both monocular and binocular viewing evoked C2 with comparable amplitude, but the latency of the component is slightly increased for monocular viewing. The threshold of C2 is also higher in the case of monocular viewing.

FIGURE 3.2. V.E.Ps recorded to half and full-field stimuli. From Jeffreys (1989).



VEPs recorded from midline electrode (Oz) to bottom half-field (full lines), upper half-field (dashed lines) and full-field (dotted lines) stimulation by a 0.3 deg. chequerboard pattern. Stimulus duration 250ms.

C2 is only evoked by the appearance of a visual stimulus, not by its disappearance or displacement. The component reaches maximal amplitude with only brief presentations of patterns (10-20 msecs). This is independent of stimulus duration. C2 was also found to be very sensitive to pattern pre-adaptation.

C1 is seen to have a dual composition, consisting of two subcomponents of similar latencies and scalp distributions. However, these subcomponents display different stimulus related properties. For example, 'C1a' is evoked only by the pattern onset, while 'C1b' seems to be both onset and offset related. Varying stimulus patterns affects the relative amplitudes of these two subcomponents of C1.

In more recent experiments, (see Jeffreys 1989a for review) components have been reported from later parts of the pattern VEP, which (like C2) are contour specific and are evoked only by pattern onset. They achieve maximal amplitudes for very brief stimulus presentations and are highly sensitive to pattern pre-adaptation. They are however, selectively sensitive to different, relatively complex stimulus features, which is not a characteristic of C2.

The early components C1 and C2 appear to be followed by two potentials of distinct amplitude distributions which overlap in time. They also appear to be of opposite polarity in the bottom half-field pattern visual evoked potential. The 'C3' component is evoked only when the stimulus elements are presented against an untextured background. It has similar topographical properties to the C2 component but is of an opposite polarity, which is suggested to indicate a visuotopic cortical origin. The other component was found to be consistently negative and the amplitude and form of its broad scalp distribution was uninfluenced by stimulus location, suggesting a non-visuotopic origin.

Most of the constituent components of the pattern-onset VEP have been found to be contour specific, suggesting that their cortical generators are involved in the analysis or recognition of object form or shape.

The question of whether it is possible to record potentials which are specific to more complex patterns has been investigated in some studies. Those studies which have investigated evoked potential responses to facial stimuli are particularly relevant to this thesis.

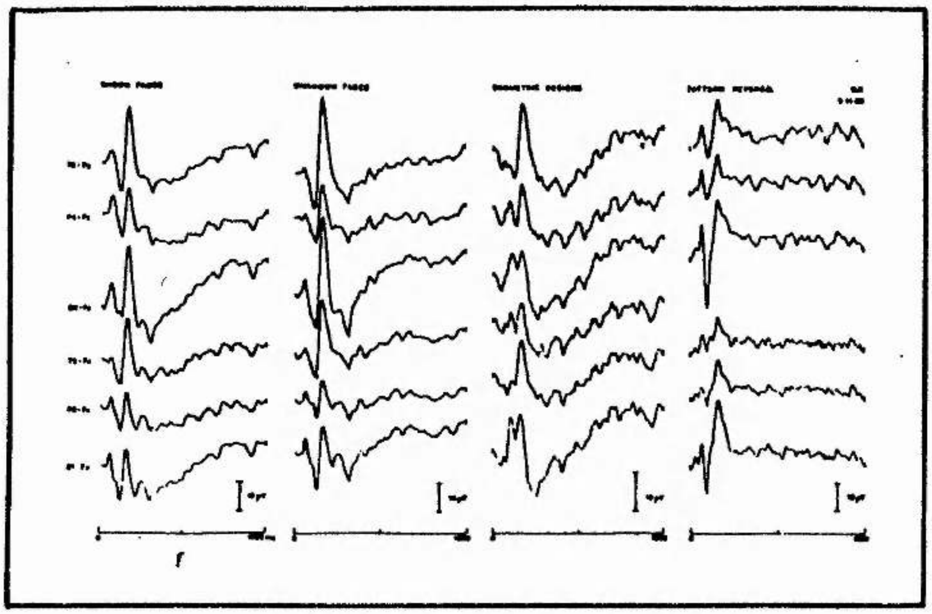
3.3 'FACE-SPECIFIC' EVENT RELATED POTENTIALS

There have been a number of studies investigating the possibility of a 'face-specific' component. In these studies, face processing has become of interest because faces are examples of complex, meaningful, non-verbal visual stimuli. There have been several investigations into the changes in E.E.G. of human subjects when representations of faces were presented, or other face-specific tasks had to be performed. An early study reported by Dumas and Morgan (1975) involved forming subjective impressions about faces (eg "interesting", "friendly"). Subjects were asked to recall this information 15 seconds later. They found a suppression of E.E.G. alpha activity that was more pronounced over the right hemisphere when faces were recalled (A decrease in alpha activity- approx 10 Hz frequency - is interpreted as increase in cortical activation).

Small (1983) also reported evoked response hemispheric asymmetries, in the parieto-occipital region, to the presentation of face stimuli. Responses to familiar and unfamiliar faces were compared to those produced by other complex geometric stimuli in a group of right-handed subjects. There was no task involved besides fixating on the stimuli. The main findings of this study were that the amplitude of response was greater at right hemisphere sites (posterior temporal, parietal and occipital) at a latency of 300msecs during presentation of known faces. This greater amplitude was also found in occipital regions with unknown faces. No such asymmetry was seen with the geometric figures or with pattern reversal (See Fig. 3.3). Small refers to this positivity as a 'P300'. The P300 is a late component which seems to reflect cognitive events. This component has been variously interpreted as a neuroelectric sign of cognitive acts such as orientation, information acquisition and evaluation, uncertainty reduction, decision making, task-relevant surprise and the confirmation or disconfirmation of expectancy (For review, see Hillyard and Picton 1978, Donchin et al 1978, Ruchkin and Sutton 1983, Munson et al 1984). Small interprets her finding of the 'P300', which is greater in the case of facial stimuli presentation, as an indication of cognitive rather than perceptual events.

In a subsequent study (Small 1986) the responses from a group of right and left-handers were compared, using the same stimuli as the previous experiment. The main findings of this study were that there was a significant asymmetry at around 300msec to all stimuli in the right-handed group and this was greater for face as opposed to other stimuli. Left-handed subjects showed no significant hemisphere assymetries. In a further study (Small 1988), these data were compared to responses observed in a prosopagnosic patient with evidence of lesions in the right posterior parietal region and above the left lateral ventrical. The stimuli used were identical to those used in the previous experiments, and again the prosopagnosic subject performed no task other than fixating on the stimuli. The results showed no significant differences between the prosopagnosic patient and a normal control group with regard to P100 amplitude, P300 amplitude or P300 latency. The main difference between the controls and the patient were that the latency of a P100 was significantly slower (around 30msec) in the case of the prosopagnosic patient, particularly at right hemisphere sites. This latency effect was present for facial and non-facial stimuli. There was also an interaction between lateralisation and stimulus condition in the case of the prosopagnosic patient - the latency of the P120 was significantly slower

FIGURE 3.3. Evoked potentials in response to known and unknown faces, geometric designs and pattern reversal. From Small (1983).



— *Evoked potentials from one individual under all four types of stimuli. Electrode derivations, as shown on left, were in the same order for each condition.*

in the right hemisphere to geometric and pattern reversal stimuli (approximately 6.5 msec later than the control group). These results were interpreted as evidence that in this particular case of prosopagnosia, the problem was at a perceptual rather than a cognitive level of processing.

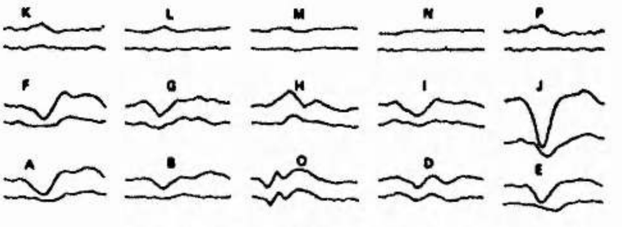
Another study of evoked potentials recorded from a prosopagnosic patient was reported by Renault et al (1989). When this patient viewed a series of familiar and unfamiliar faces occurring with unequal probability a positive P300 like potential (latency = 600-800 ms) occurred with greater amplitude to the less frequent class of stimuli. When the patient viewed a series of familiar and unfamiliar faces occurring with equal probability, however, the positive potential was equal in amplitude across stimulus category. The presence of a P300, therefore indicated that the patient could detect the difference between familiar and unfamiliar faces (at least at the covert level).

Neville et al (1982) also recorded a high P300 amplitude which was evoked by pictures of persons or places known to the subject as compared to the responses evoked to unknown stimuli. This result is questionable however, due to the lower probability of known as opposed to unknown stimuli in the experiment, since the P300 has been shown to occur in response to improbable stimuli.

Srebro (1985a, 1985b) computed the 'Laplacian derivative' of visual evoked potentials to brief presentations of computer generated faces and geometric figures. In the Laplacian technique, activity at a site of interest is compared to the activity occurring in a group of surrounding electrodes and only that activity unique to the target electrode is recorded. In the first set of experimental sessions, four right-handed female subjects memorised a face. They were subsequently presented with a series of pictures of the memorised face corrupted by varying amounts of noise. The task was to detect whether the memorised face appeared in the image. Subjects responded by pressing either 'face' or 'no face' switches. They were asked to delay their response for approximately 1s until the fixation dot blinked, in order to prevent any eye movement artefacts contaminating the EP. Preliminary experiments revealed that subjects believed there to be different faces appearing in the stimulus sequence, even though the same (previously memorised) face was used throughout. The task was thus modified to a situation where one of three responses was required;'the' face, 'a' face or 'no face'. The resultant averaged waveform which resulted when subjects reported 'the face' was characterised by an initial peak at around 75ms after stimulus onset. This was followed by a larger trough at 180ms, followed by a secondary peak at 280ms after stimulus onset (See Fig. 3.4). The waveforms resulting from 'a face' and 'no face' reports were broadly similar, but differed from 'the face' waveform from around 197ms post stimulus. Up to 100ms, all three waveforms were equal in both amplitude and wave form. For all four subjects, the evoked cortical activity was greatest in the temporal lobes and was slightly stronger in the right than in the left temporal lobe. Within each temporal lobe, the activity encompassed the posterior part of the lobe, extending approximately 5cm anteriorly towards the anterior pole of the temporal lobe. (The pattern of activity was assessed by a mapping technique described by Srebro 1985a). One experimental session was modified slightly to include the memorised face and some other faces. In this case, the pattern of activity evoked by the unfamiliar faces was the same as that evoked by the memorised face.

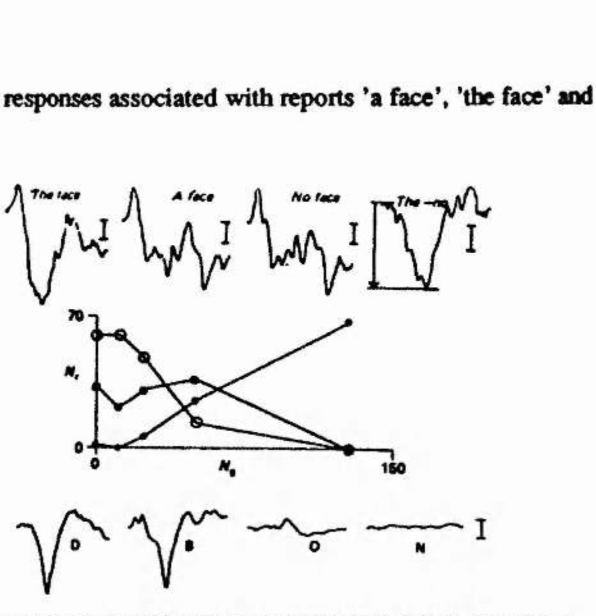
A second experiment reported followed broadly the same pattern as experiment 1, except that silhouette shapes of a triangle and a block letter 'T' were used as stimuli. These were also corrupted by varying amounts of noise and the subjects were required to respond 'shape' or 'no shape'. The subjects were three right handed females, two of whom had taken part in the first experiment. The resulting waveforms were relatively simple, with a

FIGURE 3.4. Laplacian responses associated with correct shape identification and the report 'no shape'. From Srebro (1985b).



. Laplacian responses for Expt. 2 (subject E.M.M., silhouette shape, block I, Pl. 3). Each record shows 420 ms following stimulus offset. Two Laplacian responses are shown for each centre-electrode location (letter above, Pl. 2). Top Laplacian response is that associated with the correct shape identification. Bottom Laplacian response is that associated with the report *no shape*. All records are at the same scale. Note that the Laplacian responses have similar wave forms at all centre-electrode locations except at O, over the occipital cortex, where an early negative–positive complex appears, and that the Laplacian response associated with the report correctly identifying the shape is much larger than that associated with the report *no shape* except at centre-electrode location O, where it is nearly equal in amplitude.

FIGURE 3.5. Laplacian responses associated with reports 'a face', 'the face' and 'no face'. From Srebro (1985b).



Laplacian responses and report name usage (subject R.K.C.). Top: average Laplacian responses, centre-electrode location D (Pl. 2). Each record shows 420 ms after stimulus offset, outward current downward. Scale marks: 10 arbitrary amplitude units. Report labels: *the face*, the face shown at the beginning of the experimental session was seen, *a face*, a face but not the face shown at the beginning was seen, *no face*, no face was seen. *The – no*, the response constructed by subtracting the Laplacian response associated with the report *no face* from that associated with the report *the face*. Bottom: *the – no* responses at several different centre-electrode locations (Pl. 2). Scale mark at right applies to all. Middle: N_g, number of grey-scale levels restored in the look-up table, N_r, number of reports. ●, report *the face*; ■, report *a face*; ○, report *no face*.

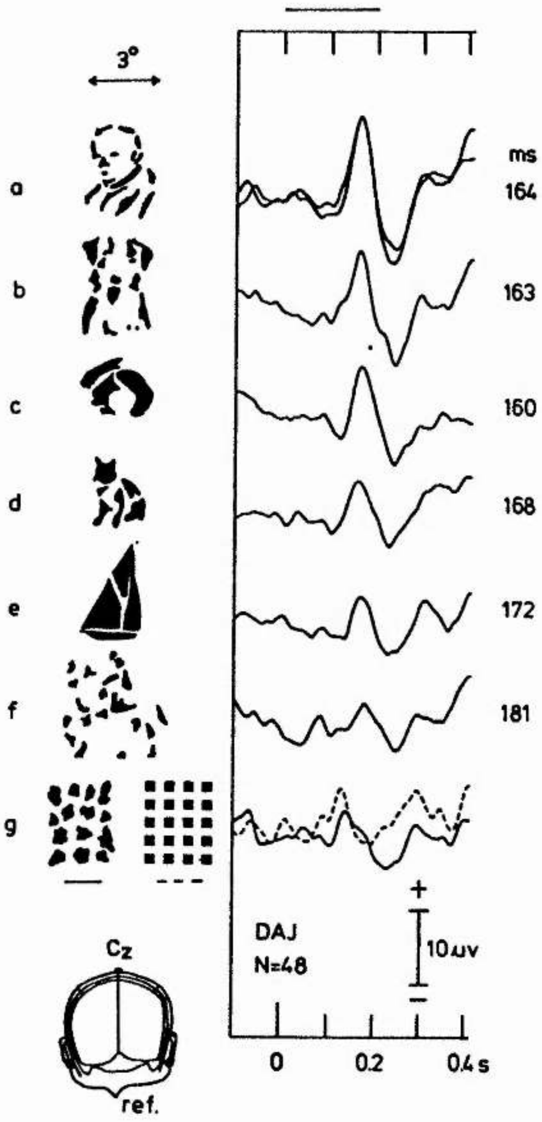
prominent trough occurring at 207ms. Cortical maps revealed that activity was greater in the right then in the left temporal lobe. There was considerable overlap between the regions of temporal lobe in which cortical activity was evoked in the two experiments. However, the activity associated with the simple shape recognition appeared as a subset of that associated with face recognition, restricted to the more anterior part of the temporal lobe (See Fig. 3.5).

The results suggested that in humans, recognition of faces and simple shapes evoke cortical activity with similar time course and topographies. but that the activity associated with face recognition encompasses a wider region of cortex, extending to more posterior regions of the temporal lobe.

Jeffreys (1989a) presents results from studies investigating evoked potentials to face and non-face stimuli. This work forms part of a wider study of the functional organisation of the human visual cortex, involving the identification of contour and pattern specific evoked potentials. Previously identified components (Jeffreys 1989b) included two relatively long-latency components of non-visuotopic cortical origin which are reported to respond selectively to distinct complex stimulus parameters. Two earlier components are also reported, originating from visuotopic occipital regions , which are sensitive to local contours (Jeffreys and Axford 1972, Jeffreys 1977). Jeffreys (1989b) presented a series of fragmentary figures, photographs, outline drawings and adapted Mooney faces during EP recording. Recordings were taken from nine subjects altogether, although the majority of the experimental results are based on two subjects, one the author himself. No task was involved other than fixating on the stimuli. The initial experiments involved the presentation of fragmentary figures of a man's head, a dog, a cat, a ship and a man on horseback. Also presented were geometric patterns and arrays of discrete, irregularly shaped elements. The more easily recognisable fragmentary figures (man's head, dog's head) evoked midline positive peaks from 160-180 msec. This is termed the 'vertex positive potential' (VPP). The peak was less evident in the case of the 'man on horseback' fragmentary figure and no such peak was recorded to the control stimuli (geometric patterns, arrays of discrete elements) See Fig. 3.6.

The fragmentary man's head was the most effective stimulus for evoking the VPP. In a subsequent experiment, fragmentary figures of the man's head and stimuli containing elements of corresponding location but different shapes were presented. These changes attenuated the VPP. The largest responses in this case were recorded from the author. In a third experiment, a variety of face and non-face stimuli were presented. The VPP was evoked with consistently larger amplitude to face stimuli, but was evoked also by some non-face stimuli. Jeffreys reports that the VPP was evoked by many different forms of face stimuli such as photographs and caricatures. Front, profile and half-profile views were all relatively effective in evoking the VPP. Representations of hands, feet, flowers and written words were ineffective. One particular experiment compared responses to a schematic face and a watch 'face'. In general, there was no response to the watch 'face' stimulus, but one subject showed no VPP to the schematic face stimulus. Varying the size of the stimulus (length 8.7 to 2.5 degrees) had no effect on the VPP, but central fixation evoked the VPP 16-20msec earlier than eccentric fixation. This result is compared to those obtained by Perrett et al (1985), who reported attenuation and/or delays in cell responses when face stimuli were manipulated in ways that affected perception. Inversion or rotation of the face stimuli resulted in delaying the VPP for 18-25msec and a slight attenuation. The VPP was eliminated when Mooney faces were presented inverted, but was still present when other faces were inverted. It is suggested that these stimuli could still be recognised as faces, whilst the inverted Mooney faces are not perceived as faces. The removal of features also affected the latency of the VPP, with delays of up to 50msec.

FIGURE 3.6. V.E.Ps recorded from Cz electrode to the illustrated figures (a-g). From Jeffreys (1989).



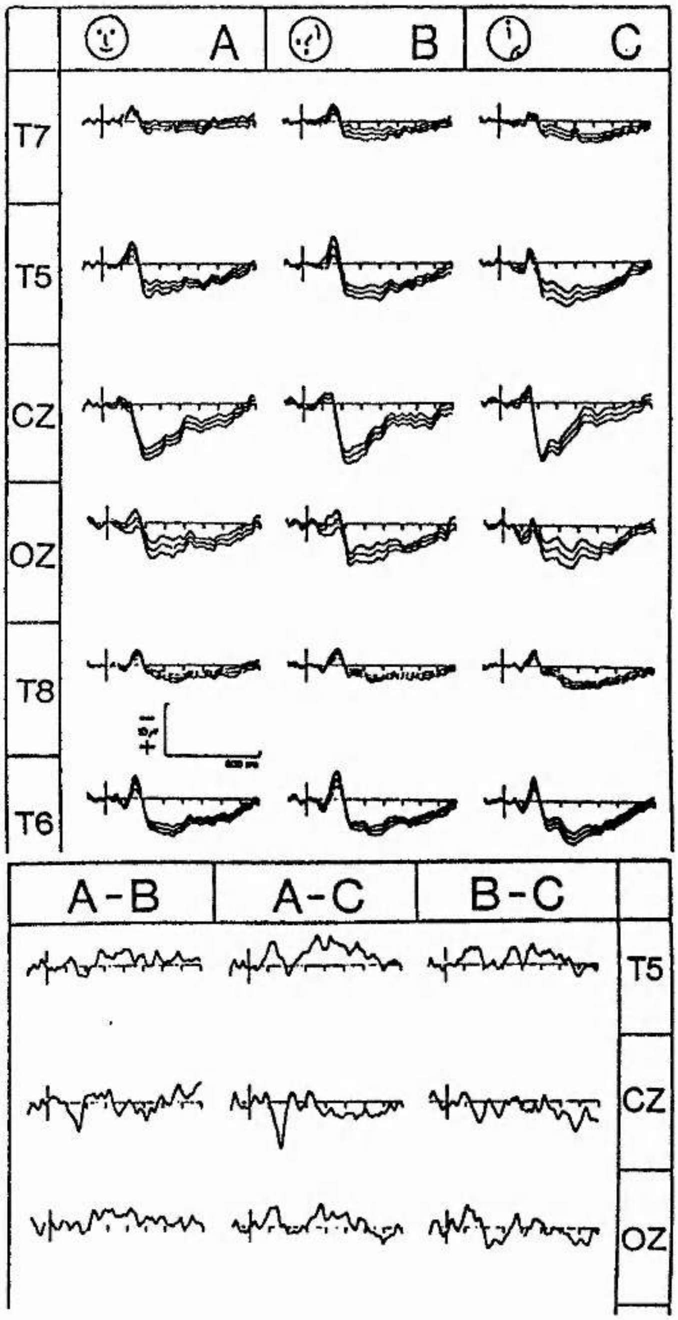
The form of the response distributions in Jeffreys studies were found to be dependent on the choice of reference (Jeffreys 1989b). Recordings were taken from a coronal row of 7 electrodes and also from a midline row of 8 electrodes. Moving from a linked earlobe reference to a nose reference was found to reverse the polarity of the VPP at sites T3 and T4. The underlying source locations of the VPP are thus unclear. Jeffreys suggests that the topography is nevertheless consistent with a site of origin in the superior temporal sulci or ventral temporal cortex. The conclusion from these experiments is that the generators of the VPP play some role in the perception of complex and meaningful stimuli, reflecting visual processing rather than any psychological response to the appearance of a face. The results reported appear to be fairly consistent with regard to a VPP maximally responsive to face stimuli.

A further study reported by Jeffreys (personal communication to D.I Perrett 1991) describes an experiment in which EPs were recorded to a series of faces of different sizes (1 to 7 degrees). Subjects were required to fixate at points 1,2,3, and 4 degrees to the left and right of, or above and below the centre of the face. The frontal view of a face produced a positivity at around 200msec. Changing the visual fixation point in the case of the smallest stimulus face had a marked effect on the size of this EP. Maximal amplitude and shortest latency was recorded for central fixation on the bridge of the nose. There was a smaller response to eccentric fixation 1 degree to the left or right of the central point, and little or no response recorded for fixation points of 2 degrees or more eccentricity.

Comparison of frontal v profile views of faces also changed the maximum point of response, with the optimal fixation point for the profile faces skewing toward the front of the face (1 degree from centre of stimulus). EPs of similar optimal amplitude were evoked for central fixation of faces of different sizes. The attenuation of the response at different fixation points is also present with varying stimulus size. The results of this experiment have yet to be replicated in other subjects.

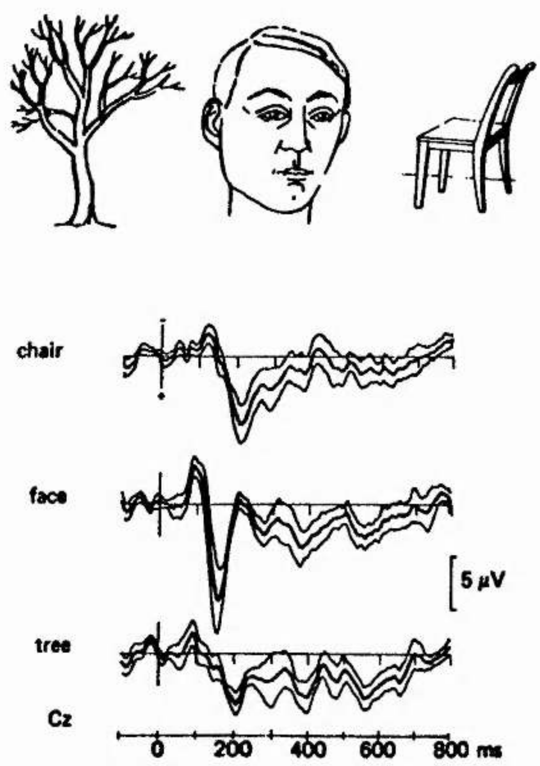
Botzel et al (1989) reported a series of experiments investigating changes in the EP corresponding to the viewing of facial and non-facial stimuli. In the first study, a highly schematic face was used as stimulus. The positions of the internal features of this face were changed to achieve a continuous degradation from 'good face' to 'poor face' to 'non-face'. No task was involved other than fixating on the stimuli. Category-specific differences were reported which were most evident in the comparison of good face and nonface stimuli. The difference curve obtained from these two waveforms indicate a greater positivity for the good face around 250msec (Fig. 3.7). Further differences were reported when another set of schematic faces were presented either normally, jumbled or inverted. A third experiment reported involved a direct comparison of facial and nonfacial stimuli (also reported in Grusser 1990). 29 subjects participated in the experiment (19 female, 10 male). The study involved no task other than fixating on a series of stimuli. These stimuli were slides of black and white line-drawings of a face, a tree and a chair. The slide series was shown twice to each subject, the second series being negatives of the first series. Fig. 3.8 shows the grand averages obtained from the viewing of facial and other stimuli at site Cz. The waveform resulting from the viewing of face stimuli was characterised by a more 'structured' waveform than that obtained with the highly schematic faces. The EP recorded to face stimuli was characterised by a positivity in the waveform between 100 and 300ms, peaking at around 150ms. The response was most pronounced at Cz. These differences were reported for the positive and negative stimuli.

FIGURE 3.7. Evoked responses to 'good face', 'poor face' and 'non-face' schematic line drawings. From Botzel et al (1989).

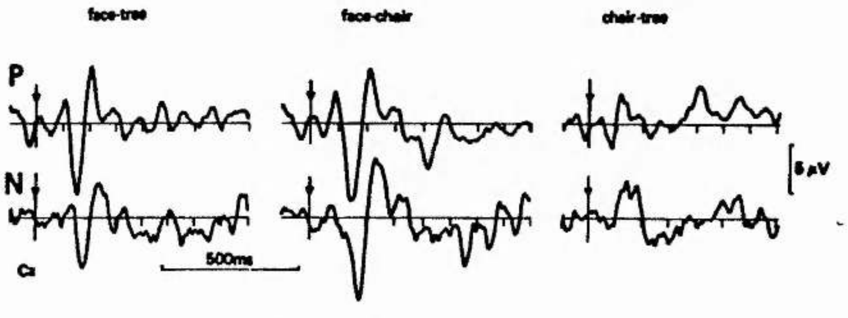


EPs obtained with patterns 1, 6, and 12 of Fig. 2. EP grand averages (± standard error) of 14 subjects. Recording electrodes as indicated. In the *lower part of the figure*, difference curves according to stimulus categories are shown for three electrodes as indicated

FIGURE 3.8. Evoked responses to face, chair and tree stimuli. From Grusser et al (1990), originally reported in Botzel and Grusser (1989).



Upper: Set of stimuli in the first experimental paradigm. Stimuli were black line drawings of a chair, face, or tree (P stimuli) or the same drawings with white lines on a black background (N stimuli). Lower: Grand averages (±standard error) of EPs recorded through electrode C_z in five female subjects; P stimuli.



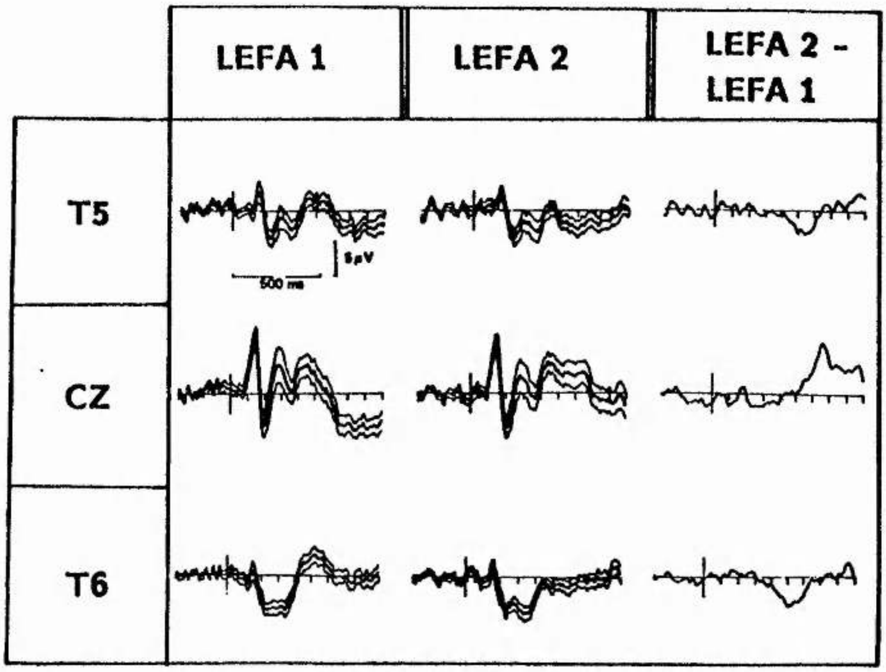
Subtraction curves of the grand averages of EPs recorded in five female subjects with electrode C_z (paradigm 1: face−tree, face−chair, chair−tree). Note the considerably larger differences when face stimuli were involved for the responses obtained between 100 and 300 msec after stimulus change (*arrow*). Data obtained with P stimuli (P) in the upper row, with N stimuli (N) in the lower row.

Also reported is another series of experiments in which black and white photographs of unknown faces as well as photographs of vases and shoes were presented. Subjects were told that they would have to recognise the slides later but no other task was required. An early negative peak emerged at around 140-160ms post-stimulus. This peak had the shortest latency and the highest amplitude at Cz when the stimulus was a face. A positive peak was identified occurring between 210 and 240 msec. The latency of this peak was shortest in the case of the face waveforms. A negative peak at around 300ms was also reported for face stimuli, which was small or absent in the waveforms elicited by nonface stimuli. This was not, however, present in all subjects, and was absent in the case of the male subjects.

Another experiment reported in the same paper involved a face-recognition task. The faces are referred to as 'known' and 'unknown'. (In fact, they were either presented prior to the experiment or not. This is an important qualification, as the task was another version of a memory/recognition task rather than an investigation into any qualitative differences in waveforms to familiar and unfamiliar faces). Subjects saw eleven faces before the experiment, and rated them on subjective characteristics such as friendliness. These were then presented ten minutes later interspersed with an equal number of previously unseen faces. The main result obtained from this study was a more sustained negativity form around 400msec in the case of the previously seen faces (Fig. 3.9).

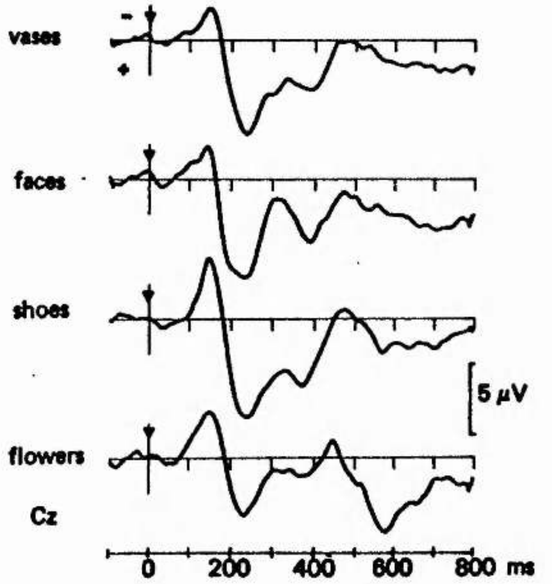
The same group of subjects in this experiment were presented with a series of famous faces interspersed with unknown faces. The subjects were required to respond with a button press only when a famous face appeared. There were only small differences between the resultant waveforms from viewing the famous and unknown faces. In any case, the comparison of E.R.Ps across the famous and unknown faces could be flawed due to the imbalance in the response requirements. This criticism can also be levelled in

FIGURE 3.9. Evoked responses to previously seen and unseen faces. From Grusser et al (1990).



Grand averages of the EPs of 15 subjects (8 men, 7 women). Recording examples from the electrodes T5, T6, and C_Z. In the middle column the responses to face photographs viewed before the tests (LEFA 2), in the left column the corresponding EPs to unknown face photographs (LEFA 1). In the right column, the difference between both curves is displayed. In the left and middle columns, the standard error is shown in addition to the grand average.

FIGURE 3.10. Evoked responses to pictures of vases, faces, shoes and flowers. From Grusser et al (1990).



EPs (grand averages) obtained at electrode C_Z in 13 subjects (4 men, 9 women). Stimuli were black and white photographs of vases, faces, shoes, and flowers. A recognition task after presentation of a flower was included. Responses to unknown stimuli averaged.

the case of a subsequent experiment (Grusser et al 1990) employing an identical paradigm, but using pictures of flowers as stimuli. The flowers were either previously learned or unfamiliar. Here, a positivity emerged between 200 and 400 msec in the case of the learned stimuli (See Fig.3.11.). This could quite easily be attributed to the response requirement and not the suggested 'quasi-physiognomic quality' that the learned flowers enjoy. A comparison is also made across the two latter experiments between the responses to flowers and faces. The most pronounced difference here was a negative peak around 280msec in the case of the face stimuli.

Another series of experiments (Botzel and Grusser 1989 also reported in Grusser 1990) introduced a memory task. The stimuli used were the pictures of unknown faces, vases and shoes used previously. In addition, a series of 'flower' slides were included in the experimental series. Subjects memorised nine slides approximately 20 minutes before the experimental recording, three from each category of faces, vases and shoes. These slides consequently appeared in random order within a series of 183 other pictures, including the flower pictures. The subjects were instructed to press a button whenever a flower slide appeared immediately after one of the memorised slides. This memory task appeared to eliminate the early category-specific differences obtained in the previous experiments. A late positive wave was reported however at around 700msec, which was most prominent when the facial stimuli were viewed and which had a maximum at Fz (Fig. 3.10). It is suggested by Botzel and Grusser (ibid) that this late component is related to the storage of information in order to make a decision. No explanation is offered as to why the early category specific differences were eliminated in this study.

A final experiment (Grusser et al 1990) reported involved the presentation of normal and inverted faces. The main finding here was an increased latency for a positive peak around

200msec in the case of the inverted stimuli. This is similar to results obtained by Jeffreys (1989b).

It is difficult to come to any firm conclusions about all the experiments reported by Grusser et al. The initial findings of category-specific differences are interesting but the responses to faces are also often indistinguishable from those to nonface stimuli, particularly in the early latency regions where differences were originally observed.

Some further studies have been reported which follow on from the initial studies reported by Grusser and colleagues. Fischer et al (1989) have presented brief descriptions of evoked potentials recorded while subjects viewed 'face' and 'tree' stimuli. The results of these studies cannot be fully discussed due to lack of detail in these abstracts. However, the main findings can be summarised. The first study involved 16 subjects being presented with representations of a line drawn face or tree. These stimuli were preceded by the corresponding written word 'face' or 'tree' or by a random dot pattern. Subjects were required to respond with a button press whenever a marker appeared on a slide. The responses to these slides were not included in the analysis. Results showed that verbal priming did not have any effect on the responses recorded to either face or tree stimuli. This result would not be surprising if the same representations were shown for several trials during the experiment. However, this is not made clear in the description. The EPs recorded to the word stimuli were reported as differing from those recorded to pictorial stimuli, but there were no differences between responses to the word 'face' and the word 'tree'. The latency of a positive peak around 200 msec was found to be shorter for faces than trees. No differences in amplitude were reported.

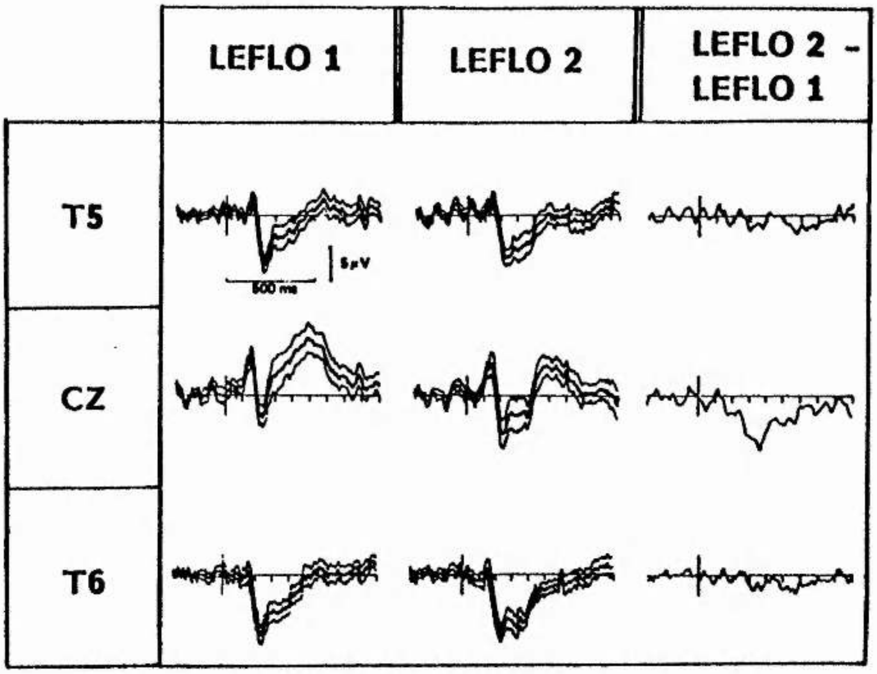
Seeck et al (1989) investigated EPs resulting from viewing human body silhouettes and inanimate object silhouettes (flowers,tools). Category differences between the resultant waveforms were reported as small, but most pronounced at tempero-occipital sites (from bi-polar recordings T4-T6, T3-T5). The differences take the form of a greater positivity in the waveform response to human silhouettes than to non-human shapes. Further to this study (Seeck et al ibid), recordings were made while subjects viewed silhouettes of human profiles, hands and abstract figures. The results of this study indicate a greater positivity for the waveforms to hand stimuli than to the other silhouettes, again around 200msec (See Figs. 3.12 and 3.13).

It is difficult to come to any firm conclusions about the results reported in these abstracts. Again, the results are not consistent with regard to a face specific component. A variety of 'biologically significant' stimuli also evoke responses that differ from those to inanimate objects.

Some studies have investigated EP responses to facial stimuli in the monkey brain. Grusser and Fuhry (1989) recorded responses from a single Java monkey implanted with epidural electrodes above the right hemisphere. The monkey was trained to discriminate between monkey/human faces and nonfaces. In the first part of the investigation, face stimuli were rewarded and in the second part, the nonface stimuli were rewarded. A difference in the resultant waveforms was reported, with a "face responsive" EP component occurring between 110 and 200 ms, with a peak latency of about 150ms (Fig. 3.14). The component is reported to be present whether face or non-face stimuli are rewarded.

A further study reported by Grusser and Fuhry (1989) involved a task in which the monkey had to distinguish between monkey and complex non-face stimuli. Again, either face or non-face stimuli were rewarded. A face responsive component emerged at around 110ms, having a positive peak at 140msec (Fig. 3.15).

FIGURE 3.11. Evoked responses to learned and unknown flowers. From Grusser et al (1990).



Grand averages (± standard error) of the EPs of 12 adult subjects (7 men, 5 women). Stimuli were learned (LEFLO 2) and unknown flowers (LEFLO 1); In the right column, the difference curves are shown, indicating a highly significant change in the EPs from learned to unknown flowers at the electrode C_z.

IGURE 3.12. Evoked responses to silhouettes of hands, ace profiles and abstract figures. From Seeck et al (1990).

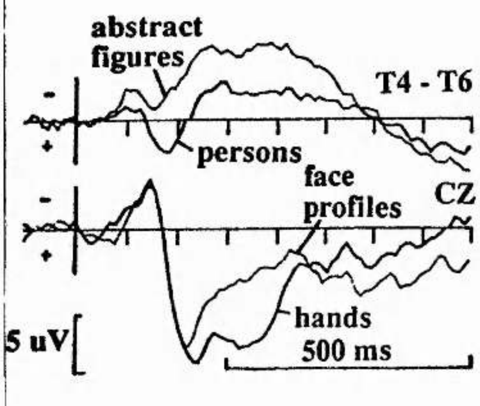


FIGURE 3.13. Evoked responses to animate and inanimate silhouettes. From Seeck et al (1990).

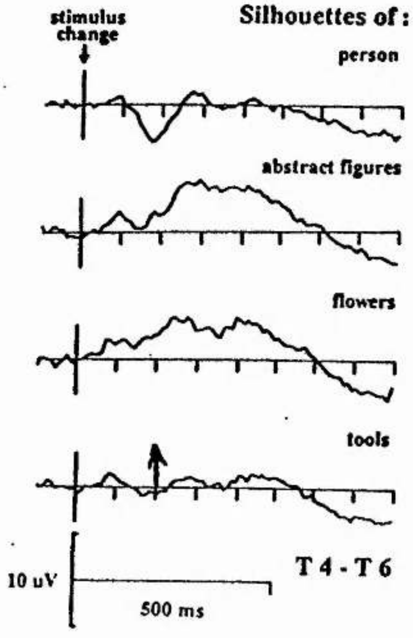


FIGURE 3.14. Evoked responses recorded from a Java monkey. Stimuli are rewarded and unrewarded monkey and human face stimuli. From Grusser and Fuhry (1990).

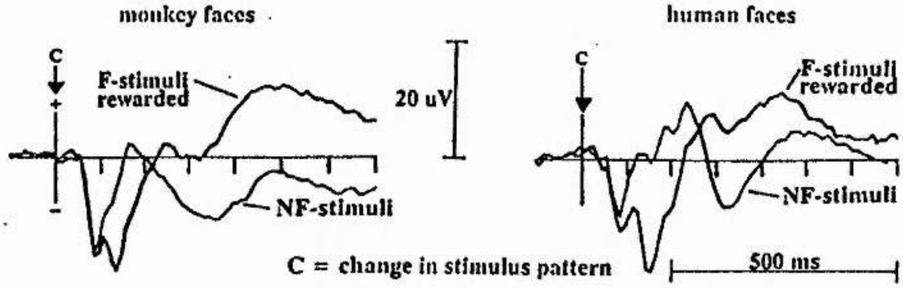
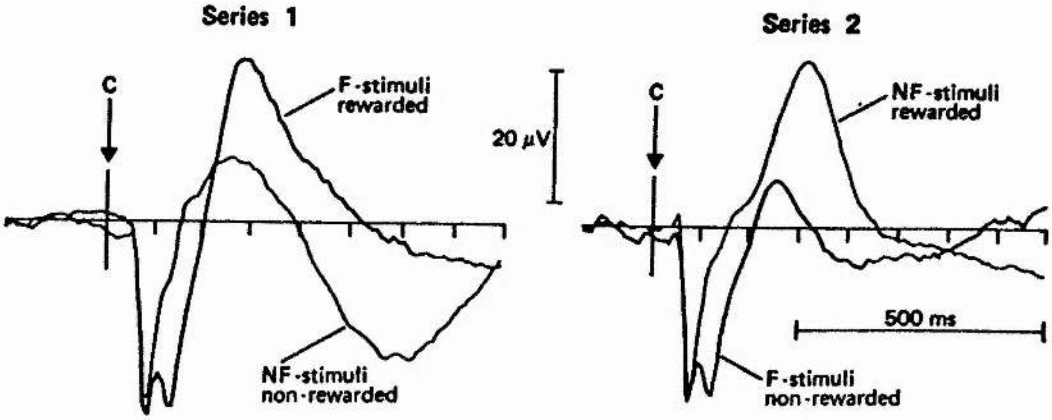


FIGURE 3.15. Evoked responses recorded from a Java monkey. Stimuli are rewarded and unrewarded monkey face and non-face stimuli. From Grusser and Fuhry (1990).



As suggested by Jeffreys (1989b), it is possible that the early EP responses to faces reported thus far are similar to neuronal responses observed in neurophysiological studies of monkey brain cell populations indicating a major role for the temporal lobe region in high level pattern representations. Throughout the studies reported thus far, as observed by Jeffreys, the evidence for face specificity is less strong than the evidence for the potential reflecting a high degree of perceptual processing. However, even if these potentials turn out not to be entirely face-specific, they still have important properties with respect to perception.

An important aspect of the work investigating stimulus specific potentials is the latency at which such potentials may occur. This is important in terms of locating and identifying the brain structures responsible for the generation of evoked potentials. It is useful in this context to refer to single neuron recordings taken from monkey brains. With regard to this review in particular, single unit recordings employing facial stimuli are most relevant.

3.4 SINGLE CELL RECORDINGS FROM NON-HUMAN PRIMATES

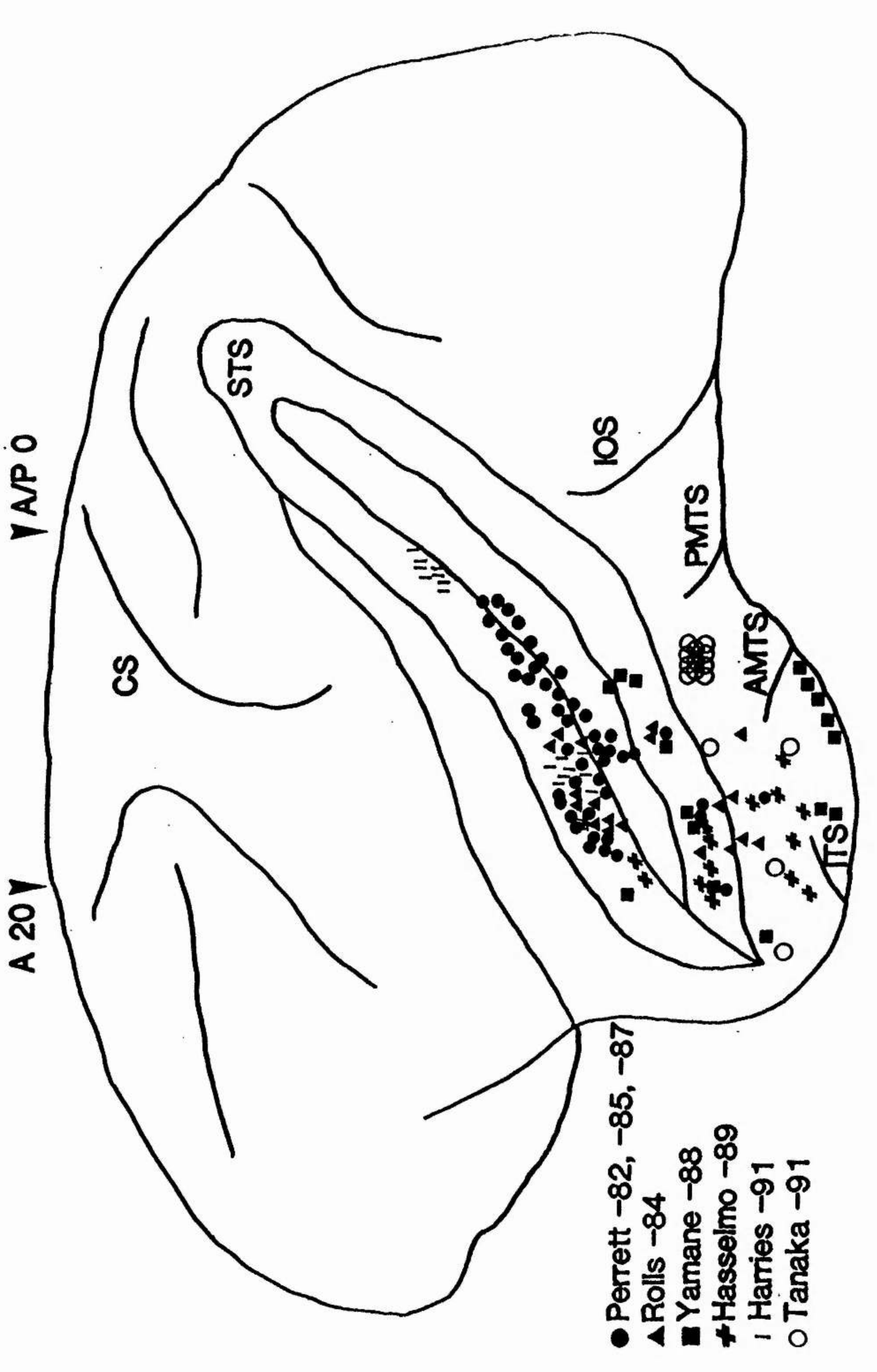
Within the cortex of the superior temporal sulcus (STS), populations of cells have been studied that respond more to the sight of faces than to a variety of other simple and complex stimuli (eg. Bruce et al 1981, Desimone et al 1984, Gross et al 1972, Perrett et al 1982,1984,1985). Some evidence does exist that special structures of the brain control the execution and understanding of facial identification. Microelectrode recordings performed in awake monkeys indicate that face specific neuronal networks exist in the primate brain located in cortical areas bordering on the central region of the superior temporal sulcus of monkey brains (Perrett et al 1982, 1984; Rolls 1984; Desimone et al 1984).

These cells have also been shown to be tolerant to changes in viewing conditions such as size, orientation and position. Some cells have also been found which are sensitive to the identity of faces (eg. Baylis et al 1985, Perrett et al 1984,1986,1987, Rolls 1984). In this case, cells respond more to the face of one individual (familiar to the monkey) than to other equally familiar faces. These cells also generalise across viewing conditions such as orientation, viewing distance and expression. Neuroanatomical studies have shown that these face responsive cells occur in particularly high concentration within two regions of the STS, areas TPO and PGa (eg. Perrett et al 1986, 1987, 1988). They are also found to a lesser degree in other parts of the inferior temporal cortex. The face responsive cells are found in patches extending vertically through the thickness of the cortex and in a tangential direction across the cortical surface. It should be noted that the STS does not only contain cells responsive to faces. Other cells within the region respond to somatosensory information or different classes of movement. Thus the area is not exclusive for face processing, but the evidence suggests a face processing subsystem within one brain area. Cells sensitive to faces have also been reported in other brain areas (eg. frontal cortex, parietal cortex amygdala and brain stem) but the highest concentration of these cells is found in the temporal cortex (see Fig. 3.16 from Perrett et al 1991).

Another source of investigation which has indicated face specific brain mechanisms are humans who exhibit neuropsychological deficits. This research will be briefly reviewed.

3.5 NEUROPSYCHOLOGICAL DEFICITS

Deficits in face processing were first formally described by Bodamer (1947) who used the term 'prosopagnosia' to describe the inability to recognise familiar faces. Since then, well documented impairments in the recognition of familiar faces have been found without disturbances in the linguistic domain (eg. Grusser 1984, Jeeves 1984, Young et al


A 20
A/P 0
CS
STS
IOS
PMTS
AMTS
ITS
● Perrett -82, -85, -87
▲ Rolls -84
■ Yamane -88
✚ Hasselmo -89
I Harries -91
○ Tanaka -91

1988). There have been cases reported of prosopagnosics who can perform normally in the matching of unfamiliar faces (Landis et al 1979, De Haan et al 1987). There is also evidence that unfamiliar face recognition impairment can occur with no specific deficit in familiar face recognition (eg. Warrington and James 1967, De Renzi et al 1968).

Bauer (1984) and Tranel (1985) have shown that prosopagnosics who are unable to discriminate between familiar and unfamiliar faces in a behavioural task do produce galvanic skin responses which show a clear discrimination between familiar and unfamiliar faces. This covert recognition of familiar faces has been proposed as evidence for two separate pathways for processing facial information.

De Haan et al (1987) also report a case of covert recognition. The patient (PH) was unaware that any stimulus face were familiar to him, but he responded faster when task decisions involved familiar rather than unfamiliar faces.

Cases of prosopagnosia have rarely been found without the occurrence of other deficits (Meadows 1974, Whiteley and Warrington 1977), and it is common to find that prosopagnosics also show deficits in recognition of other classes of objects. Damasio et al (1982) suggest this is evidence that prosopagnosia is not a face specific deficit but an inability to distinguish between exemplars of a certain category. Cases have been found, however, where prosopagnosics show little evidence of object agnosia (Whiteley and Warrington 1977, Newcombe 1989, De Renzi 1986).

Cases of prosopagnosia give some support for the notion of stimulus selective processing mechanisms but as noted this evidence is controversial because most patients have a variety of recognition impairments. Damage in prosopagnosia is rarely localised to one functional system, so this does not preclude the possibility that there are specific systems for face processing.

The issue of whether there exist evoked potentials which are selectively responsive to facial stimuli is explored later in this thesis. the first experiments to be reported are concerned with how repeating a stimulus influences waveforms evoked in monkey brains.

CHAPTER FOUR

EXPERIMENT ONE: E.R.Ps RECORDED FROM MONKEYS USING FAMILIAR PICTURES IN A MATCH-TO-SAMPLE TASK

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4.1 INTRODUCTION

In the following chapter, an investigation of evoked potential responses recorded from monkeys is described. The main question of interest is can the E.R.P. repetition effect previously described in Chapter 2 be replicated in monkeys using non-verbal material? In human studies, E.R.Ps to repeated words show a sustained positive shift in comparison with non-repeated words (Rugg 1985, 1987). This modulation of evoked potentials when items are repeated has led to many insights into memory organisation (See Chapter 2 for review). The following investigation extends the enquiry to monkey evoked potentials. Most E.R.P. studies of repetition effects in humans have employed words as stimulus items, as they can be manipulated along many dimensions - familiarity, frequency, orthographically legal/illegal etc. In the study reported here using monkeys as subjects, it was necessary to find a comparable set of stimulus items. The stimuli chosen to this end were pictures. The task element of the study paralleled the human studies reported by Rugg and his collaborators (1985,1987, Rugg and Barrett 1988) as far as was possible. Rugg (1987) adopted a paradigm in which E.R.P. repetition effects could be studied with items to which no overt response was required but which were subject to an implicit lexical decision. Similarly, in this study, no overt response was required to the critical items but the monkeys made match/non-match decision to every stimulus. It was hoped by using this paradigm to extend understanding of E.R.P. repetition effects across species.

Some of the experiments reported here which involve the recording of evoked potentials from monkey brains are innovative and are presented as pilot studies. Throughout the experiments conducted, there were many difficulties encountered due to the length of training time, inconsistent performance by the monkeys and electrical problems. The number of recording sites was restricted in some experiments due to faulty electrodes which could not be repaired non-invasively. This renders the interpretation of the data problematic from the point of view of source locations of potentials. The experiments are also based on recordings from two experimental subjects, and use of one of these subjects was limited by medical problems. Despite these difficulties, some interesting and significant results were obtained which point the way to future investigations.

4.2 METHODS

Subjects:

Recordings were made from two awake, behaving juvenile rhesus macaque monkeys (Macaca mulatta), one male and one female. The monkeys were trained pre-operatively to perform a picture memory task. Training for the two monkeys was identical, but there were differences in performance levels at each stage of training. The training procedure for the female monkey is reported here.

Training:

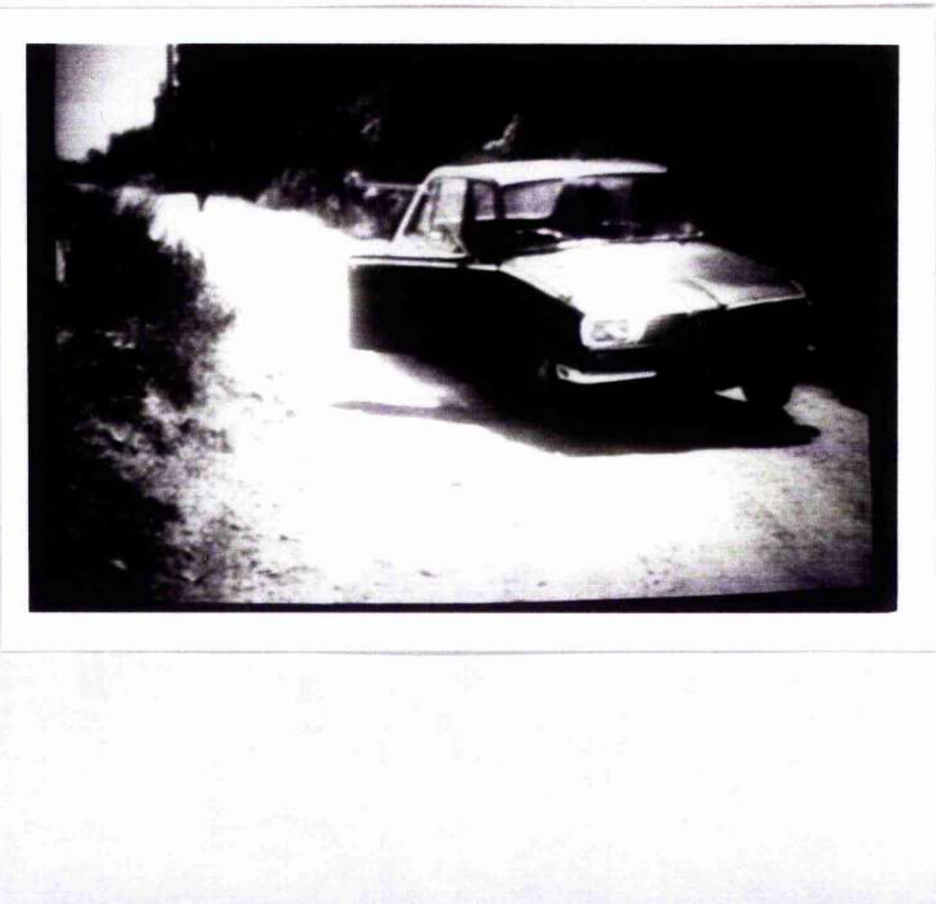
The monkey was housed in a cage, where liquid intake was restricted. Training began with adaptation to a primate chair. Whilst in the chair, perspex plates at either side of the monkeys head restricted head movement but the monkey could lick a tube ad lib to obtain fruit juice reward. During the adaptation period, the monkey could lick freely. The monkey received 50-100% of her daily food and liquid intake when in the primate chair. These adaptation periods lasted from 15 to 30 minutes per day. At the end of five consecutive days, the monkey had adapted to the chair and laboratory environment. A task was then initiated, where the monkey was taught to discriminate between a red and green L.E.D. situated five metres away at eye level. The occurrence of a green light was rewarded with fruit juice. Licking to a red light was discouraged with saline solution. The stimulus light was preceded by a 0.5 second tone and appeared for 1.0 second. The interstimulus interval was 2 seconds. This task trained the monkey to attend to a stimulus and fixate at a distance. At the end of 27 training sessions, the monkey could perform this task to a 90-100% level of accuracy. In order to enable efficient presentation of stimuli, a shutter was then placed in front of the monkey. This shutter obscured the monkey's view, and automatically opened before each stimulus presentation. This trained the monkey to fixate on the stimulus immediately in order to make a quick response decision. The monkey adapted to the shutter after seven training sessions.

In the next stage of training, real objects were used as stimuli. A variety of small items were used - eg, a glass jar, wooden blocks and some small toys. In the description of this task, the first presentation of an object is termed 'novel non-target' and a repeated object as 'repeat target'. A warning tone preceded the opening of a shutter which revealed an object as well as the L.E.D. If the object was novel non-target, a red light appeared and no reward occurred. If the object was an immediate repeat (target), the green light appeared and the monkey could lick for fruit juice reward. For the first batch of training sessions (approx. ten one hour sessions), a new set of objects was employed every day. Thereafter, the same set was used every day. After 22 training sessions, the monkey achieved an 80-100% performance rate in this task. The L.E.D was faded gradually from one training session to the next and was finally discontinued. The monkey could still perform the task with the object stimuli only. The stimuli were then changed to a series of pictures. These were projected onto a large screen five metres away from the monkey, subtending a visual angle of seven degrees. The pictorial stimuli were drawn from a set of 10,000 pictures stored on video disk (Optical Disc Corp. Laservision PAL/SECAM, University of London Audio-Visual Centre. River Video Project). They depicted a variety of animate and inanimate objects and scenes (See Fig. 4.1). Randomly chosen pictures from the first 200 pictures on the disc were presented in a previously determined sequence of 150 or 200 trials. Each picture as it appeared was (a) novel non-target (first presentation), (b) repeat target (immediate repetition) or (c) repeat non-target (repetition after intervening stimuli). Stimulus duration was one second and the interstimulus interval was two seconds to allow time to respond on target occasions. A warning tone occurred 0.5 ms before stimulus onset. An infra-red corneal reflection system to record eye movements was introduced at this stage. The apparatus was transparent and was situated in front of the monkeys left eye. Horizontal and vertical eye movements of approximately two degrees sensitivity could be recorded. When the monkey achieved 80-100% level of performance on the object matching-to-sample task (after 11 training sessions) the method of stimulus presentation was changed. The stimuli were presented on a colour T.V monitor (JVC CX-6OGB) positioned one metre away from the monkey at eye level. The display window subtended a visual angle of approximately 5 degrees. The monitor was used in order to minimise large eye-movements through scanning of the picture stimulus. At the end of 20 training sessions, the monkey could perform the task with monitor presentation to a level of 80-100%.

Throughout the entire training schedule, there were frequent "refresher" sessions on previous tasks. These were necessary in order to ensure the monkey got as much reward as possible in the chair when learning a new, potentially more difficult, task.

The training of the male monkey took a longer time than training the female. On average, 10 more training sessions were required at each stage to reach an acceptable level of performance (80-100%).

FIGURE 4.1. Examples of stimulus pictures stored on video disk used as stimuli in experiments one, two and three.



Implantation:

Female monkey (Date of surgery - 7/8/88): A skeleton implant was prepared prior to the operation using dental acrylate, with cylindrical bar holders at the front and back. Seven epidural electrodes were surgically implanted under 4.0ml sodium pentothal (Sagatal) anaesthesia. The electrodes consisted of seven steel screws with wire wrapped around them, which were screwed into holes drilled in the skull. The electrode wires were crimped onto gold-plated pins and attached to an acrylicised eight-way connector on the implant. There were three midline electrodes located at frontal, central and posterior sites and there were two additional pairs of electrodes located laterally at the central and posterior sites. All midline electrodes were placed slightly right of centre to allow for the position of the skeleton implant, and the placement of electrodes was also restricted by the inclusion of two steel wells which were intended for use in single-cell recordings. The female monkey was however only ever used as a subject in E.R.P studies. The reference was a pair of linked electrodes across the inion.

The female monkey was used as a subject for a total of 94 E.R.P recordings from the 23/10/89 to the 20/6/90, and was killed on 17/8/90.

Male monkey (Date of surgery - 1/6/89): Seven epidural electrodes were surgically implanted under 4.7ml sodium pentothal (Sagatal) anaesthesia. There were three midline electrodes located at frontal, central and posterior sites. There were two additional pairs of electrodes located laterally at frontal and central sites. The reference was an electrode at the inion. Again, the placement of electrodes was restricted by the inclusion on the implant of two steel wells for the purpose of single-cell recordings, but the sites chosen were as near as possible to standard placements for E.E.G. electrode recordings.

Prior to using the male monkey as an experimental subject for E.R.P. recordings, he had been used as a subject for single-cell recordings. Between the 27/6/89 and the 1/9/89, a total of seventeen single-cell recording tracks in the right hemisphere were carried out in the region of superior temporal sulcus.

Forty E.E.G experimental sessions were subsequently carried out from the 2/9/89 to the 25/10/89, during which time the monkey was also used for two further single-cell investigations. Five of the total E.R.P. recordings were made during the time when single-cell recordings were in progress (though single cell and E.R.P. recordings were not taken simultaneously).
During the last single cell recording the monkey had a localized Jacksonian epileptic fit. This was attributable to the passage of a guide-tube (1 mm O.D, used to protect the single-cell microelectrode) through a sub-region of motor cortex. The monkey's visual processing was assumed to be unaffected due to the confinement of fit location and its brevity (30s). Experiments employing E.R.P recording were therefore continued.

At the end of experiment two, studies of human E.R.P.s were initiated. During this time the male monkey was again used for single cell studies for the period 13/11/89 to the 3/5/90,). Since the subject had three further Jacksonian fits during this time despite the use of an anti-epileptic drug Mysoline (1ml administered daily i.m), all experimentation was stopped. The monkey was killed on the 21st of September 1990.

At the end of the experiments, the monkeys were given a lethal dose of barbiturate anaesthetic and perfused with phosphate buffered saline and 10% formal saline. The exact positions of the electrodes was determined from stereotaxic measurements taken from the implant after removal from the skull. The measurements were assessed relative to two orthogonal axes corresponding to saggital and interaural planes. The co-ordinates for all the electrodes from which recordings were taken are shown on Table 4.1.

Equipment:

All channels were recorded through a D150/D160 signal amplifier system with a bandwidth of (0.03-30hz) and sampled on-line at a rate of 4ms per point. Sampling began 100ms before visual stimulus onset and continued for 924ms thereafter. The waveforms were displayed on-line on a computer screen (PC386:AT compatible DEL 3165X). Horizontal and vertical movements of the left eye were relayed by the infra-red recorder and were sampled at the same rate and period as the other channels.

Stimuli

The stimuli used for this experiment were drawn from a set of pictures stored on the same video disk that was used for training. The first 200 pictures on the video task had also been used in training the monkeys. Each picture had been previously seen by the monkeys approximately 10 times. These 'familiar' pictures were used as stimuli in the first experiment.

Procedure

Female monkey

Choice of recording sites was restricted due to faulty signals from some electrodes. Therefore, during experimentation, recordings were taken only from the frontal and central midline electrodes and the left posterior electrode. The reference was located at the inion.

Male monkey

Recordings were taken from the frontal, central and posterior midline sites. The reference was located at the inion.

TABLE 4.1. Stereotaxic co-ordinates of electrode sites relative to saggital and interaural planes.

Female monkey:

Fz	8mm lateral	34mm anterior
Cz	6mm lateral	13mm anterior
LP	23mm lateral	17mm posterior
RP	25mm lateral	9mm posterior

Male monkey:

Fz	4mm lateral	29mm anterior
Cz	6mm lateral	3mm posterior
Pz	6mm lateral	15mm posterior

Stimulus presentation: During every experimental recording period, the monkeys were presented with a set of 100, 150 or 200 images, selected at random from the first 200 pictures of the video disk. The number of presentations per experimental period was varied according to the monkey's daily performance. Presentation of large numbers of stimuli was only possible when the monkeys were attentive and performing well. The monkeys responded with a lick whenever an immediately repeating stimulus occurred. Within each series, pictures were also repeated after a lag of 7+-2 items. These conditions of presentation will hereafter be referred to as 'novel non-target' (first presentation of a picture in a single recording session), 'repeat-target' (an immediate repetition of a picture to which the monkey could lick to obtain reward) and 'repeat non-target' (a repetition after a lag of 7+-2 intervening pictures). See Fig. 4.2 for example of stimulus sequence.. Within a series of 200 pictures, there were 60 novel non-targets, 88 repeat targets and 52 repeat non-targets. The stimulus condition order was the same for every recording.

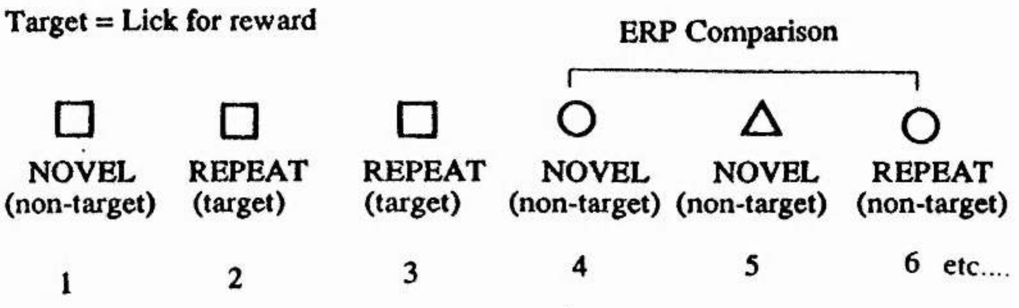
Analysis

The analysis programme called up every trial recorded in a session. Trials with incorrect responses were automatically eliminated from the analysis, as were trials containing eye movements exceeding a pre-determined cut-off point of 2047μv. This automatic elimination was necessary in order to minimise contamination of the waveforms by 'lick' or eye movement artefacts which could distort the responses to a considerable degree. Each trial was also viewed individually in order to reject those containing large eye movements just under the automatic cut-off point.

The waveforms generated for each trial were averaged per day across condition (novel non-target, repeat-target, repeat non-target). The resultant averaged waveforms were then put through a filtering programme to eliminate 50hz electrical interference. All these

FIGURE 4.2. Example of stimulus sequence in matching-to-sample task. Task used in experiments one, two, three, four and five.

EXAMPLE OF STIMULUS PRESENTATION SEQUENCE: Matching-to-sample task.
Stimulus conditions = novel (non-target), repeat (target) and repeat (non-target).



150 or 200 presentations per experimental session. For every 50 presentations, there were 15 novel non-targets, 13 repeat non-targets and 22 repeat targets. Average lag between novel non-targets and repeat non-targets was 7+-2 presentations.

daily averages were then put into weighted grand-averages. The comparison of interest was that between the E.E.G. responses to novel non-targets and repeat non-targets.

The grandaverages obtained from daily recordings were subjected, when necessary, to repeated measures ANOVAs, with factors of picture condition (novel non-target, repeat non-target) and site (female monkey Fz Cz and LP, male monkey Fz Cz and Pz). Greenhouse-Geisser corrections for inhomogeneity of variance (Keselman and Rogan 1980) were applied to restrict degrees of freedom when appropriate. The same degrees of freedom were used for Tukey post-hoc comparisons where necessary.

4.3 RESULTS

Behavioural Data: Average reaction times and % correct per condition for both monkeys are illustrated in Figs 4.3-4.6.

Female monkey: The average reaction time to target stimuli was 527msec (SD=148). Two error rates were calculated (a) licking to novel non-target stimuli and (b) licking to repeat non-target stimuli. The % correct for novel non-target pictures was 86% and to repeat non-targets was 67%. Correct responses to target stimuli was 67%.

Male monkey: The average reaction time to target stimuli was 447 msec (SD=143). The % correct for novel non-target pictures was 88.4% and for repeat non-targets was 76 %. Correct responses to target stimuli was 43%.

E.R.P. Data:

Female monkey: There were 555 novel trials and 401 repeat-non-target trials available for analysis after rejection of incorrect and contaminated trials. The grandaveraged waveforms from fifteen experimental sessions are shown in Fig. 4.7. The pattern of

FIGURE 4.3. Accuracy scores for repeat non-target stimuli. Female (F) and male (M) monkeys. Experiments one and two.

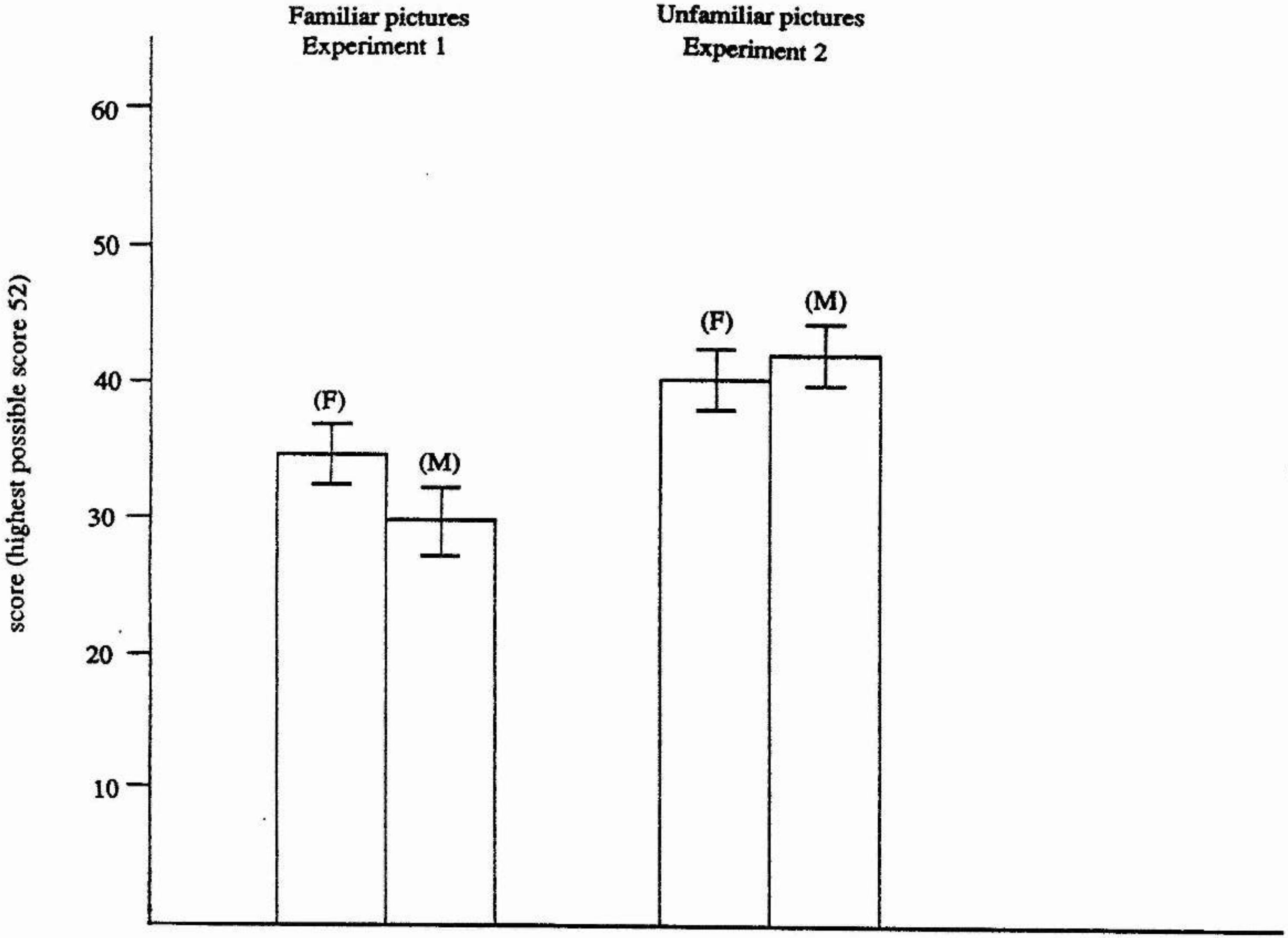


FIGURE 4.4. Accuracy scores for novel non-target stimuli. Female (F) and male (M) monkeys. Experiments one and two.

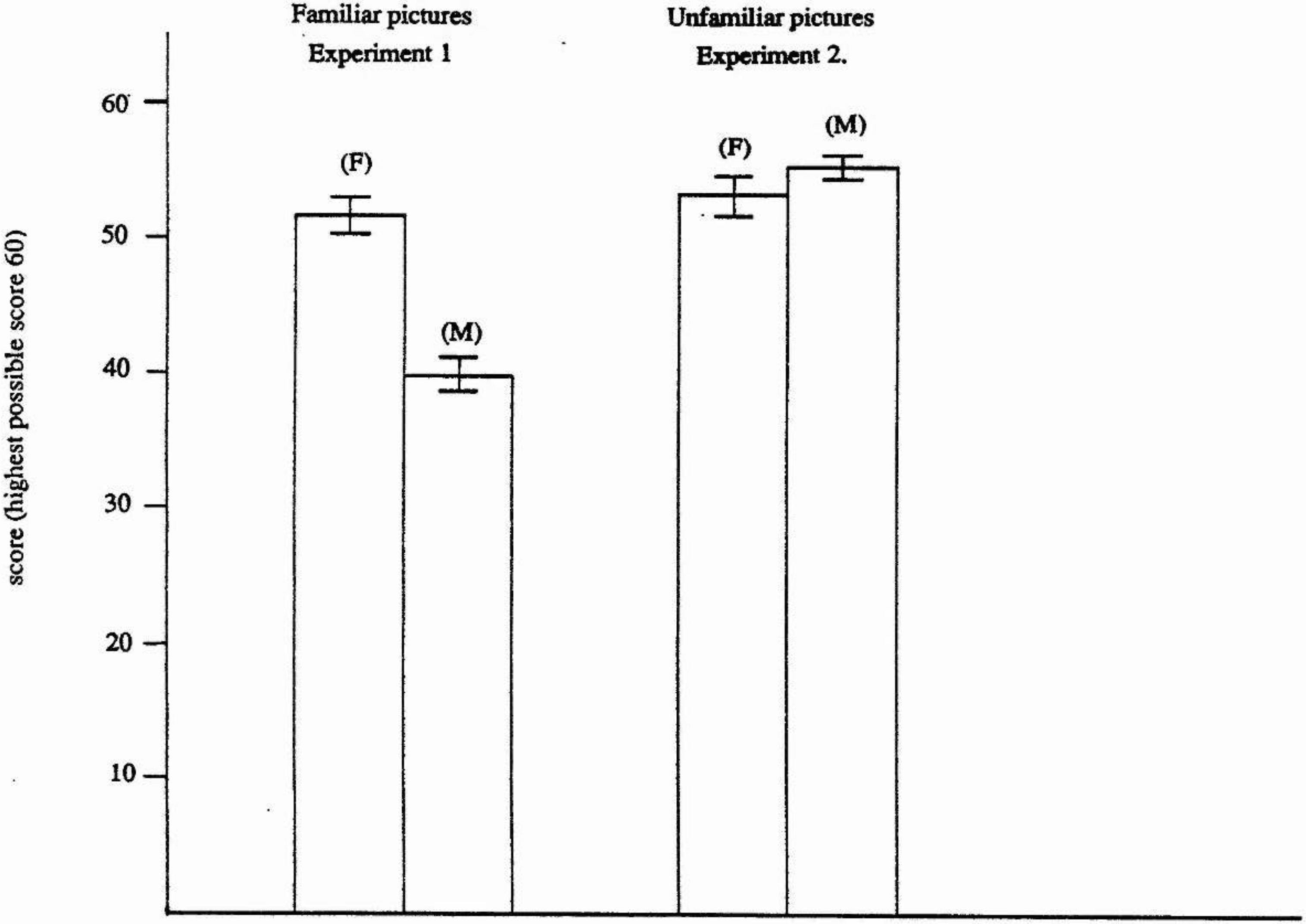


FIGURE 4.5. Accuracy scores for repeat target stimuli. Female (F) and male (M) monkeys. Experiments one and two.

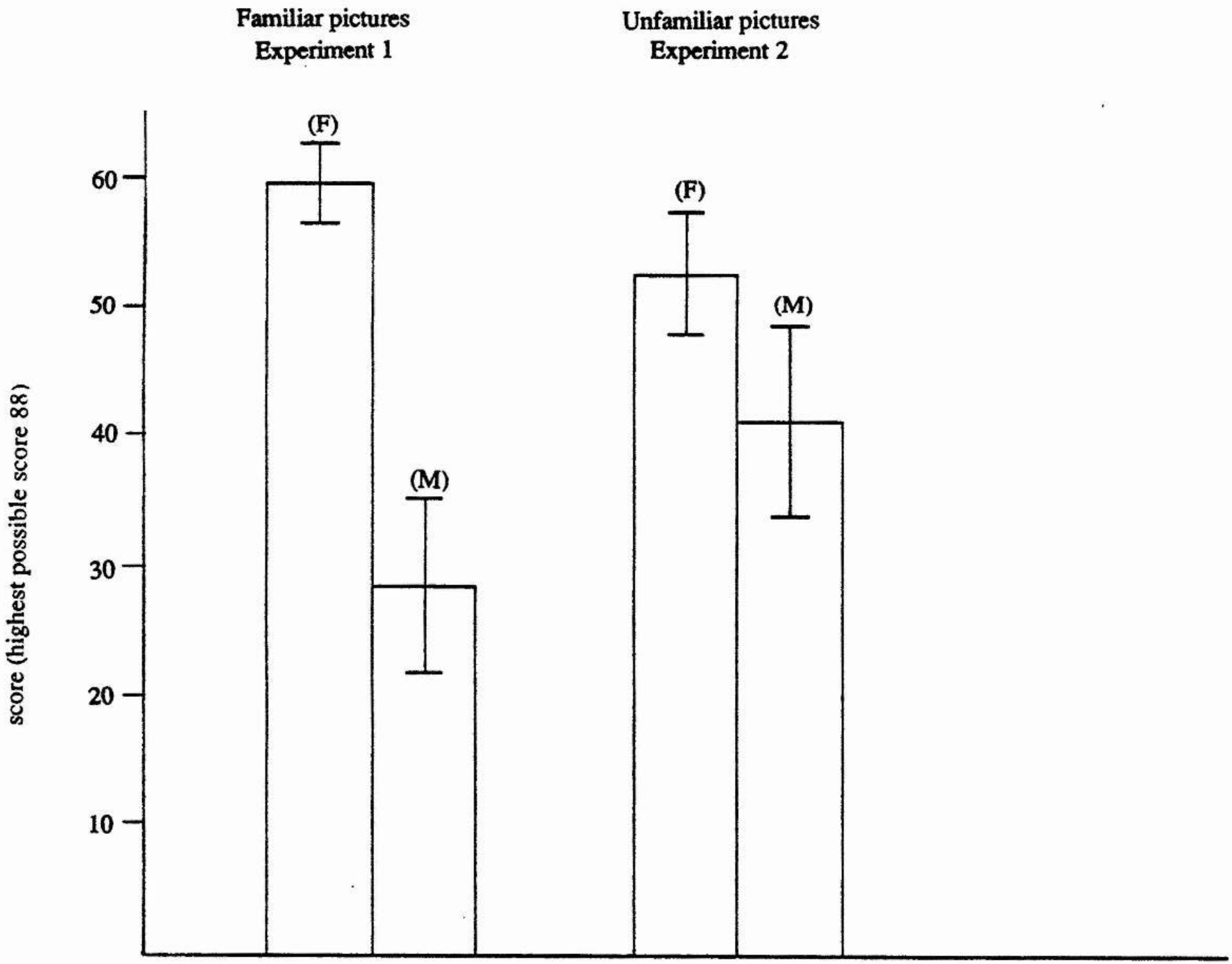


FIGURE 4.6. Average reaction time (RT) in milliseconds for target pictures. Female (F) and male (M) monkeys. Experiments one and two.

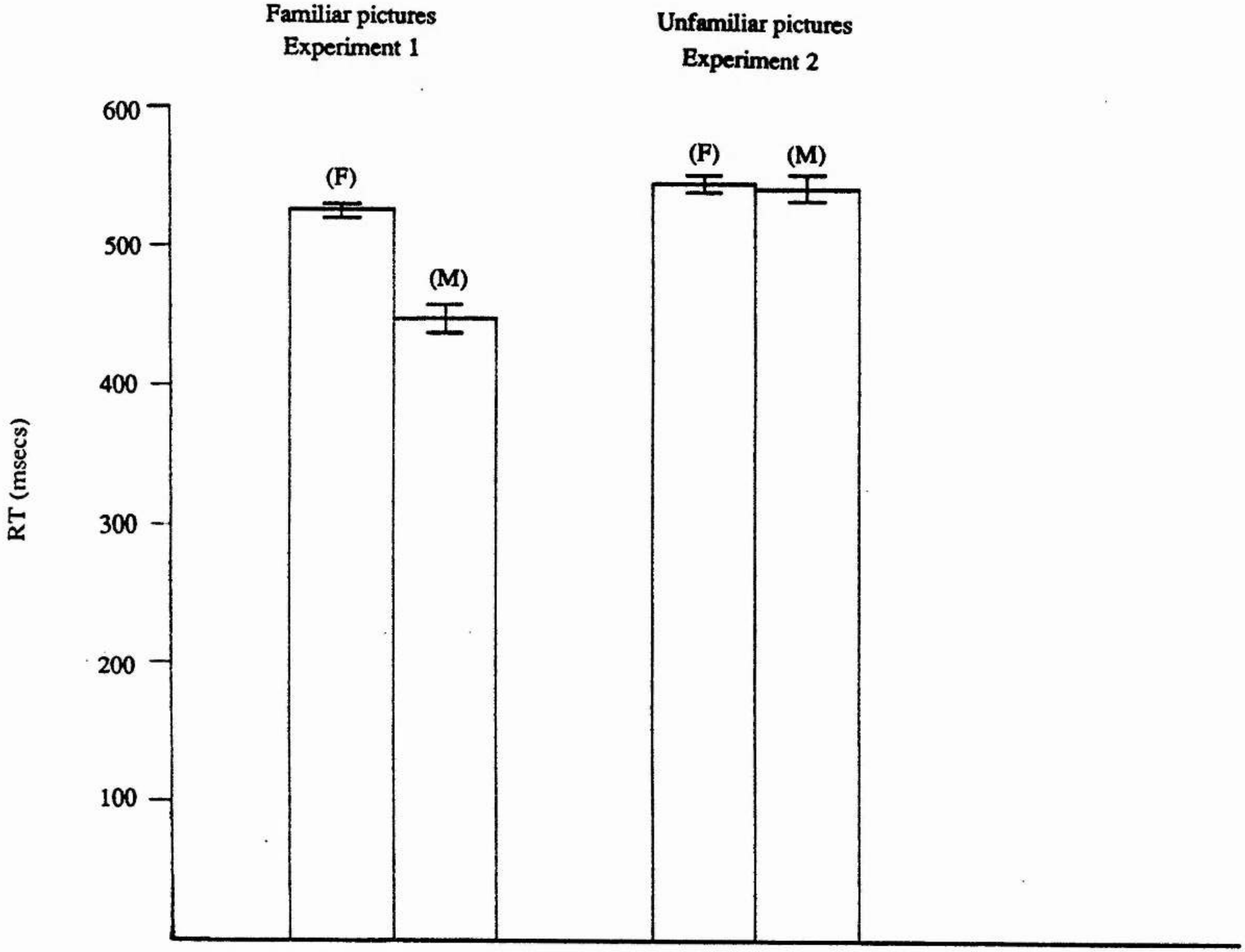
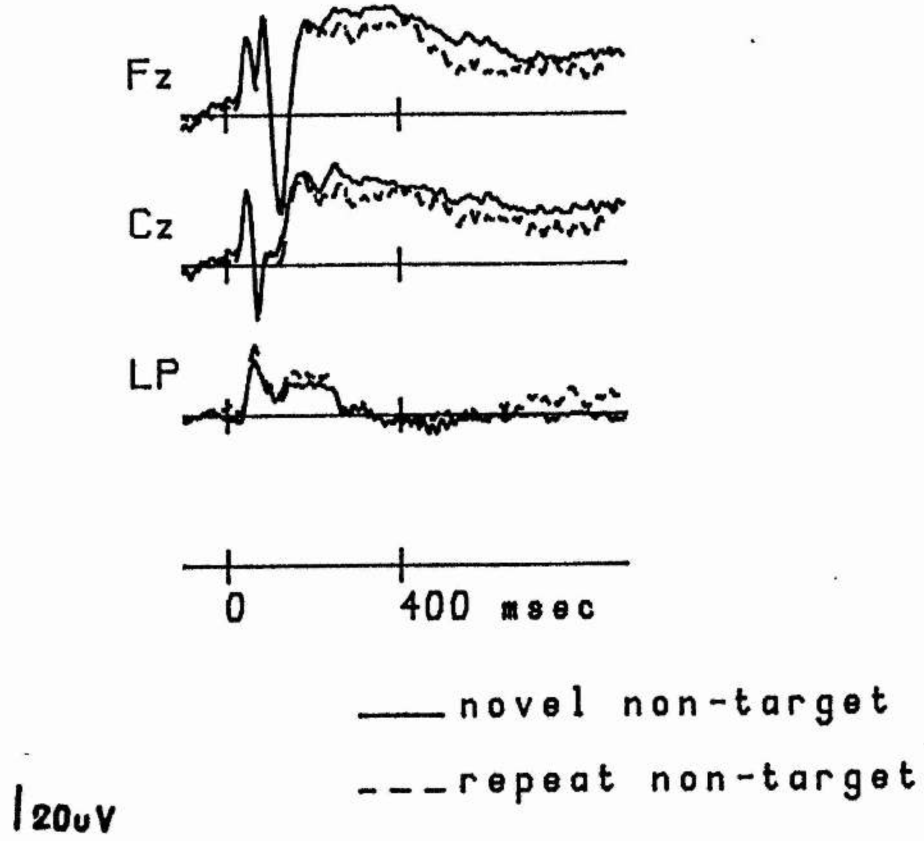


FIGURE 4.7. Experiment one. Grand-average evoked responses to novel non-target and repeat non-target familiar pictures. Female monkey.
No. of trials in both conditions: Novel non-target = 555, Repeat non-target = 401.



response shows little difference between novel and repeat non target waveforms. Both novel and repeat waveforms show a sustained positivity at frontal and central sites from around 200msec, with the repeat non-target waveform being slightly more positive. The waveforms come together until around 500 msec where again the repeat non-target waveform is slightly more positive.

Repeated measures ANOVA using factors of picture condition (novel/repeat-non-target) and site (Fz Cz LP) were carried out on the data within two selected latency regions; 200-400msec and 500-700msec. These latency periods were selected for analysis in order to examine further the apparent small differences between novel and repeat-non-target waveforms. The mean amplitudes within these regions across site and picture condition are shown in Table 4.2.

TABLE 4.2. Experiment one. Mean amplitude (v) at each electrode site for selected latency ranges of E.R.Ps from each picture condition. Female monkey viewing familiar pictures.

Female monkey

RANGE:200-400msec.

Condition	Fz	Cz	LP
Novel non-target	34.7	28.7	2.9
Repeat non-target	29.1	23.7	3.6

RANGE:500-700msec.

Condition	Fz	Cz	LP
Novel non-target	20.5	20.6	-0.88
Repeat non-target	15.5	18.8	-1.03

TABLE 4.3. Experiment one. Mean amplitude (v) at each electrode site for selected latency ranges of E.R.Ps from each picture condition. Male monkey viewing familiar pictures.

Male monkey

RANGE:400-600msec.

Condition	Fz	Cz	Pz
Novel non-target	4.07	0.00	0.00
Repeat non-target	3.14	-0.01	-1.14

RANGE:700-900msec.

Condition	Fz	Cz	Pz
Novel non-target	2.04	0.00	0.00
Repeat non-target	-7.06	-0.01	1.65

200-400msec

There was no effect of picture condition (novel non-target/repeat-non-target) (F=0.448 df=1,14 p=0.513). There was a main effect of site (F=54.2 df=1.6,22.1 p<0.001). This was due to reduced response at the LP electrode site. There was no interaction present between the factors.

500-700msec

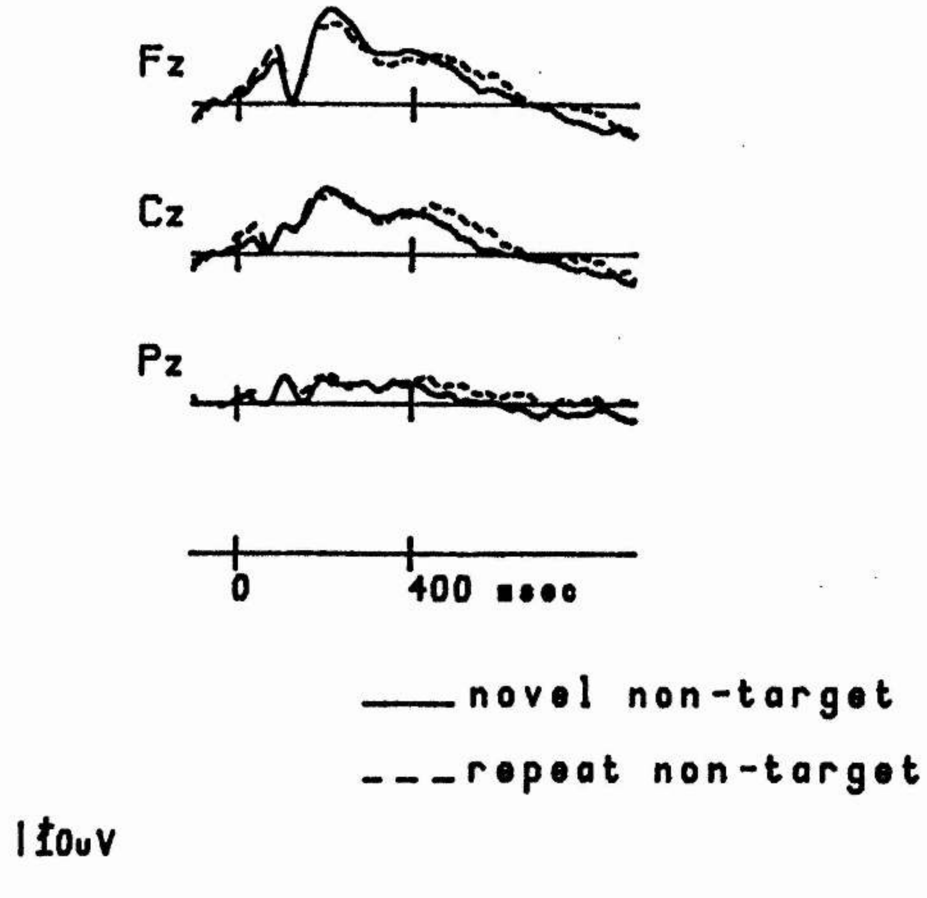
Again, there was no effect of picture condition (F=0.578 df=1,14 p=0.458). There was a main effect of site (F=49.223 df=1.8 24.6 p<0.001) due to reduced response at the LP electrode. There was no interaction between the factors.

Male monkey: There were 226 novel trials and 164 repeat non-target trials available for analysis after the elimination of incorrect and contaminated trials. The grandaveraged waveform from nine experimental sessions are shown in Fig. 4.8. The grand average waveforms follow an identical pattern up to around 500msec post-stimulus, where the repeat non-target waveform is slightly more positive than the novel waveform. Repeated measures ANOVA using factors of picture condition (novel/repeat-non-target) and site (Fz Cz Pz) was performed on the data from the 400-600 msec and 700-900 msec latency ranges of the waveform. The mean amplitudes across condition for these latency ranges are shown in Table 4.3.

400-600 msec

There was no effect of picture condition (novel/repeat non-target) (F=0.194 df=1,8 p=0.67) and no effect of site (F=2.946 df=1.2,9.6 p=0.115). There was no interaction between the factors (F=0.065 df=1.3,10.5 p=0.865).

FIGURE 4.8. Experiment one. Grand-average evoked responses to novel non-target and repeat non-target familiar pictures. Male monkey.
No. of trials in both conditions: Novel non-target = 226, Repeat non-target = 164.



700-900 msec

There was no effect of picture condition (novel/repeat non-target) (F=0.887 df=1,8 p=0.372) and no effect of site (F=3.51 df=1.2 9.8 p=0.284) There was no interaction between the factors (F=1.757 df=1.1,8.9 p=0.221).

4.4 DISCUSSION

There was no difference between the waveforms resulting from viewing novel and repeat non-target familiar pictures. This was true in the case of both monkeys. This lack of effect could be explained by the fact that the pictures used as stimuli were familiar to both monkeys. The pictures had been seen several time by both animals during the training sessions. Behavioural repetition effects have been reported that last as long as a year (Kolers 1976) and effects lasting for days or extending over many intervening stimuli are not uncommon (eg. Feustel et al 1983, Jacoby and Dallas 1981, Scarborough et al 1977). Any long-term repetition effects could thus have obscured the results of experiment 1. In order to resolve this question, a further set of experiments were carried out using unfamiliar pictures as stimuli.

CHAPTER FIVE

EXPERIMENT TWO: E.R.Ps RECORDED FROM MONKEYS USING UNFAMILIAR PICTURES IN A MATCH-TO-SAMPLE TASK

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EXPERIMENT TWO: E.R.Ps RECORDED FROM MONKEYS USING UNFAMILIAR PICTURES IN A MATCH-TO-SAMPLE TASK

5.1 INTRODUCTION

In experiment one there was no difference between the E.R.P. waveforms resulting from viewing novel and repeat non-target pictures. This lack of any E.R.P repetition effects could be explained by the fact that the pictures used as stimuli were highly familiar to the experimental subjects. A further experiment was therefore carried out using identical procedures, except that unfamiliar pictures were used as stimuli.

5.2 METHOD

Stimuli: The stimuli were again selected at random from the video disk. In this case, they were selected from later sections of the disk (picture no.201 onwards), which had never been used in training sessions. A different set of pictures was used for each experimental recording.

Procedure: The procedure was identical to that reported for the previous experiment. The monkeys performed the same task of responding to repeat targets.

5.3 RESULTS

Behavioural Data: The average reaction times in msec and % accuracy for both monkeys are shown in Figs. 4.3-4.6.

Female monkey: The average reaction time was 547 msec (SD=157). The % correct for novel pictures was 88.1%, and for repeat non-target pictures was 77.3%. The % correct for target stimuli was 60%.

Male monkey: The average reaction time was 542 msec (SD=160). The % correct for novel pictures was 91.4% and for repeat non-targets was 81%. The % correct for target stimuli was 46.4%.

The accuracy data was compared with that of experiment 1 across monkeys and each condition (novel non-target, repeat target and repeat non-target).

Novel non-targets:

There was a significant difference between accuracy rates to novel non-target familiar and novel non-target unfamiliar pictures (F=26.948, df=1, p<0.001). Responses were more accurate when unfamiliar pictures were presented. There was also a significant difference between the two monkey's performance (F=12.896, df=1, p<0.01), with the female monkey scoring higher. There was also an interaction between the two factors (F=30.899, df=1, p<0.001). Post-hoc testing (Newman-Keuls) revealed that the female monkey scored higher on familiar pictures than the male monkey (Q=9.247, p<0.01), but there was no difference across monkeys with unfamiliar pictures. The male monkey scored significantly higher with unfamiliar pictures than with familiar pictures (Q=10.692, p<0.01). There was no difference for familiar and unfamiliar pictures in the case of the female monkey.

Repeat non-targets

There was a significant difference between accuracy scores with familiar and unfamiliar pictures (F=12.086, df=1, p<0.01), with higher scores for unfamiliar pictures. There was no difference in accuracy scores across monkeys, but the male monkey scored better on unfamiliar repeat non-targets than on familiar repeat non-targets (Q=4.818, p<0.01).

Repeat Targets

There was no difference in accuracy across familiar and unfamiliar repeat targets. There was a significant difference between monkeys (F=3.476, df=1, p<0.001), with the female monkey scoring higher than the male monkey. The difference between monkeys with familiar pictures was also significantly greater than accuracy for unfamiliar pictures, with the female monkey scoring higher than the male monkey (Q=6.114, p<0.01).

E.R.P. Data. Effects of repetition.

Female monkey: There were 356 novel trials and 274 repeat non-target trials available for analysis after elimination of incorrect and contaminated trials. The grandaveraged waveform from 10 experimental sessions are shown in Fig. 5.1. No difference emerged between the grand averaged novel and repeat non-target waveforms.

Male monkey: The grandaveraged waveforms from nine experimental sessions are shown in Fig. 5.2 . 405 novel trials and 316 repeat non-target trials went into the grand average. The waveforms to novel and repeated stimuli diverge at around 200 msec at frontal and central sites. This divergence continues throughout the remainder of the sampling period and is most apparent at the frontal and central sites. Repeated measures ANOVAs were carried out on the data within selected latency regions of 200-400msec and 400-700msec with factors of picture condition (novel, repeat non-target) and site (Fz,Cz,and Pz). The mean amplitudes across condition for these latency regions are shown in Table 4.4.

FIGURE 5.1. Experiment two. Grand-average evoked responses to novel non-target and repeat non-target unfamiliar pictures. Female monkey.
No. of trials in both conditions: Novel non-target = 356, Repeat non-target = 274.

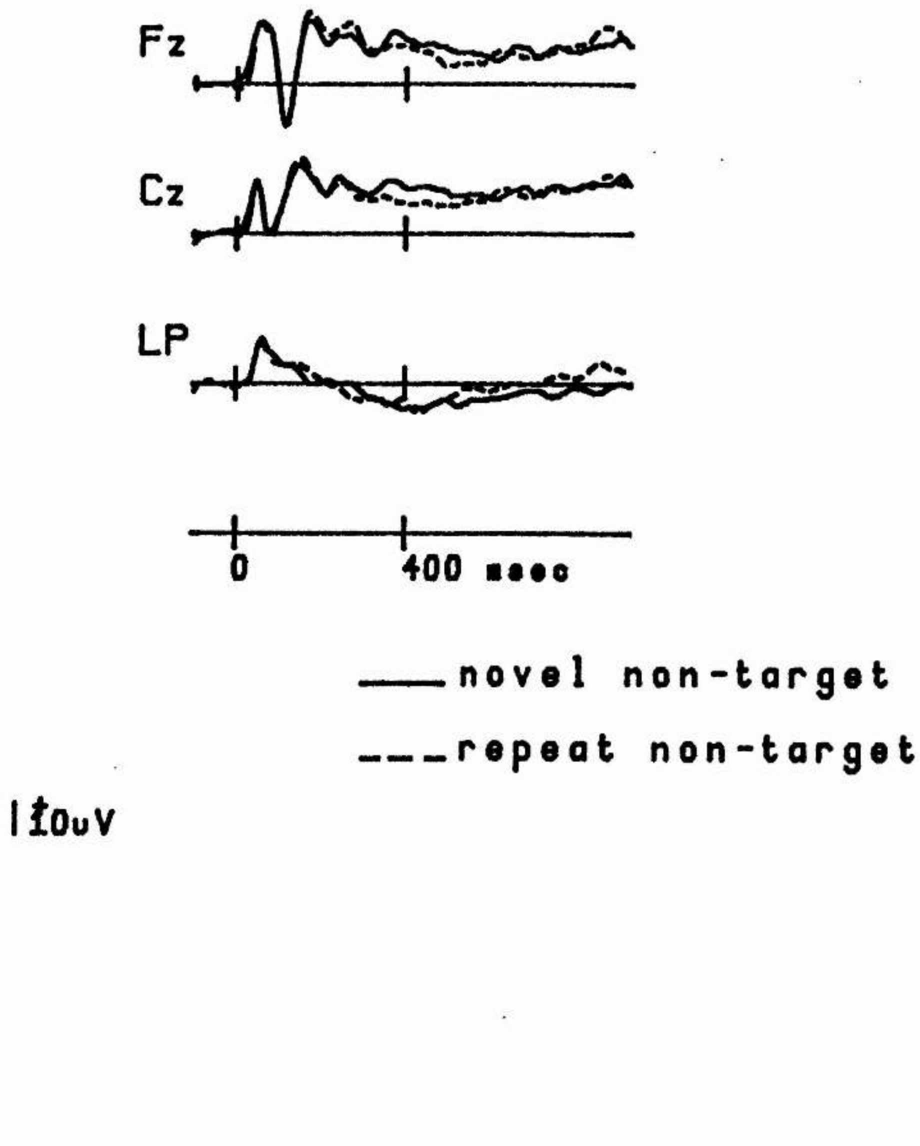


FIGURE 5.2. Experiment two. Grand-average evoked responses to novel non-target and repeat non-target unfamiliar pictures. Male monkey.
No. of trials in both conditions: Novel non-target = 405, Repeat non-target = 316.

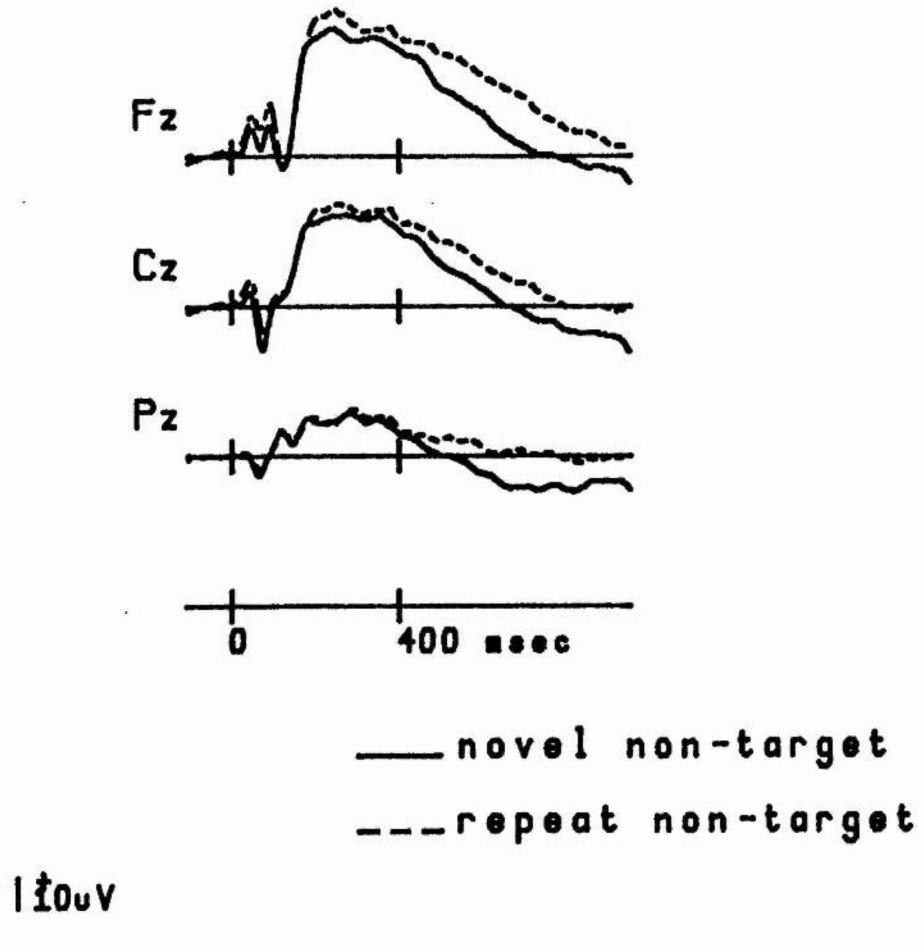


TABLE 4.4. Experiment two. Mean amplitude (v) at each electrode site for selected latency range of E.R.Ps from each picture condition. Male monkey viewing unfamiliar pictures.

Male monkey

RANGE:400-700 msec.

Condition	Fz	Cz	Pz
Novel non-target	24.8	16.3	1.47
Repeat non-target	36.3	24.4	7.15

400-700 msec

There was a significant effect of picture condition (F=7.783, df=1,8 $p<0.05$) and a significant effect of site (F=45.5 df=1.5,11.7 $p<0.001$). Repeated pictures evoked a significantly more positive waveform than novel pictures. The effect of site was due to greater positivity at frontal and central sites than at the posterior site.

200-400 msec

There was no main effect of picture condition. There was however a significant interaction between picture condition and site (F=7.991 df=1.4,10.9 $p<0.05$). Post-hoc comparisons revealed that there was a significant difference between novel and repeated pictures at the frontal site.

In summary of the data investigating repetition effects with unfamiliar pictures, there were no measurable effects in the case of the female monkey. Data from the male monkey indicated significant effects of repetition. These were restricted to the frontal recording site from 200-400msec and were widespread from 400-700msec.

5.4 DISCUSSION

The use of unfamiliar pictures as stimuli in the repeating picture paradigm had a considerable effect for one of the monkey subjects (the male). The effects of repetition on the waveforms are similar to those seen in human studies using lexical stimuli, in that the repeated stimuli evoked a more positive waveform than the novel stimuli, the greatest difference occurring at around 400 msec.

In the case of the female monkey, there were no effects of repetition on the E.E.G. The inconsistency of results across monkeys is interesting. The result could possibly be linked to the difference in accuracy and reaction time across monkeys. The female monkey scored consistently better from the start of training, one might therefore have expected a repetition effect to have been more prominent in this subject. This was not the case.

The difference in performance and E.R.Ps might have reflected differences in 'strategies' used by the subjects to solve the task. One reflection of this possibility is the observation that the female subject consistently performed more accurately than the male on novel non-targets and repeat targets than the male monkey. This could indicate a difference in attention levels between the two monkeys to the novel non-target stimuli. This may have affected the resultant waveforms.

Also, the male monkey scored slightly higher on repeat non-targets (although this was not significant) than the female monkey in the case of unfamiliar pictures. It is notable that this is the condition in which the repetition effect emerged.

Alternatively, the inconsistency in the E.R.P. repetition effect across subjects could have been due to the fact that remembering the later repeat non-target stimuli may have been too difficult for the monkey subjects. Both monkeys were generally less accurate with these stimuli than with novel non-targets or repeat targets. It should be noted, however, that the presence of an episodic image is not the sole factor contributing to repetition effects (see experiments three and nine). That is, even when subjects can explicitly remember stimuli it is still possible to fail to obtain behavioural or E.R.P. repetition effects.

The question of how much the 'memorability' or meaningfulness of stimuli contributes to repetition effects is important and needs to be addressed in order to come to any conclusions about the monkey experiments. Although there have been some studies in humans using meaningful and non-meaningful words as stimuli, there have been none which directly investigate how manipulation of the semantic content of pictures affects evoked potentials. The next chapter describes an experiment conducted to explore this issue

CHAPTER SIX

EXPERIMENT THREE: E.R.Ps RECORDED FROM HUMANS USING MEANINGFUL AND NON-MEANINGFUL PICTURES

CHAPTER SIX

EXPERIMENT THREE: E.R.Ps RECORDED FROM HUMANS USING MEANINGFUL AND NON-MEANINGFUL PICTURES

6.1 INTRODUCTION

The aims of this study were firstly to determine whether the E.R.P repetition effect seen previously with lexical and facial stimuli would be apparent in human recordings with the use of complex meaningful pictorial stimuli. Secondly, to investigate the extent to which this repetition effect would be affected by the use of "meaningless" pictorial stimuli.

The study reported here investigates evoked potential repetition effects using non-verbal picture material as stimuli. Two kinds of pictorial material were selected to provide a parallel with the orthographically legal/illegal letter string distinction in lexical E.R.P. experiments. In order to obtain a comparable dimension of meaningfulness / meaninglessness, one set of stimuli depicted a variety of everyday objects and scenes ('meaningful stimuli'). The other stimulus set was obtained by a process of 'pixellation' ('meaningless stimuli'). This technique rendered pictures into relatively meaningless arrays of coloured blocks, whilst maintaining the original luminance, colour, contrast and low frequency distribution of light. High frequency edges were introduced which inhibit the perceptual interpretation of the image (See Harmon 1973). These pixellated pictures share some of the characteristics of orthographically illegal non-words, in that they retain many of the features of normal pictorial stimuli (colour, intensity variation, pattern etc.) but have no relation to pre-existing representations in memory ie. are essentially "meaningless" and assessed on physical features only.

It was predicted that if the E.R.P repetition effect previously described is a function of general memory, repetition of pictorial material will modulate the waveforms in a similar way. That is, the waveform generated by repeated pictures will be more positive around 400msec than the non-repeated pictures. It is further predicted that the use of pixellated (meaningless) images will attenuate or even obliterate this repetition effect. This line of reasoning follows on from the results obtained by Rugg and Nagy (1987) where repetition effects were attenuated when orthographically illegal letter strings were employed as stimuli. Any similarities in the resultant waveform perturbations to those seen in studies using verbal stimuli will help to clarify and extend understanding of the encoding and retrieval processes involved in visual memory.

6.2 METHOD

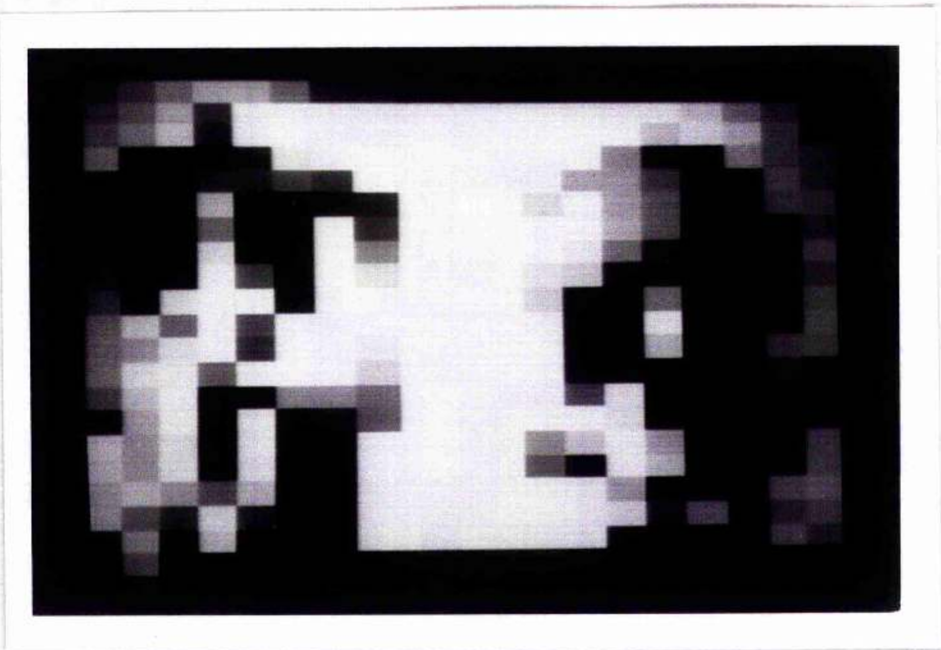
Subjects

Six male and six female adults (age range 19-30) were subjects. All had normal or corrected to normal vision.

Stimulus Material

Each stimulus set consisted of static pictures, stored on a video disk, depicting various people, objects and scenes. Two presentation conditions were used. In the first condition (normal pictures), 200 unmodified images were used for stimuli. The second condition (pixellated pictures) involved the presentation of a further 200 images which were degraded into abstract blocks of colour by means of the pixellating function of a video mixer (CVI, Fairlight). This procedure rendered each image unrecognisable compared to the respective normal pictures, but retained the mean luminance and colour of the original (See Fig. 6.0 for example).

Examples of normal and pixellated pictures stored on video disk used as stimuli in Experiment three



Stimulus Presentation

Images, which were displayed on a TV monitor, subtended a visual angle of 7.5^{0} at a distance of 1m. A 0.5s warning tone sounded before each stimulus presentation so that subjects could orientate towards the screen and minimise movement. Each image was presented for 1s and presentations were separated by a 1s interval (screen blank).

Procedure

There were 200 pictures in an experimental series. Of the 200 pictures, 60 were classed as 'novel'(first presentation in the series); 88 were 'targets` (immediate repeats of the preceding picture) and 52 were 'repeat non-targets'(repeated within the series after a lag of 7+-2 items).

Subjects were instructed to fixate on the monitor and refrain from moving their eyes or body during stimulus presentations. They were further instructed to respond by pressing a button held in their preferred hand, whenever they saw an immediately repeating stimulus. No response was required to non-immediate repeats. Comparison of E.R.Ps resulting from repeated (non-target) and novel stimuli could thus be compared in the absence of overt responses to these critical items.

Recording E.R.Ps

E.E.G. was recorded from electrodes (Ag/AgCl) placed at sites Fz, Cz, and Pz according to the 10-20 convention (Jasper 1958) and at left (LT) and right (RT) temporal sites, 75% of the distance from Cz to T_3 and T_4 respectively. The right mastoid was employed as reference and the midpoint between Fz and Cz was grounded. Electrode impedances with respect to ground were always less than 5kOhms. All channels were amplified with a bandwidth of 0.03-30 Hz (3dB points). Signals were digitized at the rate of 1 point per 4ms commencing 100ms before stimulus presentation and continuing for a further 924ms.

Electrodes placed on the outer canthus of the left eye and above the right eyebrow recorded EOG. Only trials associated with correct responses and on which no eye movement artefact occurred, were included in the analysis.

Analysis of E.R.Ps

The waveforms were analysed by measuring mean amplitude (with respect to the mean of the 100ms prestimulus baseline) within selected latency regions. The data were analysed using repeated-measures ANOVA, incorporating the Greenhouse-Geisser correction for inhomogeneity of covariance (Keselman & Rogan 1980). For each selected latency region, a three-way ANOVA was performed with factors of picture type (pixellated/normal), condition (novel/repeat) and electrode site (Fz Cz Pz LT and RT). Post-hoc analyses were carried out where necessary (Tukey). A significance level of $p<0.05$ was adopted for all post-hoc tests. E.R.Ps elicited by targets were subjected to a separate set of analyses.

6.3 RESULTS

Behavioural Data

Analysis of subjects` reaction times to the target stimuli revealed no effect of stimulus type, i.e subjects responded with equal speed in the normal and pixellated picture tasks. Formal analysis of hit rates was not conducted because of ceiling effects in both pixellated and normal picture tasks. False alarm rates did not exceed 2% with either stimulus type.

Waveform analysis (Novel v Repeat non-target)

Approximately 34% of trials were discarded due to contamination of eye movement artefact and small number of incorrect responses. Grand-average waveforms of the E.R.Ps elicited by the novel and repeated (non-target) stimuli in the normal and pixellated picture tasks are shown in Figs 6.1 and 6.2. The effects of repetition appear thus; (1) A modulation of the waveform around P200 such that E.R.Ps elicited by repeated items are more positive than those elicited by novel items. This modulation appears to a much greater extent with normal picture stimuli. (2) A sustained positivity to

FIGURE 6.1. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat non-target normal pictures.
No. of trials per condition: Novel non-target = 417, Repeat non-target = 382.

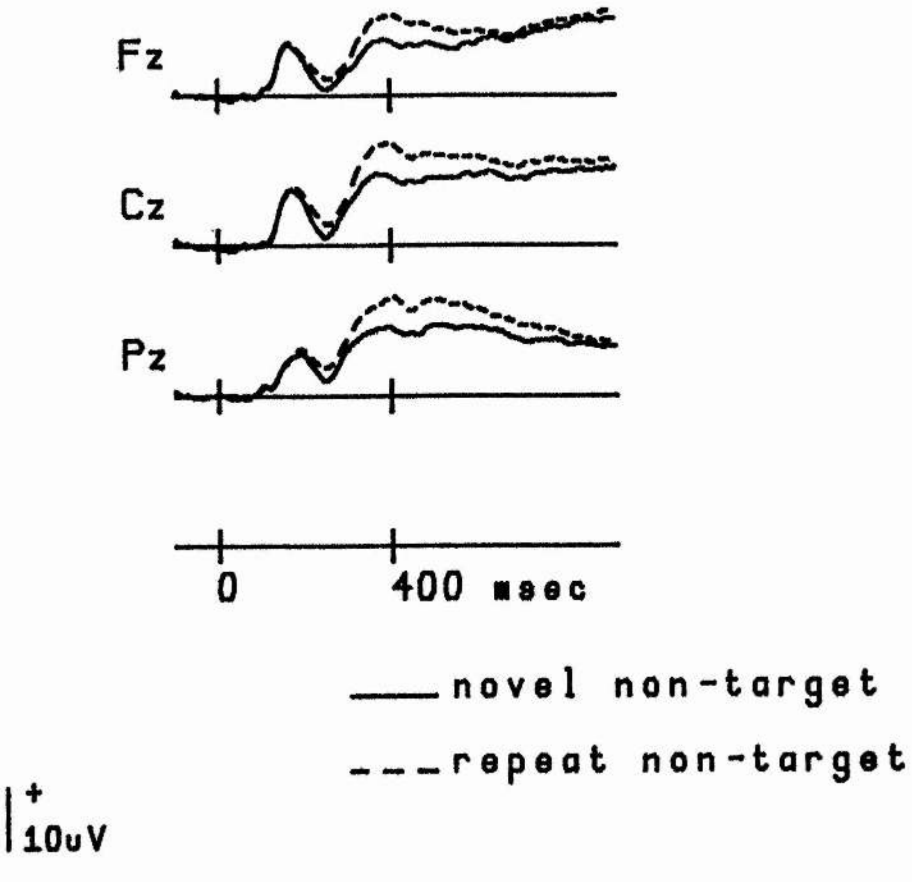
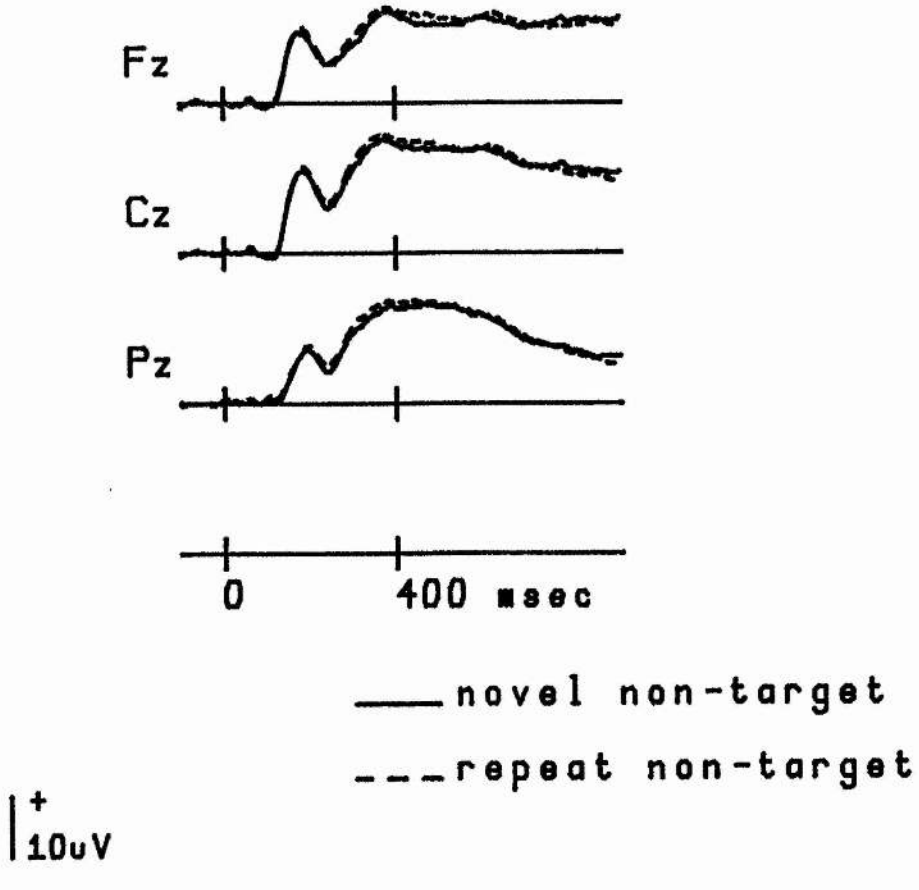


FIGURE 6.2. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat non-target pixellated pictures.
No. of trials per condition: Novel non-target = 421, Repeat non-target = 370.



repeated items from around 300ms evident in the waveforms elicited by normal pictures. This effect is most prominent at central and posterior recording sites.

In order to clarify the effects of picture type and repetition, three-way ANOVAs were conducted on selected regions of the waveforms. These were the area around the P200-N300 deflection (200-300ms) and the region around the later slow wave (300-600ms), where effects of repetition were most apparent.

200-300ms

Analysis of this region gave rise to a significant overall effect of picture type ($F=9.7$ $df=1,11$ $p<0.05$) and a significant main effect of repetition ($F=5.6$ $df=1,11$ $p<0.05$). Planned comparisons (Tukey) revealed that there was a significant effect of repetition for both normal and pixellated stimuli, with an increased positivity for the repeat waveforms.

There was also a significant interaction between picture type and site ($F=26.3$ $df=3.3,36$ $p<0.001$). This interaction reflects the greater positivity for pixellated picture waveforms, maximal at Fz Cz and Pz and almost absent at Oz and lateral sites.

300-600ms

In this case, the effect of repetition was again significant ($F=11$, df 1,11 $p<0.01$) but there was no overall effect of picture type. There was also a significant interaction between picture type and repetition ($F=11.2$ df 1,11 $p<0.01$). Post-hoc analysis revealed that there was a significant difference between the waveforms generated by novel and repeated normal pictures. There was no such difference in the pixellated picture condition. Post-hoc testing also revealed that the waveform generated by novel normal pictures was significantly more negative than that generated by novel pixellated pictures. There was no significant difference between the repeated normal and pixellated picture waveforms.

This indicates that the effect of repetition with normal pictures is due to a sustained negativity in the waveform to novel presentations.

There was a significant effect of site (F=9.7 df=1.6,17.7 p<0.01) and interactions between picture type and site (F=13 df= 1.7,18.2 p<0.01) and between picture type, repetition and site (F=3.7 df=2.4,26 p<0.05).

The main effect of site was due to effects being maximal at Cz and Pz. There was no overall effect of picture-type, but post hoc tests on the picture type/site interaction revealed that pixellated picture waveforms were more positive at frontal central and posterior sites. The three-way interaction between repetition, picture type and site reflected greater differences between novel normal and pixellated waveforms at Fz Cz and Pz than at Oz and lateral sites.

In summary, comparison of the waveforms generated by novel and repeat presentations demonstrated significant differences in both selected latency regions. The difference was apparent for both normal and pixellated pictures in the 200-300ms latency range, but was confined to normal pictures from 300-600ms. The differences are due to a greater negativity for novel waveforms as opposed to repeat waveforms.

Novel v Repeat-target presentations

Figs. 6.3 and 6.4 display the comparison of novel non-target waveforms and repeat target waveforms in the normal and pixellated picture conditions. The waveforms consist of initial P200, N300 and P400 components followed by a target-related negativity around 500ms and a sustained positive wave for the remainder of the sampling period. The effects of repetition appear thus; (1) A modulation of the waveform around P200 such that E.R.Ps elicited by target items are more positive than those elicited by novel items.

FIGURE 6.3. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat target normal pictures.
No. of trials per condition: Novel non-target = 417, Repeat target = 649.

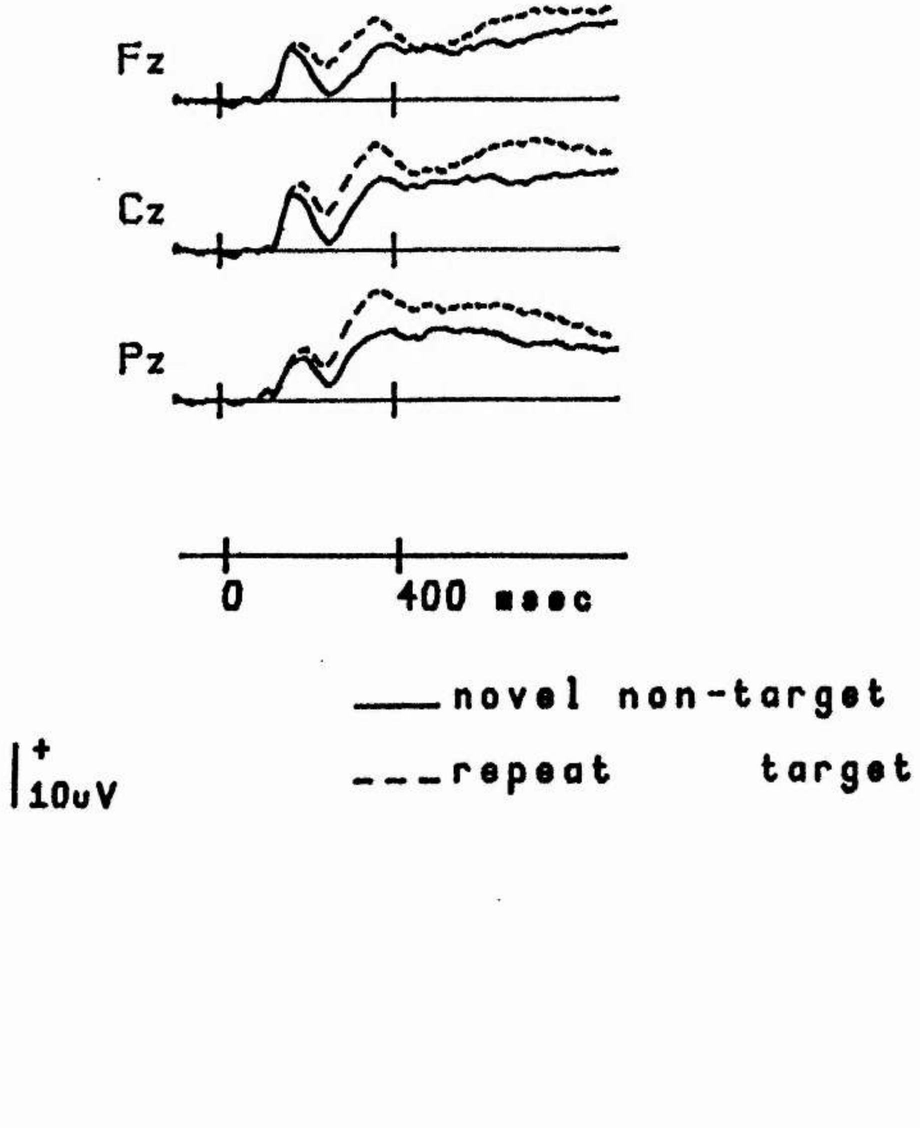
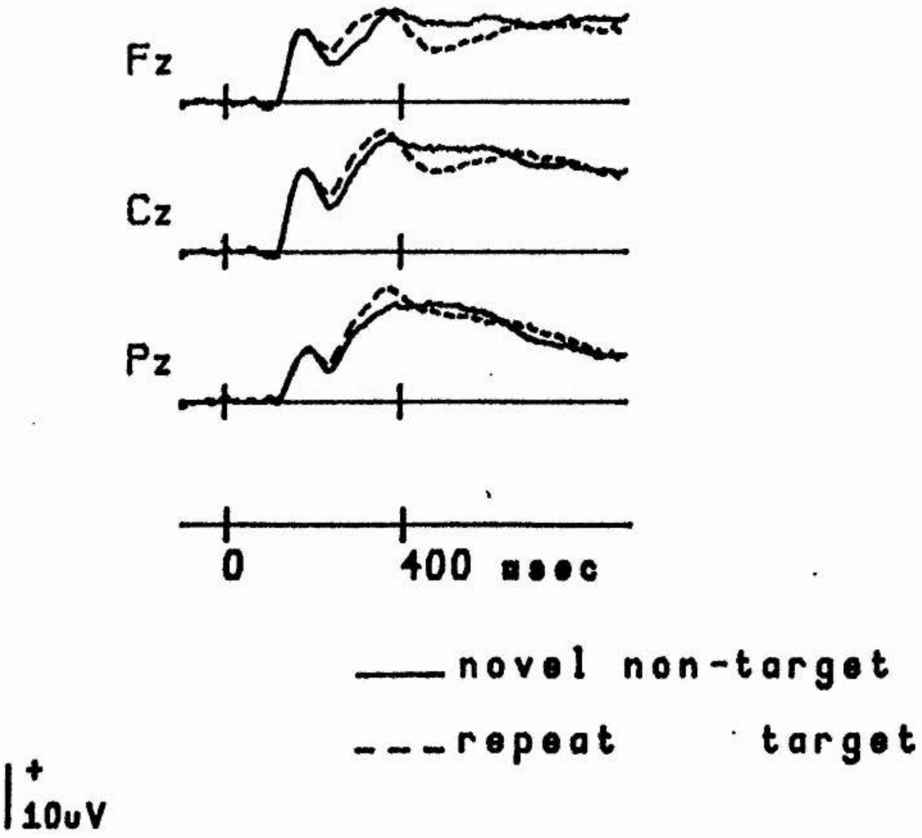


FIGURE 6.4. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat target pixellated **pictures.**
No. of trials per condition: Novel non-target = 417, Repeat target = 617.



This modulation appears to a greater extent with normal picture stimuli. (2) A sustained positivity to repeated items from around 400ms in the waveforms elicited by normal pictures. This effect is most prominent at central and posterior recording sites. (3) A reversal of novel and target waveforms in the pixellated picture condition from around 400-600ms, with a greater positivity for the novel waveform. This is most apparent at frontal and central sites.

In order to clarify the main repeat-target effects, three-way anovas were conducted on those regions of the waveform where effects were most evident; 200-400ms, 400-600ms and 600-800ms.

200-400ms

Analysis of this region revealed a significant main effect of picture-type (F=7.8 df=1,11 p<0.05) and of target (F=23.6 df=1,11 p<0.01). Planned comparisons demonstrated that these effects reflected the greater positivity of target waveforms as compared to novel waveforms in both the normal and pixellated picture conditions.

There was also a main effect of site in this region (F=8.6 df=1.8,20 p<0.001) and interactions between picture-type and site (F=23.4 df=2.1,23 p<0.001) and target and site (F=8.6 df=2.8,30 p<0.001). The main effect of site again reflected maximal amplitude at frontal, central and posterior sites. The picture type x site and target x site interactions reflected a greater overall positivity for the pixellated picture waveforms at Fz Cz and Pz, which was absent at Oz and lateral sites.

For novel picture waveforms, there were no site differences. The target picture waveforms were more positive at Fz Cz and Pz than at Oz and lateral sites.

There was also a three-way interaction between picture type, immediate repetition and site (F=3.77, df=2.5,27 p<0.05). This was due to the greater negativity of normal picture novel waveforms than pixellated novel waveforms, maximal at frontal and central sites.

400-600ms

Within this latency region, there were no overall picture type, or target effects. There was however, an interaction between picture type and target (F=15 df=1,11 p,0.01). Post-hoc analysis revealed that the interaction between picture type and target was due to a significant difference between novel and target waveforms in the normal picture condition. The reversed difference between novel and target waveforms within this latency period in the pixellated picture condition was not significant. Also,the novel waveform in the pixellated picture condition was more positive than in the normal picture condition.

There was also a significant interaction between picture type and site (F=9.6 df=1.9,20.7 p<0.01). This was due to the amplitudes of normal picture waveforms being maximal at Pz, while pixellated picture waveform amplitudes were maximal at frontal, central and posterior sites.

600-800ms

There was no main effect of picture type in this latency period. There was a main effect of target (F=9.9 df=1,11 p<0.01) and a significant interaction between picture type and target (F=13.4 df=1,11 p<0.01). Post-hoc tests revealed that this interaction was due to a significant difference between the waveforms generated by novel and immediate repeat instances in the normal picture condition only.

There was also a significant main effect of site (F=29.7 df=1.5,16.8 p<0.001) reflecting greater amplitudes at Fz Cz and Pz than at Oz and lateral sites. There were also significant interactions between site and picture type (F=3.9 df=2.3,25.4 p<0.05) and site and target (F=3.8 df=2.4,26.4 p<0.05). These interactions were due to the effects of picture type and target being maximal at Fz Cz and Pz and almost absent at Oz and lateral sites.

In summary of the novel v target data, from around 200ms, the novel presentation waveforms are more negative-going than the target waveforms. This is evident in both the normal and pixellated picture conditions. For the normal pictures, there is a larger, more sustained difference between novel and target waveforms, lasting to the end of the sampling period. The effects are maximal at central and posterior sites.

6.4 DISCUSSION

While the repetition of both normal and pixellated pictures modulated E.R.Ps in this experiment, the use of normal pictures had a considerably greater effect in terms of magnitude and duration. The data clearly show that the repetition of normal pictures results in a different pattern of E.R.P. modulation than that observed with the repetition of pixellated pictures. This is most notable in the later regions of the waveforms from around 400ms post-stimulus. Here, there was a large and sustained positivity in the case of the repeated normal pictures, which was absent in the case of pixellated pictures. The repetition of pixellated pictures gave rise to a smaller, earlier-occurring effect. These are important results for two reasons. Firstly, it confirms that repetition effects can be obtained using complex pictorial stimuli. Secondly, the repetition effects obtained were similar to those seen in studies employing meaningful and non-meaningful words as stimuli.

Small, early differences were found between the novel and repeat condition waveforms in the pixellated picture memory task. This result is comparable to studies using orthographically illegal non-words as stimuli (Rugg and Nagy 1987). It was suggested that this early component is related to pre-lexical processes, such as the identification of letters. The late component which was confined to orthographically legal non-words, was proposed to be related to accessing lexical memory. It is possible that the early effect obtained in this study is similarly attributable to early cognitive processes, leading to the detection of a repetition *per se* and is thus common to both normal and pixellated pictures. The later component, which is confined to normal pictures, may be related to accessing a unitized code for the normal pictures which is not available for the pixellated pictures. Such an interpretation would not require that a separate semantic memory system be invoked to explain differences in repetition effects between meaningful and non-meaningful stimuli. The quantitative difference in repetition effects may reflect some automatic extra processing of the meaningful stimuli, but qualitatively, the repetition effects observed with both types of stimuli may reflect those aspects of the E.R.P. which are sensitive to repetition.

It is important to note that the late differences between the normal and pixellated picture waveforms is due to the greater negativity of the novel normal picture waveform as compared to the novel pixellated picture waveform. Comparison of repeat non-target waveforms across pixellated and normal pictures reveals no differences in the later part of the waveforms. This indicates that the repetition effect results from some modulation of the waveform evoked by the first presentation of a stimulus, possibly the N400 component previously discussed. As noted in chapter two of this thesis, this negativity may be interpreted as reflecting the integration of an unfamiliar stimulus with its context. On repetition, less integration is required and this is reflected by the attenuated negativity of the waveform. The fact that this negativity is greater in the case of the normal picture waveform may reflect the availability of more semantic codes for the items portrayed.

Rugg et al (1988) found that differences in the E.R.P. to novel and repeat words were present, but considerably smaller for a task in which targets were detected on the basis of global physical features (upper or lower case). There were, however, significant novel/repeat differences in lexical decision tasks. These results indicate the importance of attention being drawn to the identity of the word stimuli for sustained E.R.P. repetition effects to emerge. The pixellated picture task reported here could be considered to involve a shallow processing of the superficial characteristics of the stimuli. As previously mentioned, they are therefore comparable to orthographically illegal nonwords. The analysis of pixellated pictures is also comparable to that involved in an upper/lower case identification task. No stimulus identification occurs beyond the analysis of physical features. It should be pointed out that there are some differences between the upper/lower case task and the task employed in the study reported here. While it was not necessary for subjects to attend to the semantics of words in the case task, the stimuli used were in fact meaningful. In the study reported here, the pixellated pictures had no obvious semantic connotations. This could explain a small late repetition effect obtained in the aforementioned case task (Rugg et al ibid). No such effect was evident with the use of pixellated pictures.

Another important difference between studies involving the analysis of superficial characteristics of words and the present experiment is the suggestion that it is not possible to form a lasting episodic representation for the pixellated pictures. The late repetition effect obtained only with the meaningful pictures could be explained by subjects being unable to form an episodic memory for the pixellated stimuli, lasting over a lag of seven intervening items. Examination of the behavioural data shows that subjects are able to remember the pixellated pictures over a short time when there are no intervening items. This is important, in that the overall pattern of the resultant waveforms corresponds to those seen in the analysis of the novel/repeat non-target data. Thus, the effects of stimulus repetition either at short or long lags (0-7 intervening items) are different for normal and pixellated pictures. This reduces the possibility that the normal/pixellated waveform differences are due to an inability to form an episodic memory representation for the pixellated stimuli. However, there is a target related component present in the repeat waveform which may have obscured any sustained repetition effects for the pixellated pictures. In order to resolve this question, a second small experiment was conducted, in which memory for the pixellated items over longer lags was investigated.

6.5 EXPERIMENT 3A.

Method

Subjects: Nine postgraduates from the University took part in the experiment.

Stimuli and apparatus: The apparatus, stimuli and stimulus presentation sequence for this experiment were identical to that employed in experiment three, but on this occasion, subjects were instructed to respond whenever they saw a repeated picture within the series. They were told that some of the pictures would repeat immediately (with no intervening items) and that more would repeat after some intervening items.

Results

Accuracy: For normal pictures, subjects scored an average of 98% correct with immediately repeating targets. The accuracy rate for targets after intervening items was also 98%. For pixellated pictures, the score for immediate repeat targets was 98% and for later targets was 80%. The false alarm rate for normal pictures was 8% and for pixellated pictures was 11%.(See Table 6.1).

Reaction time: The average reaction time to normal immediate repeat targets was 476ms and later repeats, was 641ms. For pixellated pictures, the average reaction time to immediate repeats was 517ms and to later repeats was 733ms.

Two two-way anovas were conducted on the accuracy and reaction time scores. The factors were immediate repeat/later repeat presentations and normal/pixellated pictures. With regard to accuracy,measured by hits and false alarms, there was a significant difference between immediate and later repeat responses (F=2717.6, df=8, p<0.001). There was also a significant difference in response accuracy to normal and pixellated

TABLE 6.1. Experiment three (a). Reaction times (rt) in milliseconds and accuracy scores (% correct) for eight subjects in normal and pixellated picture recognition test. Immediate repeat scores and later repeat scores. Fa= false alarms.

	Normal pictures		Pixellated pictures	
	accuracy	rt	accuracy	rt
immediate repeats	98%	476 (16.3)	98%	517 ms (24.4)
later repeats	98%	641 (21.0)	79%	733 ms (18.2)
	(fa=8%)		(fa=11%)	

pictures (F= 32.835, df=8, $p<0.001$). There was a significant interaction between the factors (F=20.038, df=8, $p<0.01$). A post-hoc test (Newman-Keuls) revealed that there was a greater difference in accuracy scores to immediate and later repeats in the pixellated picture condition ($p<0.05$).

Examination of the reaction time data showed a significant difference in response time to immediate and later repeats (F=783.458, df=8, $p<0.001$). There was also a significant difference between response times to normal and pixellated pictures (F=33, df=8, $p<0.001$). There was a significant interaction between the factors (F=6.1, df=8, $p<0.05$). A post-hoc test (Newman-Keuls) revealed that there was a greater difference in response times to immediate and later repeats in the pixellated picture condition ($p<0.05$).

In summary, subjects were both faster and more accurate when detecting the immediate repeats than the later repeats. They were also faster and more accurate at detecting both immediate and later repeats in the normal picture condition. Differences in accuracy and reaction time across immediate and later repeats were greater in the pixellated picture condition.

The most important result of this second experiment was that although memory for normal pictures over the longer lag was superior in the case of the normal pictures, pixellated pictures can be recognised to a level significantly above chance over an intervening period of 7 items. This confirms that subjects are able to form an episodic memory for the pixellated stimuli after the longer lags. It should be pointed out that the task employed in the second experiment was tapping into more explicit memory than that in experiment one, where responses were not required to the later repeats. However, the accuracy score does show that the creation of (temporary) memory representations for meaningless stimuli is possible. This ability to form episodic images for pixellated stimuli is, however, independent of the sustained waveform differences between novel and repeated pictures resulting from the viewing of normal and pixellated pictures. The non-availability of a unitized code for the pixellated stimuli on first presentation may explain this. Episodic images are available for both normal and pixellated stimuli and it may be this availability that results in the small early repetition effect for both picture types. The additional dimension of 'meaningfulness' or access to unitised codes, is needed for the manifestation of the later, more substantial repetition effect.

It is worth noting that no specific semantic decisions were required in either the normal or pixellated picture recognition task in the main E.R.P. experiment. It is possible, since only immediate repeats required a response, that subjects could perform the task with both normal and pixellated stimuli by attending to superficial features only. However, the large differences in the novel waveforms to normal and pixellated stimuli would seem to suggest some 'automatic' extra processing of the meaningful pictures.

The similarity between the results reported here for pictures and the results obtained in word studies leads to the question of whether words and pictures share a common representation system in memory. Pictures would seem to have faster access to semantic representations than words as demonstrated in a study reported by Potter and Faulconer (1975) who found that subjects were faster at categorising pictures than words, but could name a word faster than a picture. This implies different orders of access to the representations for pictures and words. However, the E.R.P. repetition effects observed in this study are very similar to those obtained using legal/illegal nonword repetition.

In light of these results, it is difficult to argue that the locus of repetition effects is in a semantic memory system over and above episodic contributions. However, the large differences in waveforms resulting from the initial processing of normal and pixellated pictures implies access for meaningful pictures to the underlying architecture of the picture recognition system, which is denied to the pixellated pictures.

In summary, the first instance of a picture in this study (novel presentation) elicited a greater and more sustained negativity than a repeat presentation. This occurred to a smaller and less sustained extent when pixellated pictures were used as stimuli. The necessary access to semantic memory representations, in particular some unitised code, in order for late E.R.P. repetition effects to emerge is common for both words and pictures.

The results of this experiment have interesting implications for E.R.P. memory research and theory. They also have provided a possible explanation as to why E.R.P. repetition effects did not emerge in the monkey recordings using pictorial stimuli. As previously mentioned, the pictures used as stimuli portrayed objects and scenes which could never have been encountered by the monkey subjects. They could therefore have been 'meaningless' and appeared as nothing more than patterns of light and colour. The next chapter deals with a further experiment using monkey subjects using more meaningful stimuli.

CHAPTER SEVEN

EXPERIMENT FOUR: E.R.Ps RECORDED FROM A MONKEY USING FACIAL STIMULI IN A MATCH-TO-SAMPLE TASK

CHAPTER SEVEN

EXPERIMENT FOUR: E.R.Ps RECORDED FROM A MONKEY USING FACIAL STIMULI IN A MATCH-TO-SAMPLE TASK

7.1 INTRODUCTION:

Repetition effects do not necessarily depend on an overt memory for particular stimuli, but they can be eliminated with the use of meaningless stimuli (see Pixellated picture experiment). Access to some sort of semantic code appears to be necessary in order for repetition effects to emerge. The lack of consistent repetition effects in the monkey subjects could possibly be due to the nature of the pictorial stimuli used in the experiments reported here. The vast majority of the pictures depicted objects and scenes of a type which were completely unknown to the experimental animals. It is possible that these representations appeared as little more than patterns of light and colour to the monkeys. Responses could be made to immediately repeating stimuli on these pictorial features alone. However, if repetition effects depend on access to some semantic code or memory representation, they may have been eliminated due to the abstract nature of the stimuli as they would appear to the monkeys. This line of reasoning suggests the possibility that repetition effects could be similarly eliminated in human subjects if the stimuli were equally abstract. As previously mentioned, an experiment using lexical stimuli has demonstrated that the use of 'orthographically illegal' nonwords eliminates the substantial E.R.P. repetition effects observed with real words (Rugg and Nagy 1987). Also, the results of the experiment comparing repetition effects with normal and pixellated pictures reported in this thesis confirm the fact that EP repetition effects are sensitive to the nature of the stimulus. It was reasoned from this that the use of stimuli which are more salient to the primates may allow more consistent repetition effects to emerge. The stimuli chosen to this end were faces. Monkeys share with man the ability to discriminate individual faces (Rosenfeld and Van Hoesen 1979). Also, as previously described (chapter three), populations of neurons in the STS of the monkey have been described which respond selectively to face stimuli (Gross et al 1972, Perrett et al 1982,1984, Baylis et al. 1985).

The following is a report of an investigation into non-human primate evoked potentials using pictorial facial stimuli. This is examined (a) in the context of repetition effects and (b) any face specific potentials which may emerge. The use of facial stimuli was prompted by the reasoning that they would be more salient to the monkey. If E.R.P. repetition effects depend on access to semantic codes, then they might emerge with the use of facial stimuli as opposed to pictures which are generally meaningless to monkeys. The method of investigation was identical to that used in previous experiments using familiar and unfamiliar pictures. The stimulus sequence previously reported enables the comparison of E.E.G. responses to novel non-target faces with responses to repeat non-targets. The novel non-target responses to facial stimuli can also be isolated and compared to previous results using non-facial stimuli (experiments 1 and 2).

7.2 E.R.P. REPETITION EFFECTS WITH FACIAL STIMULI

E.R.P. recordings from humans using facial stimuli have previously been reported in the context of the repetition effect. Smith and Halgren (1986) had subjects view a series of unfamiliar faces before recording E.R.Ps. After electrode application, these faces were presented again, interspersed with a set of 'new' faces. They found a negative component (N445) associated with the new faces which was much attenuated when the repeated faces were presented. This component did not emerge in a similar design using meaningless visual patterns. Smith and Halgren interpreted the negative component as being specifically associated with face repetition priming. It is possible however, that the use of meaningful visual patterns other than faces could produce comparable results. A similar negativity was observed with the pictorial material used in experiment three of this thesis (Chapter six).

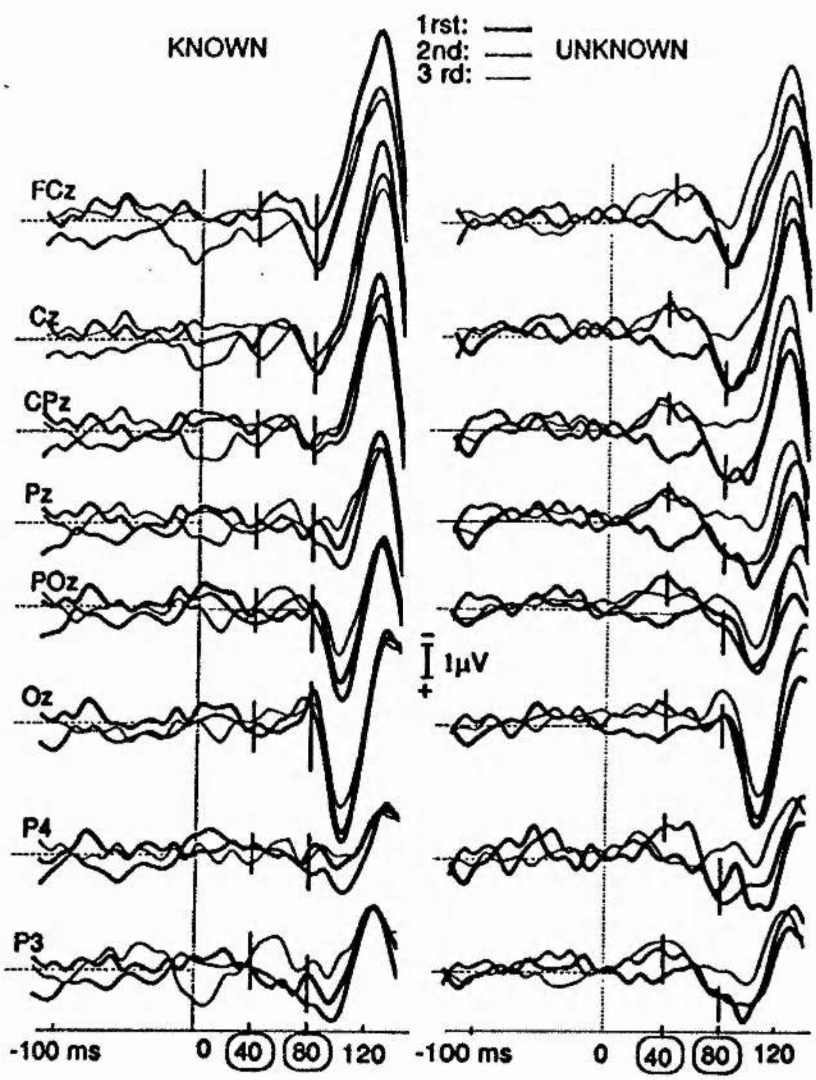
Another study of face priming with E.R.Ps was conducted by Barrett et al (1988), in which an identity matching task was used. Photographs of well-known celebrities and unfamiliar faces were viewed one after another in pairs. Subjects decided whether the second face in each pair was the same as the first or different. Different views of the faces were used from one instance to another. Faces that were seen only once were associated with two main negative components relative to the repeated items; an early effect (120-160ms) seen only with familiar faces, and a later more widespread effect for both familiar and unfamiliar faces (>250ms). In the latency range 350-450ms, the effect was greater in magnitude for the familiar stimuli. Barrett et al concluded that the match/non-match differences reflect multiple processes, including the modulation of the N400 component associated with the first presentation of a face.

A study conducted by Debruille and Renault (1990) compared E.R.Ps using known and unknown faces in a familiar/unfamiliar classification task with twelve normal and one prosopagnosic patient. For normal subjects, repetition of known and unknown faces resulted in a more positive waveform between 250-600ms. The familiarity of the faces also modified the E.R.P. between 350 and 600ms. For the prosopagnosic patient, repetition resulted in a more negative waveform, which began later and was longer for unrecognised well-known rather than unknown faces at right parieto-temporal sites.

Another experiment reported by Debruille Breton and Renault (personal communication 1991) investigated how familiarity and repetition affect evoked potentials in human subjects. Twelve right handed subjects were presented with 40 known and 40 unknown faces. The task was to move the index finger over an electrical cell, to the right for known faces and to the left for unknown faces. Each face was displayed for 400ms, separated by an interval of 3.5-4.5 seconds. The task was repeated three times in order to manipulate the repetition level. E.R.Ps were recorded from a longitudinal branch and a transverse branch of electrodes crossed on Pz. A linked earlobe reference was used. For each category of face and for each repetition level, a prominent fronto-central negative peak appeared, peaking at 120ms (See Fig. 7.1). For unknown faces, N120 amplitude increased from the first to the third presentation. In contrast, amplitude decreased for the known faces. For the first presentation N120 was significantly larger for known than for unknown faces. This difference disappeared from the second presentation. There were also early differences (pre 100ms) between the known and unknown face waveforms. The repetition of known faces did not produce any differences before 100ms, but E.R.P. modifications were seen with the unknown faces between 24-64 ms and 64-104 ms. Within the 24-64 ms latency region, E.R.Ps to second and third presentations were superimposable and both more negative than E.R.Ps to the first presentation. These differences were widespread over the scalp. From 64-104 ms, E.R.Ps to the third presentation were more negative than E.R.Ps to the first presentation. These differences were also widespread over the scalp. The authors conclude that there is a differential effect of repetition level for known and unknown faces. They postulate that the locus of these effects could be a thalamic far-field generator, in particular, a pulvinar generator. They reject the possibility that the effects could be of retinal origin due to the widespread nature of the E.R.P. modifications. The effects also occur too early for a cortical origin.

There have been no experiments reported which directly investigate repetition effects in non-human primates using facial stimuli. The following account includes investigations into whether the use of facial stimuli in a repetition paradigm would produce any effects on monkey E.R.Ps. In particular, whether the repetition of facial stimuli would result in the modulation of the N400 typically seen in human subjects when words or pictures are

FIGURE 7.1. Evoked responses to repeated presentations of known and unknown faces. From Debruille et al (1991).



repeated. In addition to the question of whether repeating faces would have any effect on the evoked responses, the waveforms resulting from viewing faces may be compared to those resulting from viewing the non-face pictorial stimuli.

7.3 METHOD

Stimuli: A set of stimulus faces was available on the video disk used in the previous monkey experiments. The face picture numbers were listed and a programme was written to select 200 of these pictures at random from the disk during each experimental recording. These pictures were a variety of coloured facial representations; photographs, line-drawings, sculptures etc. The size and views of the faces varied and many included whole body views.

Subjects: One subject used for this experiment (the female monkey that served as subject in previous experiments). The male subject was not used because it had developed epilepsy.

Procedure: The procedure was identical to that reported in previous primate experiments. The face pictures were again classed as novel non-targets, repeat targets and repeat non-targets. The monkey responded with a lick to immediately repeating pictures only. Recordings were taken from midline frontal and central sites and the left posterior site. The reference was located at the inion.

7.4 RESULTS

Behavioural Data: The mean reaction time to face targets was 523 msec (SD=150). The % correct for novel non-targets was 94.1 % and to repeat non-targets was 88.2%. The % correct for targets was 70%.

E.R.P. Data:

Novel non-targets v Repeat non-targets.

The grandaveraged waveforms from ten experimental sessions is shown in Fig. 7.2. It shows quite clearly, that there were no discernable effects of repetition on the waveforms.

Face/non-face picture comparison:

The grandaveraged waveforms resulting from viewing novel instances of faces were compared to those obtained previously from viewing novel instances of non-face pictures (experiment 2). The resultant comparison is shown in Fig. 7.3. There were 326 novel non-target face trials and 356 novel non-target non-face trials. In order to examine more closely the early peak differences between face and non-face picture waveforms, a peak by peak analysis was performed on the data. This involved measuring the latency and amplitude of the first positive peak and the first negative peak for every individual averaged recording. These latency and amplitude values were then analysed using a two way ANOVA with factors of picture type (face/non-face) and site (Fz, Cz, LP).

First positive peak: In the context of previous experiments reporting stimulus specific components, the early positive peak for faces as opposed to non-faces at the posterior site is of interest. Peak latency analysis revealed that this peak occurred at around 66 msecs for the non-face stimuli and at 71 msecs for the facial stimuli. The first peak at the frontal and central sites occurred at 82 msecs (Fz) and 56 msecs (Cz). There was no overall effect of stimulus type on the latency of this first peak. There was a significant effect of site (F=32.716, df=1.7,30.1 $p<0.001$) reflecting the fact that the first positive peak was significantly later at Fz than at LP. There was no interaction between picture type and site.

FIGURE 7.2. Experiment four. Grand-averaged evoked responses to novel non-target and repeat non-target face pictures. Female monkey.
No. of trials in both conditions: Novel non-target = 326, Repeat non-target = 241.

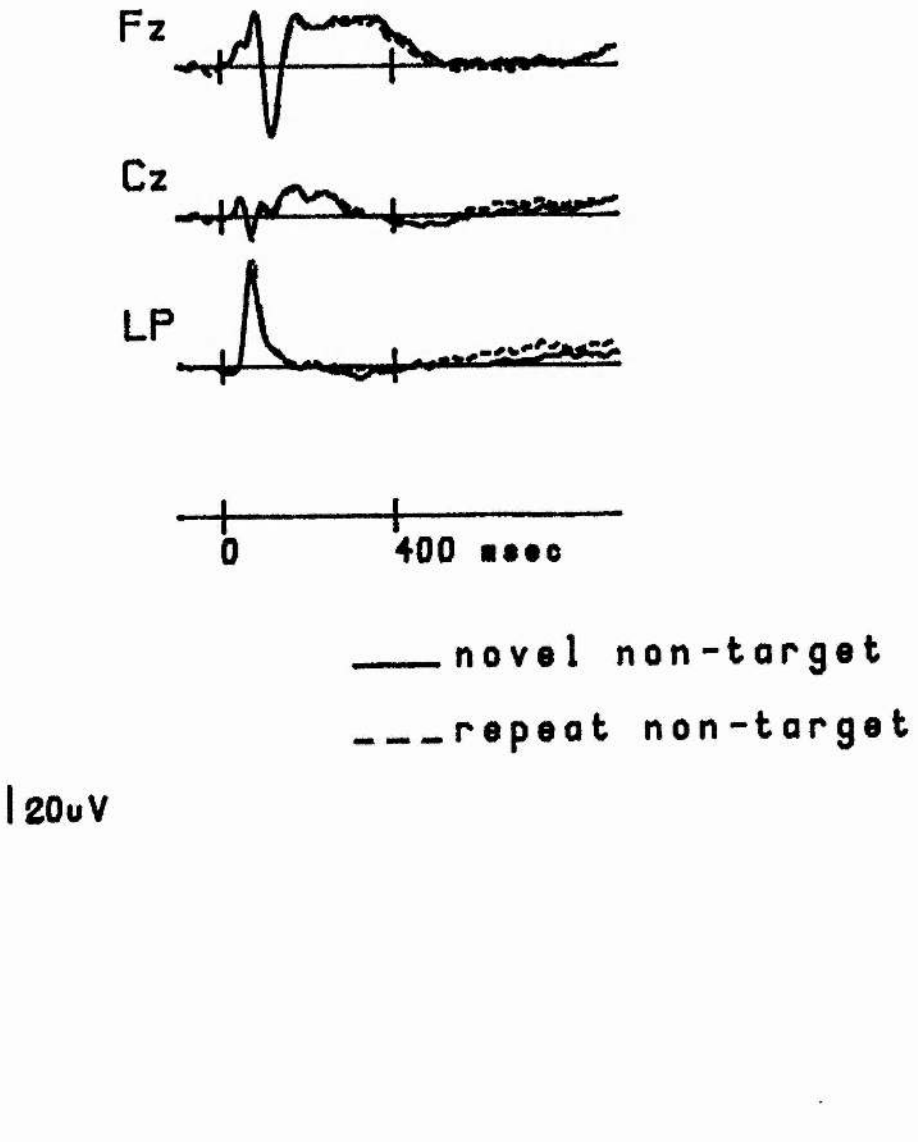
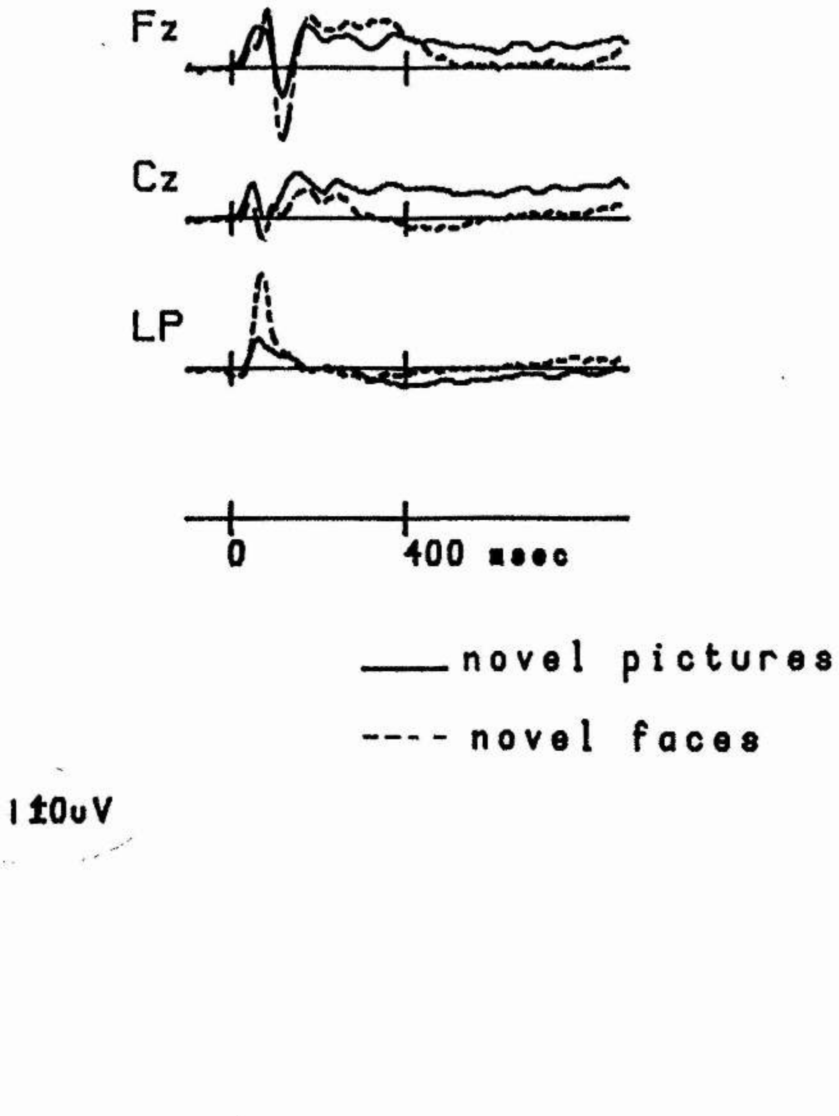


FIGURE 7.3. Comparison of grand-averaged evoked responses to novel non-target face (experiment four) and non-face stimuli (experiment two).
No. of trials in both conditions: Novel non-target faces = 326, Novel non-target non-faces = 356.



Peak amplitude analysis for the first positive peak revealed that there was a significant difference between face and non-face picture peaks (F=10.713, df=1,18 p<0.01). There was also an effect of site (F=14.397, df=1.2, 21.3 p<0.01) reflecting a higher amplitude for this peak at the posterior site. There was also an interaction between picture type and site (F=9.172, df=1.2,21.3 p<0.01) reflecting a larger amplitude for the face picture peak at the posterior site.

First Negative peak: A large negative peak occurs most prominently at the frontal site at 118 msecs. A smaller negativity occurs at the central site at 80 msecs. There is no apparent negative peak at the posterior site. Peak latency analysis revealed that there was no effect of picture type on this first negative peak. There was unsurprisingly an effect of site (F=62.037, df=1.3, 23.0 p<0.001) reflecting the later occurrence of the negative peak at the frontal site as compared to the central site. There was no interaction between picture type and site.

Peak amplitude analysis for this first negative peak revealed a significant effect of picture type (F=4.802, df=1,18 p<0.05), with the amplitude of the face picture peak being more positive than the non-face picture peak. There was also a significant effect of site (F=71.4, df=1.5,26.6 p<0.001). There was also a significant interaction between picture type and site (F=6.799 df=1.5,26.6 p<0.01) reflecting a greater difference between face and non-face picture peaks at the frontal site.

Latency Interval Measurements

A repeated measures ANOVA was conducted on selected latency regions of the waveforms using factors of picture type (face/non-face) and site. Analysis of the region from 55-100msec revealed a main effect of picture type (F=9.556 df=1,18 p<0.01). This reflected the greater positivity of the waveform resulting from the viewing of face stimuli. There was also a significant effect of site (F=26.7 df=1.2,22.1 p<0.001). There was also a significant interaction between picture type and site (F=4.455 df=1.2,22.1 p<0.05). Within the 100-140msec region of the waveform, there was a main effect of picture type (F=5.517 df=1,18 p<0.05) reflecting a greater negativity for the face as opposed to the non-face peak. There was also a significant effect of site (F=96.2 df=1.8,32.7 p<0.001). There was also a significant interaction between picture type and site (F=7.186 df=1.8,32.7 p<0.01).

7.5 DISCUSSION

The results of this present experiment would seem to indicate that the repetition of facial stimuli does not have an effect on the E.E.G. of monkey subjects. Before coming to this conclusion however, it is worth noting that the facial stimulus set used may still have been too abstract or complex. The stimulus set included a lot of line-drawn or painted pictures which may not have been meaningful to the monkey. A final stimulus set was thus constructed which consisted of faces photographed under identical lighting conditions with no extraneous elements. Also included were pictures of faces which were familiar to the monkey from real life.

The results of the comparison across experiments two and three of novel unfamiliar pictures and face pictures were interesting. The greater early positivity for the face waveform may have paralleled similar results from human E.E.G. recordings reported by Jeffreys and Musselwhite (1987) and Botzel and Grusser (1989). The results reported here are potentially more interesting, as microelectrode recordings of rhesus macaque monkeys have demonstrated that some cells respond selectively to the appearance of a face (Perrett 1985,1987). The greatest positivity recorded for faces in this study was also at the posterior site. While there are numerous problems associated with the localisation of source areas of E.R.Ps, the response at this site is consistent with the STS location of many of the face selective cells which have been found (Perrett ibid). In order to further investigate this possible 'face' potential, the next study included a within-experiment comparison of EP responses to face and object stimuli.

CHAPTER EIGHT

EXPERIMENT FIVE: E.R.Ps RECORDED FROM A MONKEY USING FACIAL AND NON-FACIAL STIMULI IN A MATCH-TO-SAMPLE TASK

CHAPTER EIGHT

EXPERIMENT FIVE: E.R.Ps RECORDED FROM A MONKEY USING FACIAL AND NON-FACIAL STIMULI IN A MATCH-TO-SAMPLE TASK

8.1 INTRODUCTION

In a final attempt to examine any potential repetition effects in primates, another stimulus set was constructed. This time, the set was specially made to include faces which were familiar to the monkey. Within the same experiment, a set of object pictures were presented in order to further clarify any face/non-face differences in the waveforms.

8.2 METHOD

Subject: Recordings were made from an awake, behaving female juvenile macaque monkey. The monkey had served as subject in the previously reported primate experiments.

Stimuli: Video pictures of faces were recorded of several volunteers from the psychology department. The faces were all frontal views. These images were then frame-grabbed and transferred to a video-disk. Also included on the video disk were photographs of a variety of objects which were familiar to the monkey, having been used as part of training. These images were then sorted into two sets. Set one included 15 pictures of faces which were highly familiar to the monkey (experimenters, laboratory technicians) and 15 pictures of a variety of familiar objects which had been used during training. Set two differed from set one in that the depicted faces were unfamiliar to the monkey and were interspersed with a different set of familiar objects. The pictures were presented in monochrome on the video monitor used in previous experiments (1 and 2).

Procedure: Recordings were taken from the frontal and central midline electrodes and the left and right posterior electrodes. The reference was located at the inion.

During every experimental recording period, the monkey was presented with the familiar face/object series and the unfamiliar face/object series. The order of presentation of the two test series was varied across recording sessions. As in the task outlined previously, the monkey responded with a lick whenever an immediately repeating stimulus occurred. Both faces and objects appeared in random order with equal probability. There were also equal numbers of target faces and target objects. Within each series, face pictures were also repeated after a lag of 7+-2 items.

Analysis

The waveforms generated for each trial were averaged across picture type (familiar faces, unfamiliar faces and objects) and also across condition (novel, repeat non-target).

8.3 RESULTS

Novel v Repeat non-targets

The comparison of waveforms resulting from viewing novel non-target and repeat non-target face pictures showed little difference between the two (Fig. 8.1). This was true of familiar and unfamiliar faces. The waveforms diverge slightly from around 200msec to 600msec, and again from 600 to 800msec. This is most apparent at the frontal site. Analysis indicated that there were no significant differences in these regions.

Faces v Objects

Behavioural Data:

Average reaction time and accuracy were calculated for responses to target faces and objects (See Fig. 8.2 and Table 8.1). The average reaction time to target face stimuli was

FIGURE 8.1. Experiment five. Grand-averaged evoked responses to novel non-target and repeat non-target faces. Female monkey.
No. of trials per condition: Novel non-target = 143, Repeat non-target = 114.

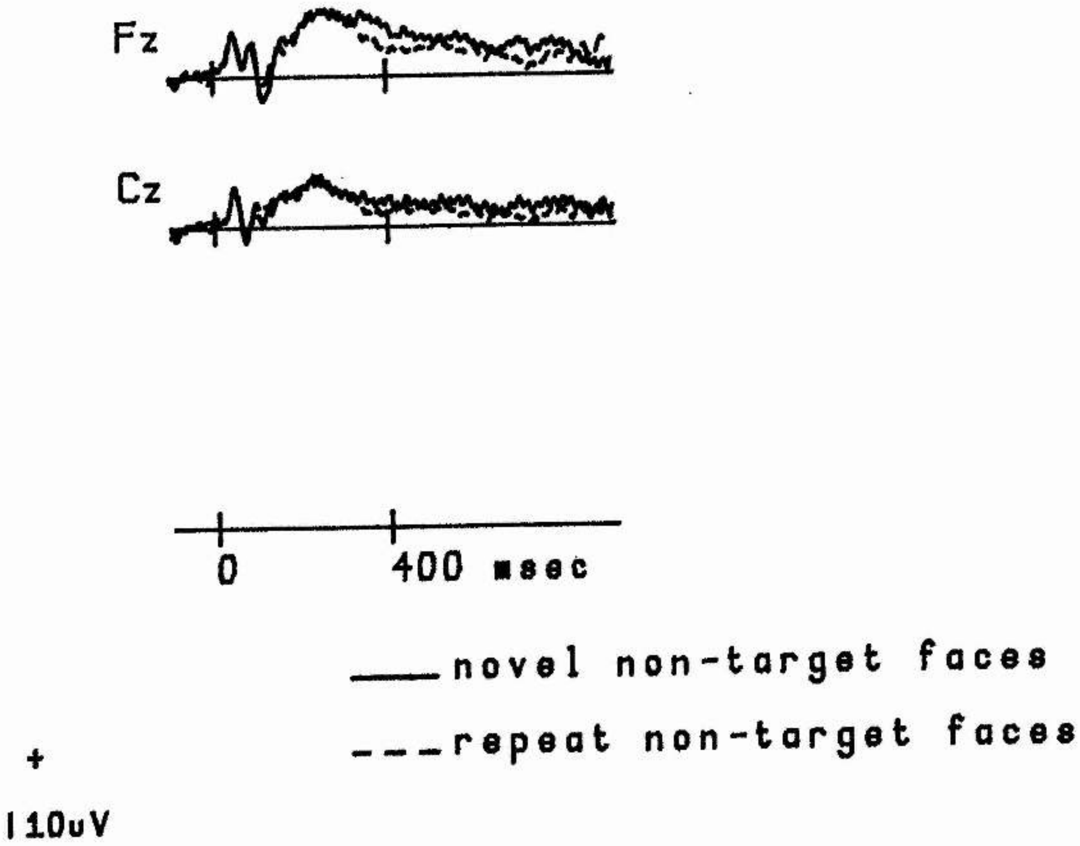


FIGURE 8.2. Experiment five. Average reaction time (RT) in milliseconds for repeat target object and face pictures. Female monkey.

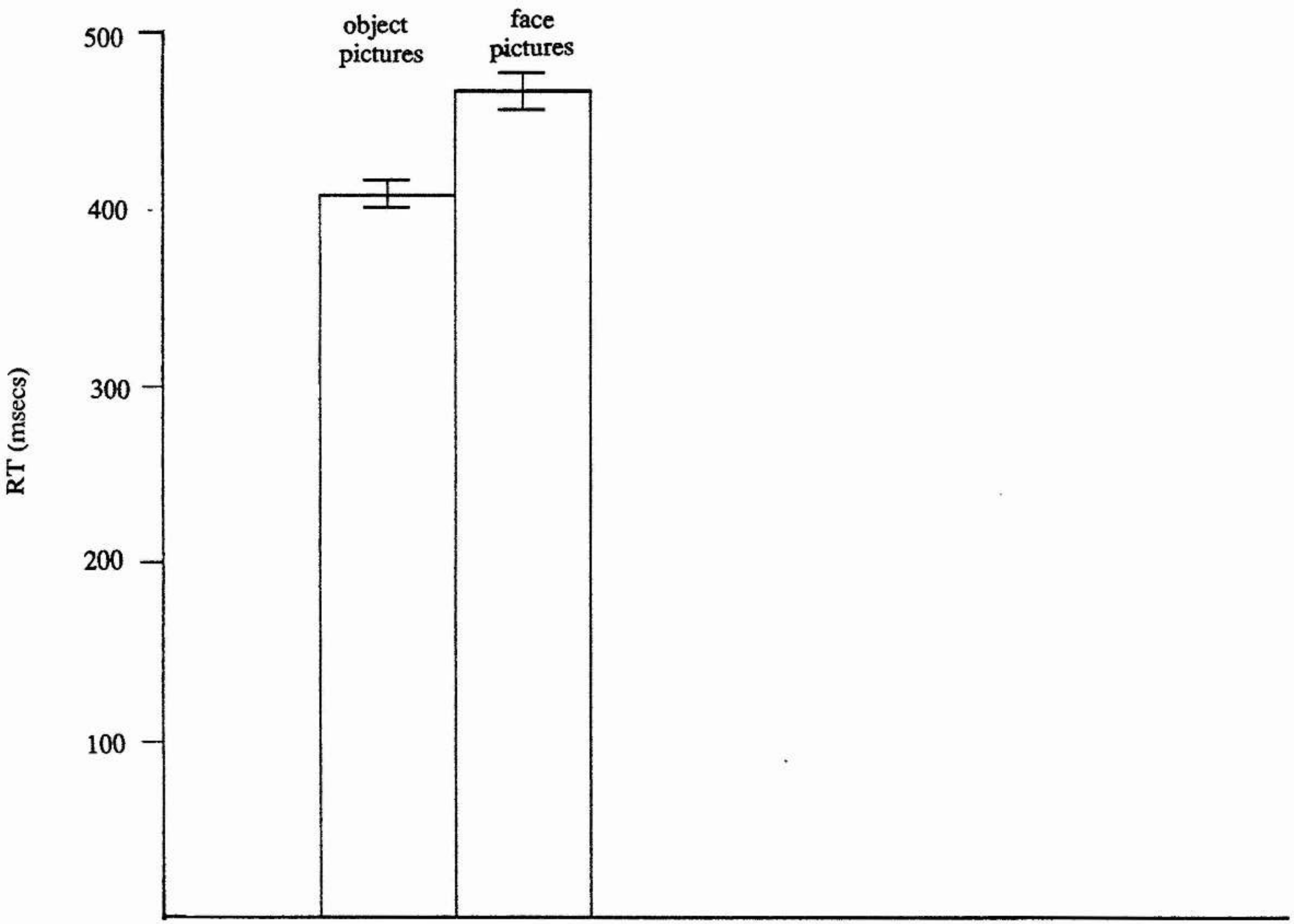


TABLE 8.1 Experiment five. Average reaction time (rt) in milliseconds for repeat target face and object picture stimuli. Accuracy (% correct) across stimulus condition. Female monkey.

		Faces	Objects
Novel non-target	accuracy	92%	95.5%
Repeat target	accuracy	84.4%	85%
	rt	446.6 ms	409.9 ms
Repeat non-target	accuracy	75.7%	

467 msecs (sem=7msec). For object targets, the average reaction time was 410 msecs (sem=10msec). A t-test revealed that there was a significant difference between reaction times to faces and objects (t=-4.574 p<0.001 df=272).

The % correct for face stimuli was 92% for the novel non-targets and 75.7% for the repeat non-targets. The % correct to target stimuli was 84.4%. The % correct for object stimuli was objects was 95.5% for the novel non-targets and 85% for the targets. A paired t-test revealed that there was a significant difference in accuracy scores to face and object targets (t=2.177 p=0.047 df=14).

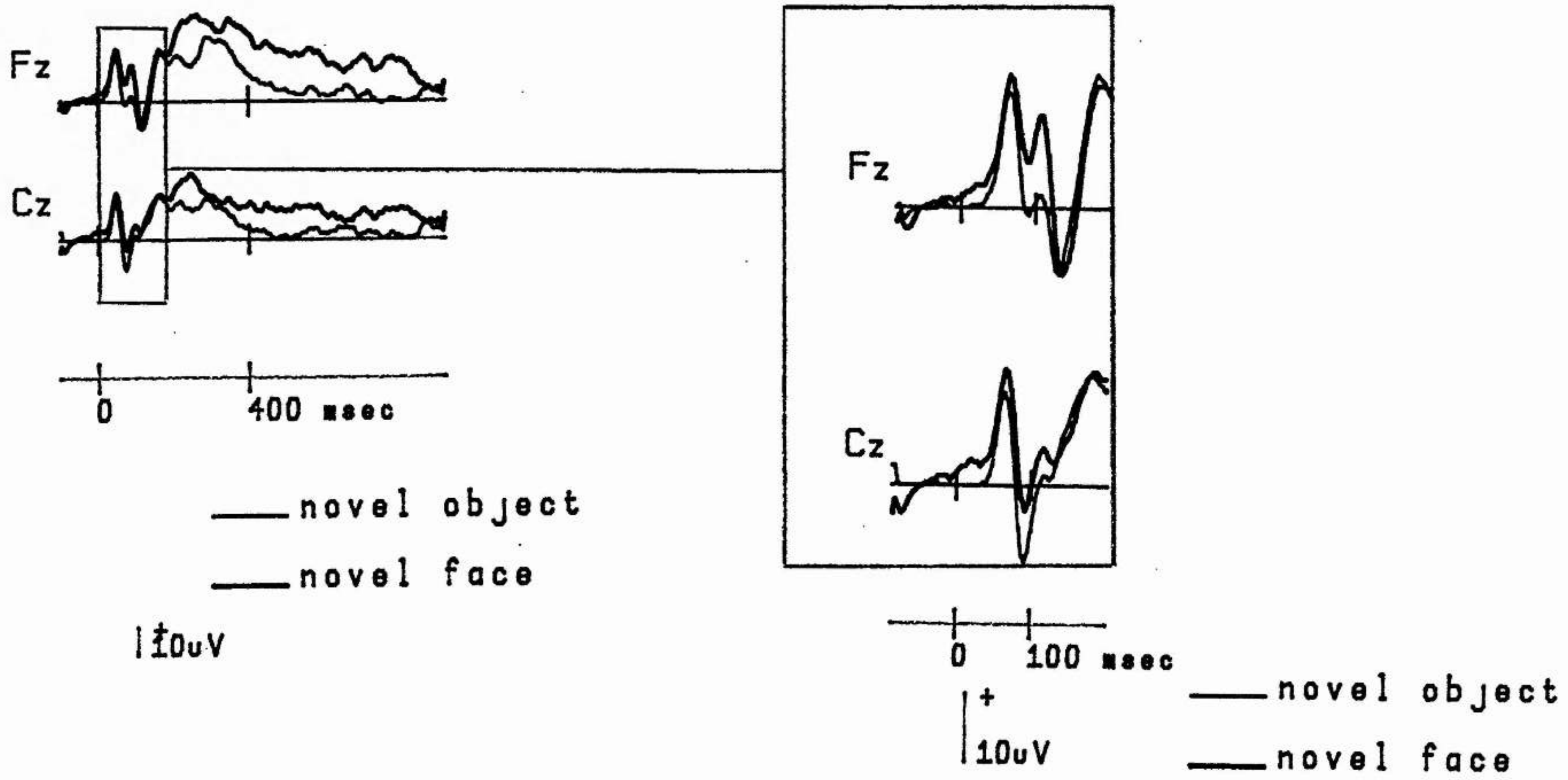
In summary, the subject was both faster and more accurate with object stimuli.

E.R.P. data

The grandaverage waveforms elicited by viewing objects v faces are shown in Figs. 8.3 (a) and (b). There were 143 novel non-target face trials and 171 novel non-target object trials in the grand average. The effects of picture type are most apparent at frontal and central sites. The waveform modulation begins early at around 45ms with a positive peak and a negative peak at around 85ms. Between 85 and 100ms there is a greater positivity for the face waveform, most apparent at the frontal site. The waveforms diverge at around 200-300ms and again at around 350-600ms, with the face waveform being more positive.

The data were analysed within selected latency regions using two-way anovas with factors of familiarity (familiar/unfamiliar), picture type (face/nonface) and electrode site. Posthoc tests were carried out where necessary (Tukey). The significance level adopted for all such tests was .05.

FIGURE 8.3. Experiment five. Grand-averaged evoked responses to novel non-target face and object stimuli.
No. of trials per condition: Novel non-target face = 143,
Novel non-target object = 181.



Familiar v Unfamiliar faces:

Preliminary analysis comparing waveforms to familiar and unfamiliar faces revealed that there were no discernable differences between these two classes of stimuli. Therefore, analysis continued with a general face/object comparison, irrespective of familiarity.

Faces v Objects:

The data from fifteen recording periods were analysed. The latency regions for analysis were selected on the basis of previous findings. That is, early regions were selected in order to examine any possible modulation such as that obtained by Grusser (ibid) and Jeffreys and Musselwhite (ibid) and also the previous comparison between face and non-face stimuli reported above. Later periods of the waveform were also analysed to confirm the impression gained from the appearance of the grand-average waveforms.

Within every latency period analysed, there were significant effects of site. This was due, in the main, to effects being small or absent at the left posterior electrode. This was due to a faulty signal at this site, and therefore, analyses were repeated eliminating recordings from this site.

The first significant effects arose within the latency period 85-100msec. There was a widespread significant effect of picture type (F=4.768 df=1,14 $p<0.05$), with waveforms to faces being more positive. There was also a significant effect of site (F=34.8 df=1.4,20.3 $p<0.001$). Post-hoc testing (Tukey) revealed that this reflected greater negativity of the waveforms at the right posterior site.

Analysis of the latency period 100-150 msec revealed no main effect of picture type. There was however, a significant interaction between picture type and site (F=4.587

df=1.8 25.7 p<0.05). Post-hoc tests revealed that this was due to a significantly greater positivity for face waveforms at Fz. Analysis of the 150-250msec portion of the waveform revealed no significant differences between face and object waveforms at any site. Between 250 and 300msec there was again a significant effect of picture type (F=5.4 df=1,14 p<0.050) with face waveforms showing greater positivity. A site x picture type interaction (F=7.477 df=1.6 22 p<0.01) reflected that the effect of picture type was least at the posterior site. Finally, analysis of the later portion of the waveform from 350-700msec showed no main effect of picture condition, but there was an interaction between picture type and site (F=4.73 df=1.4 19.5 p<0.05). Post-hoc comparisons showed that face waveforms were significantly more positive than object waveforms at the frontal site.

Peak analysis

In order to examine more closely the early face/object waveform differences, a peak by peak analysis was performed on the data. This involved measuring the latency and amplitude of the first positive peak, the first negative peak and the second positive peak for every individual averaged recording. These latency and amplitude values were than analysed using a two way ANOVA with factors of picture type (face/object) and site (Fz and Cz).

First positive peak

The first positive peak for the object waveform occurred at 48 msec latency at an amplitude of 16.8μv. The first positive peak for the face waveform occurred at 50.6 msec and at an amplitude of 20.5μv. There was no significant difference between the latencies of this first positive peak for face and object waveforms. There was no main effect of amplitude across picture type either, but there was a significant interaction for amplitude between picture type and site (F=5.142, df 1,14 p<0.05). This reflected the fact that there was a significant difference between the amplitudes of the first positive peak of face and object waveforms, with the face peak being more positive.

First negative peak

The first negative peak occurred at 77.8 msec with an amplitude of -8.7μv in the case of the object waveform and at 79 msec with an amplitude of -0.5μv in the case of the face waveform. There was no difference in the latencies of the face and object negative peak, but the object waveform peak was significantly more negative than the face waveform peak (F=7.956 df 1,14 $p<0.05$). There was also an interaction between picture type and site for this first negative peak (F=38.6 df 1,14 $p<0.001$), reflecting a larger difference in amplitude at the frontal site.

Second positive peak

The second positive peak occurred at 100 msec with an amplitude of 2.8μv in the case of the object waveform and at 97.5 msec with an amplitude of 9.8μv in the case of the face waveform. There was no difference in the latency of this second positive peak for face and object waveforms. There was a significant difference in amplitude (F=6.066 df 1,14 $p<0.05$) reflecting greater positivity for the face peak. There was also an interaction between picture type and site (F=8.764 df 1,14 $p<0.01$) reflecting a greater difference between the face and object waveform peak at the frontal site.

8.4 DISCUSSION

Repetition Effects

Repeating facial stimuli had no effect on the resultant E.R.P. waveforms. This was true even in the case of faces which were familiar to the monkey. It would appear that at least in the paradigms used in these experiments, reliable repetition effects do not emerge in E.R.P. recordings from monkeys.

The behavioural task employed provides no guarantee of the particular cognitive strategy that the subject uses to solve the task and receive reward. It is possible, despite the employment of salient facial stimuli, that the female subject performed the matching task with reference to simple pictorial cues (e.g. colour and pattern of edges) much as humans did with pixellated pictures in experiment three). The difference between monkey subjects in the presence of E.R.P. repetition effects could thus be interpreted as reflecting the different cognitive strategies employed (the male subject accessing meaningful representations of the stimuli).

It is also possible that the neural processes which contribute to repetition effects in humans are not available to monkey subjects. It could be possible that the attachment of verbal codes to stimuli is important in order for E.R.P. repetition effects to emerge. This interpretation could explain the differences obtained in E.R.Ps when meaningful and meaningless stimuli are used (Chapter 6, Rugg and Nagy 1987). Orthographically illegal words or pixellated pictures (Chapter 6) are not easily pronounceable and therefore are not verbally labelled. Monkeys do not have access to verbal codes. While this may explain the general lack of repetition effects in the E.R.Ps recorded from monkeys (Experiments one, three and four), it still remains to be explained why they were obtained in one monkey subject with the use of unfamiliar pictorial stimuli (experiment two).

Face/Object Differences

The differences in task performance in terms of reaction time and accuracy for face v object stimuli are important in the interpretation of any differences in the corresponding E.R.Ps. They would seem to suggest that processing of the facial stimuli was more difficult than processing object stimuli. It is possible that this may be due to the general similarity between the stimulus faces in terms of configuration, size etc. Although the monkey's accuracy performance with facial stimuli was significantly above chance, it was significantly less than that obtained with object stimuli. The fact that the main differences in the waveforms appear early - 85 to 100msec - is important as this occurs long before reaction times.

The differences between the face and object waveforms could also be explained by the physical differences between the face and object pictures. While care was taken to equate the size and luminance of the face and object stimuli, the faces were all frontal views. Thus they were all relatively symmetric and similarly positioned. The differences which emerged between face and object waveforms were however, remarkably similar to those observed in the previous comparison of face and nonface pictures. As noted, these face pictures were extremely varied in view and medium.

The comparison of results from experiments four and five is restricted due to the development of a faulty posterior electrode in experiment five. The face-responsive peak observed in experiment four was maximal at this recording site. It is possible that a posterior maximum would also have been evident in experiment five. The most significantly different part of the wave form for the 'face-responsive' peak occurred slightly earlier (71 msec at LP, 82 ms at Fz) in experiment four than in experiment five (98 msec at Fz). This difference could be due to the two sets of stimuli used across experiments. In experiment four, the face pictures were highly varied in view and medium of depiction while in experiment five, the faces were all frontal views photographed against a uniform background. Why this should delay the potential is difficult to say, but the uniform face pictures may have required marginally more processing time/effort. Furthermore changes in the E.R.P topography, and amplitude could have been due to the activation of additional generators required in the analysis of the more varied stimuli in experiment four.

The topography of face-responsive components recorded from human subjects is discussed by Jeffreys (1989a). He reported that the array of a coronal row of seven electrodes extending from the left mastoid to the right mastoid resulted in the subject's V.P.P having a fairly symmetrical monophasic distribution, maximal at the vertex. However, when the recordings were taken from the seven electrodes with regard to a nose reference, the V.P.P was seen to reverse polarity at T3 and T4 electrodes, from positive above to negative below. This in interpreted by Jeffreys as indicating that the potentials are generated by tangentially oriented dipole generators. That is, with generative areas of cortex oriented perpendicular to the scalp surface, directly beneath the site of the polarity reversal. The T3 and T4 electrode sites have been shown to be located close to the superior temporal sulcus and this then suggests bilateral source locations within the temporal sulci. It should be noted that the distribution of the response is dependent on choice of reference, and the positions of the polarity reversals cannot unambiguously determine the underlying source locations. Nonetheless, Jeffreys suggests that the coronal topography of the V.P.P is consistent with a possible origin in superior temporal sulci or ventral temporal cortex.

Botzel et al (1989) report a 'face' component which is maximal at the region around the Cz electrode. It is suggested that this potential does not originate in the tempero-occipital region but in symmetrically organised deep temporal structures. In this region, the cross electrical dipoles may change during the evoked responses such that a passive summation occurs most strongly at the Cz electrode. Alternatively, it is suggested that the responses originate in deep limbic structures and/or responses in the gyrus cynguli. The gyrus cynguli receives inputs from the nucleus amygdalae, which has been shown to contain a number of face-specific neurons (Rolls 1984, Baylis et al 1985).

There is one preliminary report of an experiment involving the comparison of E.R.Ps elicited by face / nonface stimuli in a single monkey (Grusser and Fuhry 1989). This study can be compared to the present results, although the task requirements and electrode arrays are different. Grusser and Fuhry (ibid) found a 'face'-responsive component occurring between 110 and 200 msecs, peaking at around 150 msecs. The potential reported in the present experiments occurs earlier (85-100 msec) but can be compared with results from single-cell recordings which demonstrate selective responses to faces. Recent analysis of the latency at which discrimination for faces can occur in the monkey brain have suggested that this can be achieved as early as 70 msecs (Oram and Perrett 1991).

The difficulties encountered with recording electrodes means that any attempt at suggesting source locations for the face-responsive component is difficult. In experiment four, the 'face'-responsive peak was maximal at the posterior electrode. Although the difference in potentials to faces and objects was not significant at the anterior Fz site, an increased positivity to faces was visible at approximately the same latency. Following Jeffreys arguments the posterior maximum is consistent with a generating source located in the temporo-occipital region of the monkey brain. In experiment five, there was a significant 'face'-responsive peak at the frontal electrode. Unfortunately no records were available from the posterior electrode. It is not possible to know whether the distribution of the face-related activity was different in the two experiments.

8.5 SUMMARY OF MONKEY E.R.P. EXPERIMENTS

The four experiments reported above would seem to indicate that the repetition of stimulus items has no consistent effect on evoked responses recorded from monkeys. This was found to be true using a variety of stimuli which varied in meaningfulness - familiar and unfamiliar pictures, varied face pictures and familiar and unfamiliar face pictures. The finding of a repetition effect in the case of one of the primates (Experiment 2) is hopeful. Further manipulation of stimuli and perhaps the use of monkey face pictures may further this investigation. It is also possible that the repetition effect which is reliably observed in human subjects using a variety of stimuli is attributable to memory processes which are not available to the monkey subjects. The ability to attach a verbal code to stimuli is one candidate for this explanation.

The face/nonface differences observed in the EPs with one of the primate subjects is a more positive and interesting result. These results came from only one primate subject, but were consistent over two experiments using different face and nonface stimuli.

CHAPTER NINE

EXPERIMENTS SIX,SEVEN AND EIGHT: HUMAN BEHAVIOURAL REPETITION EFFECTS USING FAMILIAR AND UNFAMILIAR FACIAL STIMULI

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EXPERIMENTS SIX,SEVEN AND EIGHT: HUMAN BEHAVIOURAL REPETITION EFFECTS USING FAMILIAR AND UNFAMILIAR FACIAL STIMULI

9.1 INTRODUCTION

The word/nonword distinction in lexical research has proved to be important for teasing out the factors that contribute to behavioural and E.R.P. repetition effects in word recognition. It was also shown in experiment three that stimulus meaning can have a substantial effect on visual memory processes measured with E.R.Ps. This chapter describes a further investigation of the role of meaning on behavioural measures of recognition. Following the experiments four and five, the experiments described in this chapter also employ faces as complex non-lexical visual stimuli. With these stimuli it was possible to manipulate stimulus meaning along the dimension of long-term familiarity.

In order to explore further the explanatory power of the established accounts of face recognition, the identification of familiar v unfamiliar faces should be considered. The drawing of similarities between nonwords and unfamiliar faces must be tempered with the observation that there are marked differences between the two types of stimuli. For example, faces are all largely of the same configuration, a characteristic not shared by words. The distinction between words and nonwords may be more clear-cut than between known and unknown faces.

Evidence has converged from a number of sources suggesting that familiar and unfamiliar faces are processed differently. Clinical evidence from patients who exhibit face processing deficits has for some time suggested that dissociable defects may exist (Benton 1980 for overview).

The differences between familiar and unfamiliar faces is an important consideration, as there has been little light shed on the question of how faces become familiar. Familiarity cannot be thought of as being merely a result of frequency of encounters with a face. Factors such as recency as well as the quality of the stimulus and its salience to the observer must be taken into account.

In the context of the established models of face recognition previously outlined (Hay and Young 1982, Bruce and Young 1986, Ellis et al 1987) several questions can be addressed. For instance, is the repeated presentation of a face sufficient to create a 'recognition unit'? This is the argument forwarded by Salassoo et al (1985) with regard to words. They found good performance after many presentations of nonwords and call this process "codification". Faces may be more immune to a simple rule of frequency, as they are open to more subjective interpretation and it may be necessary to encounter a face in several different aspects, in order to extract the relevant abstract information which makes up the structural codes within a face recognition unit. If only one instance of a face has been seen, then there will only be a single "trace" stored which may or may not be recognised again depending on such factors as decay, context or salience of the stimulus. But lots of different instances of a new face may lead to the extraction of the important invariants. All this has obvious implications for the semantic/episodic distinction in memory research and indicates three important factors whose contribution to face recognition must be clarified. Firstly, the number of encounters necessary to result in a repetition effect should be established, as well as whether this is constant for all faces or varies according to pre-existing semantic information. Secondly, what are the time periods that can elapse between the initial presentation of an unknown stimulus and the next encounter such that a facilitation in processing is apparent? Thirdly, do encounters with familiar and unfamiliar stimuli act on the same processes or are they coded in different ways? These questions are addressed by the first three experiments reported in this review.

The task employed in the first three experiments differs from the familiar/unfamiliar judgement used by Bruce et al (1985). Instead, the decision was made to make the task one of making a famous / non-famous discrimination. This was seen as important point with regard to the use of unknown faces in the experiment. If an episodic trace from an initial presentation of an unknown face is accessed in a familiar / unfamiliar decision task, it might be expected to inhibit a "no" response because the unknown face has now taken on some of the properties of a familiar face and it may thus seem familiar. A famous / non-famous decision on the other hand, is referring to something other than familiarity - a face can be familiar and yet not famous. Thus this task was chosen in order to minimise the confusion which might arise from feelings of familiarity due to the appearance of an unknown face in the prime phase.

Theories invoking a semantic memory system, such as those involving face recognition units, would predict a repetition effect for familiar faces in both long and short-term priming situations. For unfamiliar faces, there would perhaps be a short-lived facilitatory effect due to pictorial memory, but this should not persist to facilitate responses at longer interval testing, as there are no recognition units to be "primed". Since episodic accounts see the locus of priming as being identical in the long and short-term, presentation of both the familiar and unfamiliar faces should result in a priming effect due to the retrieval of a memory trace laid down upon the first encounter. This is dependent on the decay rate of the trace and on whether the context of the later encountered stimulus deviates from the original to any great degree.

It is predicted in this study that repetition of familiar faces across short and long periods will result in priming effects. It is also predicted that repetition of unfamiliar faces will result in priming effects in short term, only.

9.2 METHOD

Subjects: 16 young adults participated in the experiment, all with normal or corrected to normal vision. All subjects were familiar with the various forms of British media ie. they watched television and read newspapers regularly.

Stimuli: A total of 384 black and white slides depicting faces varying in expression and pose, within a circular border were used during the experiment. Half of the slides were of unfamiliar faces drawn from various sources. The remaining slides depicted "famous" faces from a number of categories - politicians, popsingers, newsreaders/T.V presenters, comedians, actors/actresses, T.V personalities and sporting personalities. The stimuli were chosen carefully so that the famous and unfamiliar face slides were of similar quality and matched for "glamour" of the image.

Apparatus: A Kodak Carousel (S-AV 2000) projector was used to project slides on to a 50cm by 64cm white black-bordered screen, positioned 3 metres away from the subject. Each face was centred on a continuously present fixation dot.

Design

The prime phase of this experiment (Pre-exposure) involved the

presentation of 300 randomly ordered slides of faces, 150 of which were famous and 150 of which were unknown.

In the test phase, each famous and non-famous slide fell into one of four categories;

(a) A repeat from the pre-exposure phase: single presentation.

(b) A repeat from the pre-exposure phase: two presentations, separated by an average lag of twelve slides.

(c) Previously unseen: single presentation.

(d) Previously unseen: two presentations, separated by an average lag of twelve slides.

See Table 9.1 for an illustration of these conditions. All of the control (single presentation) and primed items were matched, by rotating items through the conditions across subjects. This ensured no confound of items and condition due to the characteristics of any particular face. It was also ensured that the semantic categories (politician, actor etc.) were mixed as much as possible, so that two members belonging to the same category rarely followed each other and directly associated personalities (eg.from the same T.V programme) never appeared consecutively. This was carried out in order to minimise the effects of any associative or semantic priming between faces.

Subjects were requested to make a famous/nonfamous decision to each face presented. They were also told that they would have seen some of the faces earlier and that some of them would repeat within this phase. They were requested to disregard the repetition and to concentrate each time on making the famous/nonfamous decision as quickly and accurately as possible.

TABLE 9.1. Experiment six Stimulus presentation conditions. ITEM = First presentation. R1 = First repetition. R2 = Second repetition.

	PHASE ONE (Pre-exposure)	twenty minute interval	PHASE TWO (Experimental)		
FAMOUS	ITEM		ITEM	twelve item interval	
			R1		
			R1		R2
UNKNOWN	ITEM		ITEM		
			R1		
			R1		R2

Procedure:

Phase one; pre-exposure.

Subjects were seated facing the projection screen. They were requested to rate a series of 96 faces for attractiveness on a five point scale, ranging from very unattractive (0) to very attractive (4). The attractiveness rating task was chosen in an effort to encourage the objective appraisal of each face whether it was famous or unknown and to maximise the chances of famous and unknown faces being processed to an equal degree. There was no limit on the time allowed to make the rating. Subjects recorded their answers on a score sheet and controlled the rate of presentation themselves. A twenty minute interval followed this first phase during which subjects engaged in a different, unrelated activity.

Phase two; Test phase.

Subjects sat facing the projection screen with their fingers resting on two microswitches. A series of slides of faces was again presented. In this case, subjects were requested to make a famous/non-famous decision about each face, pressing a right hand switch if the stimulus was famous and a left hand switch if the face was unknown. Each face was presented for 600ms and subjects were required to respond within 1500ms of stimulus onset.

Debrief:

Following phase two, subjects were shown all the slides again and asked to name the faces (real or stage names) or to indicate their occupation. The response to unfamiliar faces was simply to indicate non-recognition. Any slides which were frequently misidentified (eg. bad photographs of famous people, unfamiliar faces that resembled famous faces) could thus be eliminated from the analysis.

9.3 RESULTS

Mean reaction times were calculated from correct responses for each subject in each condition. It was not necessary to reject any of the items in the analysis on the grounds of frequent misidentification. Means of the reaction times are shown in Table 9.2 and in Fig. 9.1. A three way repeated measures ANOVA was performed on the data from all experimental conditions. The factors referred to stimuli being famous/unknown, pre-exposed/non pre-exposed and repeated/unrepeated. There was a significant effect of pre-exposure ($F=33.7$, $df=1,15$ $p<0.001$) reflecting faster reaction times to stimuli which had been pre-exposed. There was also a significant effect of intra-experimental repetition ($F=94.2$ $df=1,15$ $p<0.001$) reflecting faster reaction times to stimuli which were repeated.

There was a significant interaction between familiarity and pre-exposure ($F=7.7$ $df=1,15$ $p<0.05$). This was because pre-exposure had a greater effect on reaction times to famous faces than unfamiliar faces. A significant interaction was also present between pre-exposure and intra-experimental repetition ($F=8.9$ $df=1,15$ $p<0.01$). Repetition of stimuli in phase two led to greater facilitation when stimuli had not been previously seen.

There was also a significant difference in reaction time to famous and unknown stimuli ($F=9.7$ $df=1,15$ $p<0.01$) with reaction time being faster to famous stimuli. Separate ANOVAs were performed on the data from famous and unknown presentations in order to demonstrate the different effects of pre-exposure and intra-experimental repetition within the two classes of stimuli.

Famous Faces

ANOVA was performed on the data from famous face presentations only, with factors of preexposure (appearance or non-appearance in phase one) and of repetition (appearance once or twice in phase two). The average reaction times across conditions are shown in Table 9.2 and Fig. 9.1. Analysis of the data revealed a significant effect of pre-exposure ($F=10.4$ $df=1,15$ $p<0.01$) with reaction times being faster to pre-exposed stimuli. There was also a significant effect of repetition ($F=66$ $df=1,15$ $p<0.001$) with reaction times being faster to repeated stimuli. There was also a significant interaction between pre-exposure and repetition ($F=10.8$ $df=1,15$ $p<0.01$). Post-hoc testing (Tukey) showed that repeating the stimuli in the experimental phase resulted in greater facilitation when stimuli had not been pre-exposed ($p<0.01$).

Error scores (correct classification as famous or unknown) were calculated for all subjects in all conditions. The average hit rates in the separate conditions are shown in Table 9.3 and Fig.9.2. ANOVA was run on the data, again with factors of appearance/ non-appearance in phase one and repetition/non-repetition in phase two. There was a significant difference in hit rate for pre-exposed and previously unseen stimuli ($F=4.6$ $df=1,15$ $p< 0.05$), being higher in the pre-exposed categories. There was also a significant difference in hit rate for faces seen once or twice in the test phase ($F=18.4$ $df=1,15$ $p<0.001$) with higher accuracy scores to repeated stimuli. There was a significant interaction between the two factors ($F=10$ $df=1,15$ $p<0.01$) indicating an effect of pre-exposure on the hit rate in the test phase. The facilitation observed in the experimental phase was greater for those faces which had not been pre-exposed.

Thus the presentation of a famous face in the attractiveness rating task in phase one facilitated response time and accuracy judgement to a presentation of the same face 20

Fig. 9.1. Experiment six. Average reaction times (RT) in msecs for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

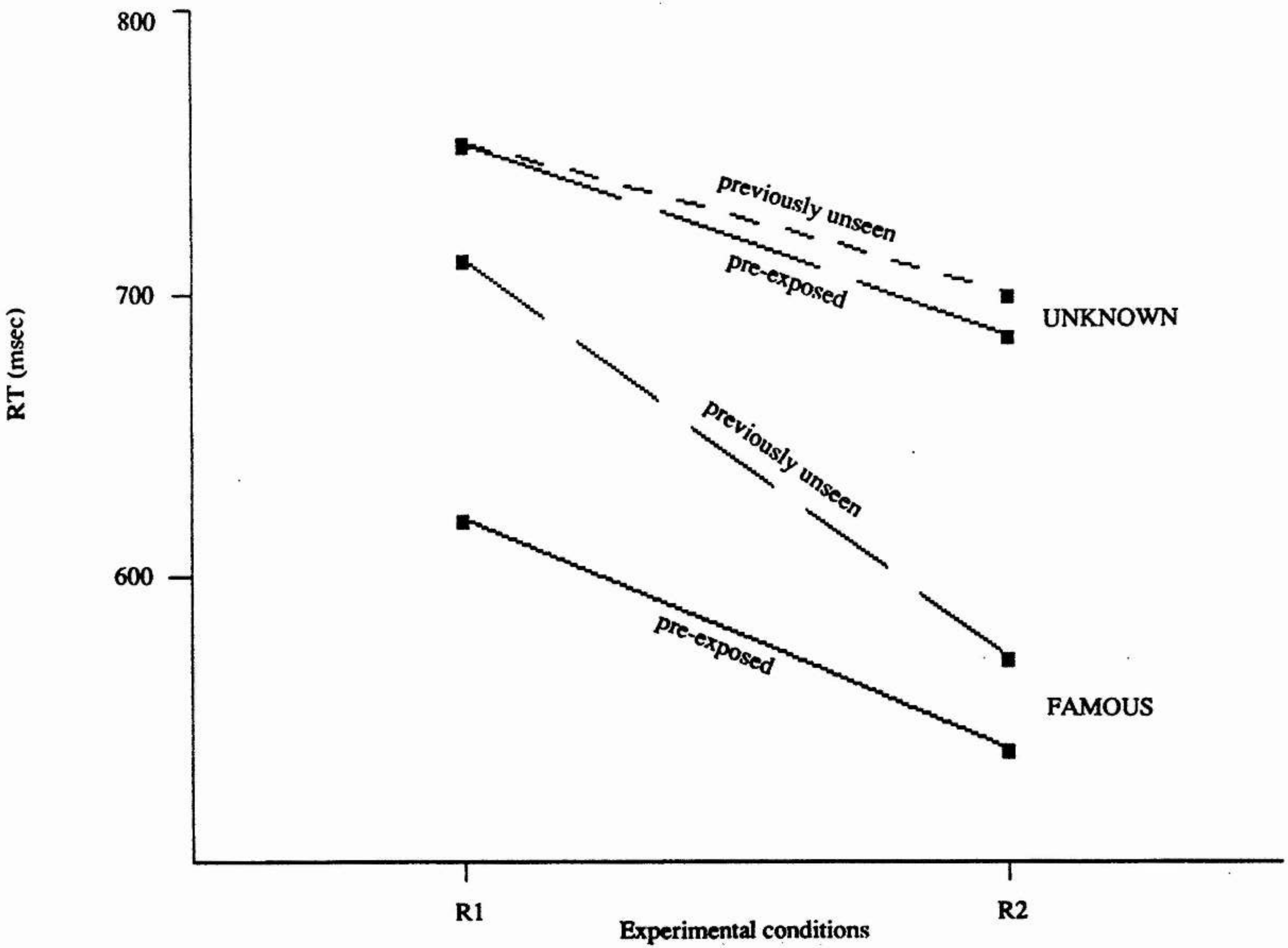


Table 9.2. Experiment six. Average reaction times in msecs for sixteen subjects in a famous/non-famous decision task. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

	PRE-EXPOSED		PREVIOUSLY UNSEEN	
	FAMOUS	UNKNOWN	FAMOUS	UNKNOWN
R1	621 *24.29*	753 *32.30*	712 *32.54*	754 *33.70*
R2	539 *20.60*	685 *29.55*	572 *20.52*	699 *30.70*

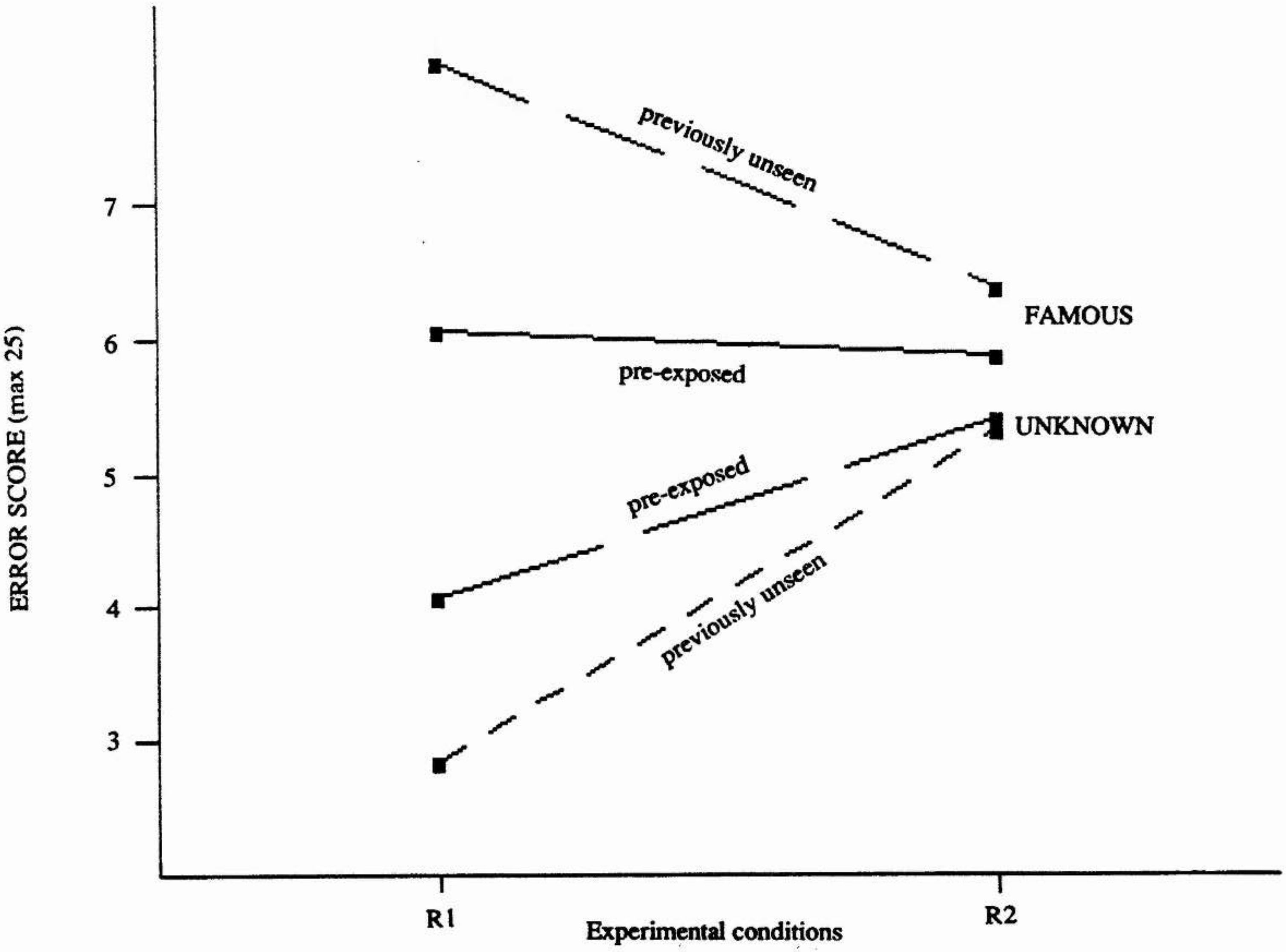
Table 9.2(a). Experiment six. Median reaction times in msecs for sixteen subjects in a famous/non-famous decision task. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

	PRE-EXPOSED		PREVIOUSLY UNSEEN	
	FAMOUS	UNKNOWN	FAMOUS	UNKNOWN
R1	592 *22.10*	729 *30.77*	670 *31.76*	735 *29.10*
R2	512 *17.82*	655 *26.37*	544 *20.78*	672 *30.46*

Table 9.3. Experiment six. Average error scores (max errors 25) for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the experimental phase.
R2 = Second presentation in the experimental phase.

	PRE-EXPOSED		PREVIOUSLY UNSEEN	
	FAMOUS	UNKNOWN	FAMOUS	UNKNOWN
R1	6.062	4.082	8.062	2.825
R2	5.875	5.375	6.375	5.312

Fig. 9.2.Experiment six. Average error scores (maximum possible 25) for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.



minutes later in a famous/non-famous decision task. There was also a facilitatory effect observed between one presentation in the test phase and another presentation twelve slides later. These factors indicating long and short-term priming were found to be interactive in that the repetition effects in the experimental phase are smaller for pre-exposed stimuli.

All of the analysis was repeated using median scores in order to eliminate the possibility of bias due to extreme scores. The results follow a highly similar pattern to those observed using mean scores in the analysis. (See Table 9.2(a).

Unknown Faces

The mean reaction times to judge a face as unfamiliar in each of the conditions are also summarised in Table 9.2 and Fig. 9.1. ANOVA using the same factors of pre-exposure / non pre-exposure, and intra-experimental repetition / non-repetition, was performed on the data from unfamiliar face presentations only. There was no significant effect of pre-exposure on the reaction times in phase two (F=0.7 df=1,15 p=0.39). There was a significant effect of repetition within the test phase (F=35. df=1,15 p<0.001), showing an advantage for repeated stimuli. There was no interaction between the factors (F=0.88 df 1,15 p=0.36).

Thus the presentation of an unknown face in an attractiveness rating task had no effect on the response time to a subsequent presentation 20 minutes later. However, the response time to a further presentation 12 slides later was facilitated. Pre-exposure had no effect on the intra-experimental repetition effect. There was also an effect of repeating stimuli within the test phase only.

The number of errors made in the famous/non-famous decision task was calculated for all subjects in all conditions (See Table 9.3 and Fig. 9.2). ANOVA run on the data with factors of appearance/non-appearance in phase one and repetition/non-repetition in the test phase. There was no significant difference between the number of errors made with pre-exposed and previously unseen stimuli (F=1.42 df 1,15 p=0.25). There was a significant difference between faces seen once or twice in the test phase (F=52 df=1,15 p<0.001) with faces seen once being processed at greater accuracy. *There was no interaction between the two factors.*

ANOVA was also performed on the data from the test phase only. The factors employed referred to stimuli being famous/unknown and repeated/unrepeated. There was a significant difference between reaction times to famous and unknown faces (F=12.3 df=1,15 p<0.01) with reaction times being faster to famous faces. There was also a significant difference in reaction times to stimuli seen once or twice (F=69.1 df=1,15 p<0.001), reaction times being faster for repeated stimuli. There was also a significant interaction present between the two factors (F=13 df=1,15 p<0.01), indicating that the facilitation in reaction time from one presentation of a face to the next, twelve slides later, was greater in the case of famous faces.

9.4 DISCUSSION

The results of experiment one support those of Bruce and Valentine (1985) in that recognising a face as familiar (famous) is primed by prior exposure to a photograph of that person. Facilitation was observed across twenty minutes (pre-exposure) and also across twelve items (intra-experimental repetition). More important however, is the interactive effect of pre-exposure and intra-experimental repetition in the case of famous faces. Pre-exposure diminished the intra-experimental repetition effect. This is of particular interest in assessing the relative contributions of episodic and semantic processes to repetition effects. Because the famous/nonfamous decision provides a reaction time measure, the method of additive factors (Sternberg 1966, 1969a, 1969b) can be used to address the question. The interactive effect implies that pre-exposure and intra-experimental repetition shared at least one processing stage. This stage could plausibly be said to involve access to a semantic code present for the famous faces which is not available for the unknown stimuli. The facilitation observed twenty minutes after the first presentation of a famous face could be seen to reflect in the main an effect of identity-specific semantic codes, whereas the 12 item lag facilitation benefits from the added, short-lived episodic aspects of the stimulus. For famous faces, additional sources of semantic information are available over and above those derived directly from the visual pattern and it is this additional information which is affected by stimulus presentation resulting in the priming effect. This conclusion is supported by the lack of any facilitation in response for the unfamiliar faces after twenty minutes - there are by definition no pre-existing face-recognition units for unknown faces, so these cannot be primed and thus show no repetition effect after twenty minutes - these faces have at most only a visually derived semantic code or episodic pictorial code. The contribution of these codes only manifests itself in the short term after a 12 item lag.

The significant difference between the facilitation observed with famous and unknown faces intra-experimentally would imply that this episodic component is smaller, but is intimately involved with the semantic component. Ratcliff and McKoon (1988) have also reported that whenever episodic priming is obtained at short stimulus-onset asynchronies, so is semantic priming. The results thus support the idea of episodic processes being embedded in semantic processes. The priming effect obtained with famous faces may be the result of a combination of system response to semantic and episodic images. Even if these are thought of as different, they cannot be thought of as completely distinct because of their interaction.

A purely episodic account of priming effects would have predicted some priming in terms of reaction time facilitation from one instance of a face, especially since the prime and target were identical, leading to easy retrieval of the stimulus trace. An episodic explanation is more readily accommodated in the short-term intra-experimental repetition effect. Bruce and Valentine (1985) suggest such short-term priming as indicating the separate pictorial memory of a stimulus - an episodic record- of the particular photograph that has been seen. In support of this idea of a pictorial code, Bruce (1982) reported that altering the pictured background context against which a previously unfamiliar face was portrayed could reduce the accuracy of subsequent recognition memory performance. In the case of the results reported here, it is possible to interpret the short-term priming effect with unfamiliar faces as reflecting this pictorial memory, a purely episodic record of the particular items presented. With regard to the famous faces however, additional information is available and even the short term facilitation is larger than that seen with unfamiliar faces. It may also be possible to propose the setting up of some kind of temporary visually derived semantic unit for unfamiliar faces - perhaps in terms of resemblances ("that looks like my old school teacher") or facial characteristics ("fat and balding-looks wealthy" etc.). However, such visual derivations may not hold, especially when subjects are not making any conscious effort to remember stimuli. Such pre-experimentally influenced subjective evaluations of the stimulus may be very important in providing the links between episodic and semantic processes.

Turning to the accuracy scores, it is interesting to note that in the case of unknown faces, subjects made more errors in judgement on the second presentation in the test phase. The task at test (famous/non-famous decision) was chosen in order to minimise confusion which might arise with a familiar/unfamiliar decision task. The memory of the stimulus from the previous presentation may inhibit an 'unfamiliar' decision. It would appear however that some confusion did arise (ie. I have seen this face before, but it's not famous) which may have had an effect on the reaction time difference between famous and unknown faces. This however, does not affect the main experimental result which showed the interactive repetition priming in long and short term for famous face stimuli, and only in the short term for unknown faces.

EXPERIMENT SEVEN

9.5 INTRODUCTION

It could be argued that the absence of repetition effects from preexposure to test for unfamiliar faces is possibly due to the different tasks subjects carried out in the prime and test phases of the experiment. Insofar as repetition effects are associated with the activation of abstract units, they should transfer across tasks and contexts. A repetition effect should be unaffected when a prime and test task are different - however, if the effects arise from the recovery of an episodic record of the priming encounter then such facilitation should exhibit some specificity to the episodic context of the priming encounter. In order to examine the possibility that the lack of effect observed with unknown faces in this experiment was due to the time period involved rather than the difference between the prime and test tasks, the experiment was repeated employing the same task in both phases.

9.6 METHOD

Subjects: 16 young adults, all with normal or corrected to normal vision. All subjects were again familiar with British media. None of the subjects had participated in experiment one.

Apparatus: The same apparatus as employed in experiment six.

Procedure: The same basic procedure was followed as in experiment one, with the only difference being that the pre-exposure phase involved subjects making a famous/nonfamous judgement about a series of faces. There was no time limit on the decision in this phase of the experiment. In the experimental phase twenty minutes later, subjects were requested to make the same famous/nonfamous decisions as quickly and accurately as possible.

9.7 RESULTS

Means were calculated from correct responses for each subject in each condition in the experimental phase. Overall means are shown in Table 9.4 and Fig. 9.3. A three way repeated measures ANOVA was performed on the data employing factors of familiarity, appearance/non-appearance in phase one and repetition/non-repetition in phase two. There was a significant effect of famous v. unknown stimuli (F=31.8 df=1,15 p<0.001) with reaction times being faster in the case of famous faces. There was also a significant effect of pre-exposure (F=19.3 df=1,15 p<0.001) reflecting faster reaction times to pre-exposed stimuli. There was also an effect of intra-experimental repetition (F=136 df=1,15 p<0.001) reflecting faster reaction times to repeated stimuli. There was a significant interaction between pre-exposure and famous/unknown (F=27.5 df=1,15 p<0.001) indicating a larger effect of pre-exposure on reaction times to famous stimuli. Famous face stimuli also promoted greater facilitation in intra-experimental repetition (F=13 df=1,15 p<0.01). The effect of repetition in the experimental phase was greater for stimuli which had not been pre-exposed (F=15 df=1,15 p<0.01).

Again, data from famous and unknown face presentations will be reported separately in order to demonstrate the different effects of pre-exposure and intra-experimental repetition within the two classes of stimuli.

Famous Faces

ANOVA performed on the data employing factors of pre-exposure/non-preexposure and repetition/nonrepetition showed a significant effect of pre-exposure (F=30.7 df=1,15 p<0.001) with reaction times being faster to pre-exposed stimuli. There was also a significant effect of intra-experimental repetition (F=282 df=1,15 p<0.001) with faster reaction times to repeated stimuli. There was a significant interaction between these two

Fig. 9.3. Experiment seven. Average reaction times (RT) in msecs for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

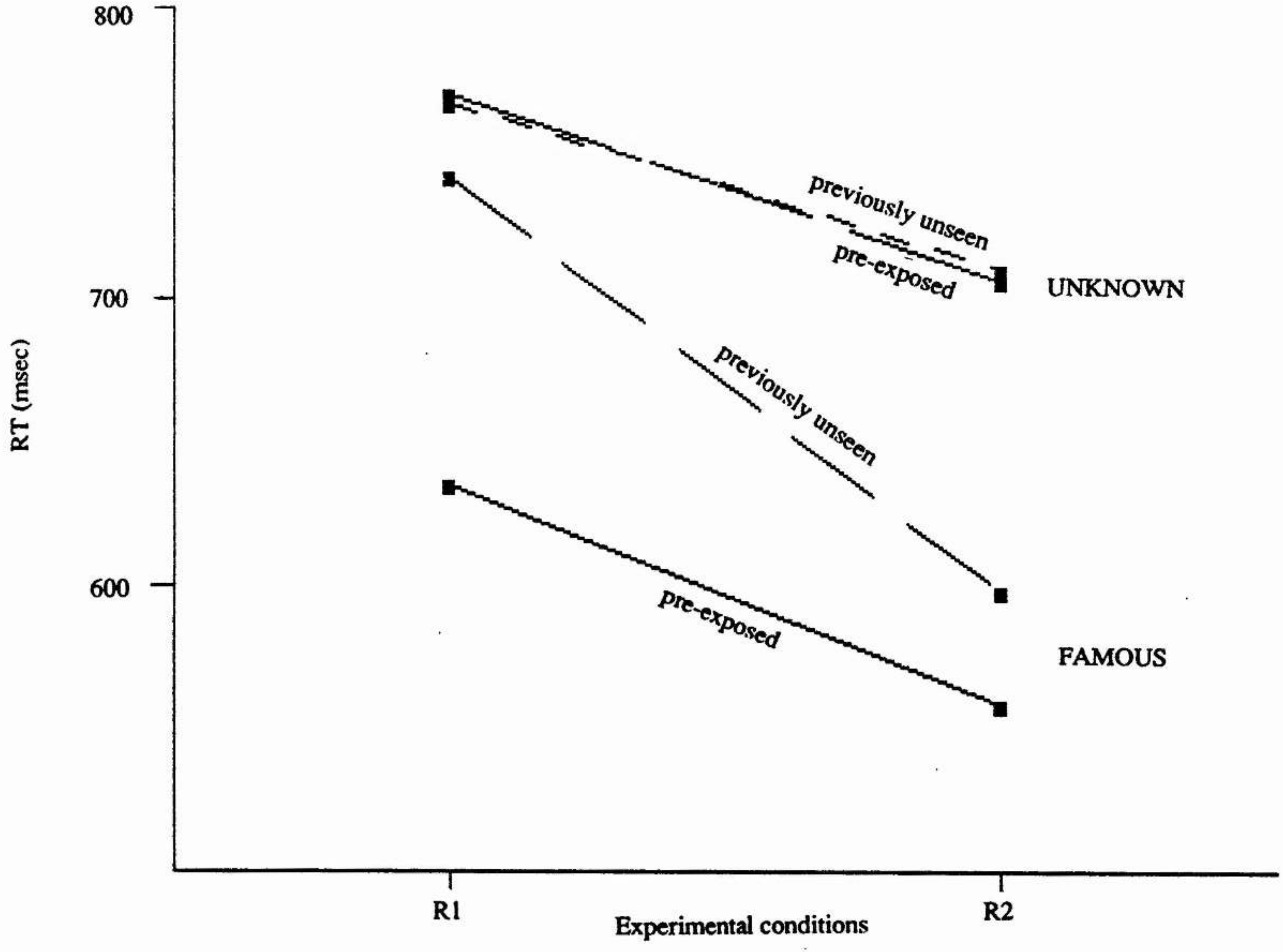


Table 9.4. Experiment seven. Average reaction times in msecs for sixteen subjects in a famous/non-famous decision task. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

	PRE-EXPOSED		PREVIOUSLY UNSEEN	
	FAMOUS	UNKNOWN	FAMOUS	UNKNOWN
R1	635 *30.00*	770 *44.51*	742 *34.50*	768 *43.00*
R2	558 *29.00*	706 *41.61*	598 *31.34*	710 *40.40*

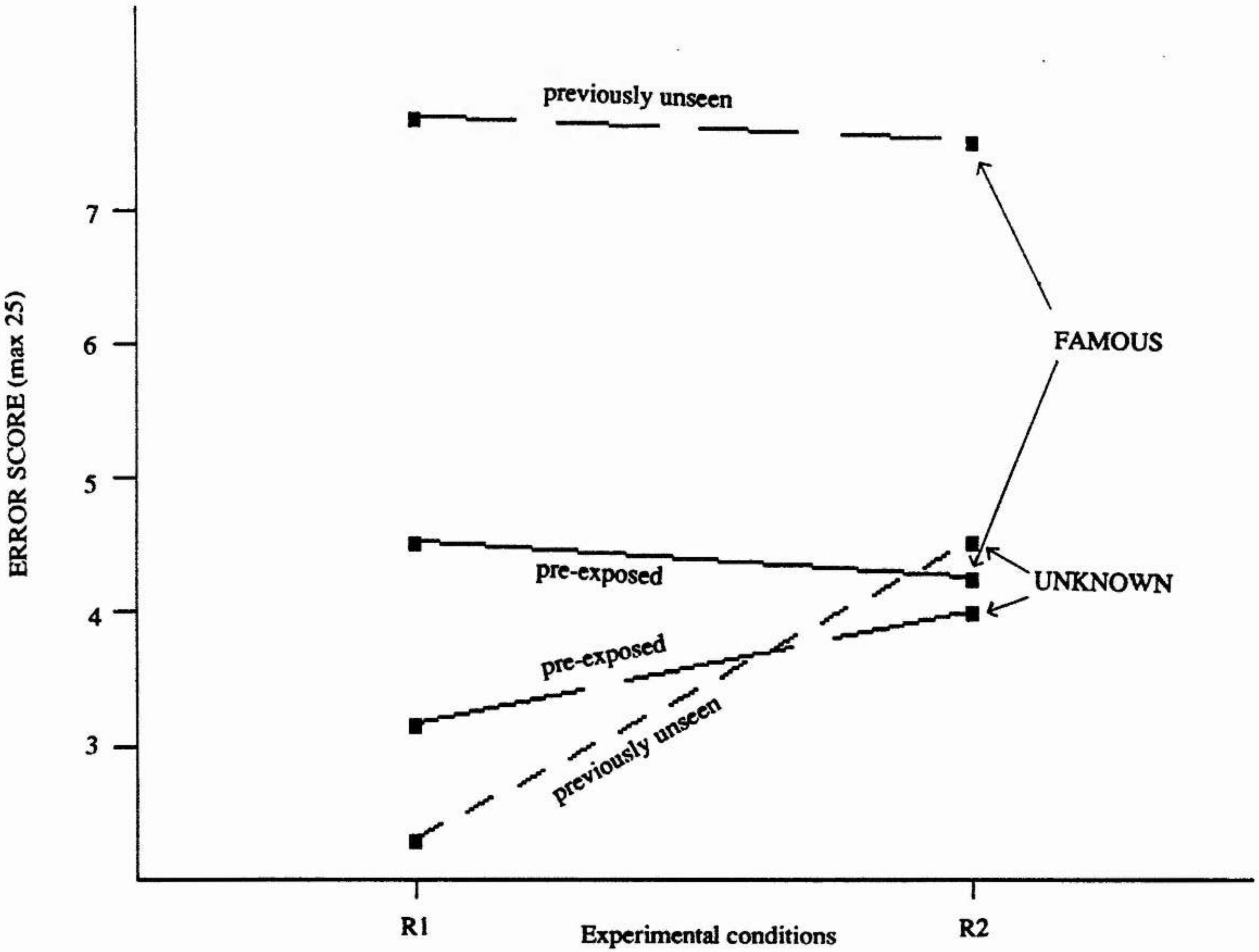
Table 9.4(a). Experiment seven. Median reaction times in msecs for sixteen subjects in a famous/non-famous decision task. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

	PRE-EXPOSED		PREVIOUSLY UNSEEN	
	FAMOUS	UNKNOWN	FAMOUS	UNKNOWN
R1	617 *33.73*	748 *43.87*	719 *36.33*	755 *44.66*
R2	542 *29.66*	679 *43.81*	570 *31.21*	704 *42.34*

Table 9.5. Experiment seven. Average error scores (max errors 25) for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the experimental phase.
R2 = Second presentation in the experimental phase.

	PRE-EXPOSED		PREVIOUSLY UNSEEN	
	FAMOUS	UNKNOWN	FAMOUS	UNKNOWN
R1	4.50	3.19	7.69	2.31
R2	4.25	4.0	7.5	4.5

Fig. 9.4.Experiment seven. Average error scores (maximum possible 25) for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.



factors (F=23 df=1,15 p<0.001) reflecting a greater facilitation in the experimental phase for those stimuli which had not been pre-exposed.

The number of errors made in the famous/nonfamous judgement was calculated for all subjects in all conditions (See Table 9.5 and Fig. 9.4.). ANOVA was run on the data with factors of appearance/non-appearance in phase one and intra-experimental repetition/non-repetition. There was a significant difference in hit rate for pre-exposed and previously unseen stimuli (F=26.4 df=1,15 p<0.001) with higher scores for pre-exposed stimuli. There was no significant difference in hit rate between faces seen once or twice in phase two (F=0.52 df=1,15 p=0.48) and there was no significant interaction between the two factors (F=0.0 df=1,15 p=0.94).

All of the analyses were again repeated using median scores in order to eliminate the possibility of bias from extreme scores. The results followed the same pattern as those observed with mean scores. (See Table 9.4(a)).

Thus the presentation of famous faces in a famous/non-famous decision task facilitated response time in the same task on presentation of the identical stimuli twenty minutes later. There was a further facilitatory effect observed upon a subsequent presentation 12 slides later. The interaction observed between the two factors reflects the fact that the intra-experimental repetition effects are smaller for those stimuli which had been pre-exposed.

Unknown Faces

The mean reaction times to judge a face as unknown in each of the conditions are also summarised in Table 9.4 and Fig. 9.3. ANOVA was performed on the data employing factors of preexposure/non-preexposure and intra-experimental repetition/non-repetition.

There was no effect of pre-exposure (F=0.0 df=1,15 p=0.89) but there was a significant effect of intra-experimental repetition (F=23 df=1,15 p<0.001). There was no interaction present between the factors (F=0.2 df=1,15 p=0.67).

The number of errors made in the famous/non-famous judgement were calculated for all subjects in all conditions. The average number of errors in the separate conditions are shown in Table 9.5 and Fig. 9.4. ANOVA was run on the data with factors of preexposure/non-preexposure and intra-experimental repetition/non-repetition. There was no significant difference in hit rate between pre-exposed and previously unseen stimuli (F=0.11 df=1,15 p=0.74). There was a significant difference in hit rate between faces seen once or twice in phase two (F= 17.4 df=1,15 p<0.01). There was no significant interaction between the two factors (F=2.2 df=1,15 p=0.15).

Thus the presentation of an unknown face in a famous/non-famous decision task had no effect on reaction times in an identical task using identical stimuli twenty minutes later. However, response time was facilitated when there were only twelve intervening items between prime and target faces. The preexposure of unknown faces had no effect on the intra-experimental repetition effect.

9.8 DISCUSSION

It can be concluded that the pattern of priming effects observed with unknown faces in experiment six was not due to the difference in task between the pre-exposure and experimental phases. It appears rather, that the difference is due to the period of delay separating the two phases. That is, it may be that a facilitatory effect can be achieved with prior presentation of an unknown face so long as there is only a short interval between prime and target, in this case an average lag of twelve intervening items. The effect does not persist to a twenty minute delay. It is worth noting also that for famous faces, *both* pre-exposure tasks substantially and equally facilitated familiarity decision tasks in the second phase.

EXPERIMENT EIGHT

9.9 INTRODUCTION

Another possible explanation of the failure to achieve long term reaction time priming effects with unfamiliar faces lies in appealing to processes of forgetting or decay of the original episodic trace. It is necessary to ensure that subjects can recognise a substantial number of "new" faces twenty minutes after encountering them for the first time. If a memory trace for the new stimulus exists after a period of twenty minutes then it can be concluded that this episodic trace alone is not sufficient to facilitate response upon a further encounter with the stimulus. A simple experiment was thus designed in order to clarify that the memory capacity for new faces was not exceeded in experiments one and two.

9.10 METHOD

Subjects: Eight young adults with normal or corrected to normal vision. None of the subjects had participated in experiments six or seven.

Apparatus: The same apparatus was used as in experiments six and seven.

Procedure: The pre-exposure phase of this experiment was identical to that in experiment two, with subjects making a famous/nonfamous judgement to a series of faces. Ninety-six faces were presented in this phase, 50% of which were famous and 50% of which were unknown faces. In the test phase of this experiment, subjects were instructed that they were going to see another series of faces and were asked to indicate whether or not they had already seen the faces in the prime phase of the experiment. Subjects answered yes or no on a score sheet and also indicated whether they were "confident" or "not sure" about their response. There was no time limit on the recognition decision.

9.11 RESULTS

The percentage hit rate corrected for false alarms was calculated for both famous and unknown stimuli. Eighty-seven percent of the famous faces were successfully recognised, while seventy-seven percent of the unknown faces were correctly recognised. See Table 9.6 for a summary of the raw hit rate and the hit rate corrected for false alarms. This difference between famous and unknown face recognition performances was found to be significant, ($p<0.01$).

9.12 DISCUSSION OF EXPERIMENT EIGHT

The resulting significant difference in famous and unknown face recognition in experiment three are unsurprising, given that internal representations for famous faces are presumably well established and additional semantic information (names, occupations etc.) may be retrieved as well as the visual memory for the face itself. This could aid later recognition - an advantage not enjoyed by unknown faces whose representations will be more context-bound. What is of interest with regard to these results is that performance on recognition memory for previously unknown faces (77% hit rate) makes it difficult to explain the lack of long-term reaction time priming with unknown faces in terms of a memory trace decay. 87% of the famous faces were successfully recognised, corresponding to an average response facilitation of 97ms in the previous experiments. 77% of the unknown faces were successfully recognised, with no corresponding facilitation in the previous experiments (a difference of 0ms). Assuming that the memory of a face contributes directly to a repetition effect, then the expected facilitation with unknown faces should be in the order of 86ms.

TABLE 9.6. Experiment eight,Raw and corrected hit rates (mean % across eight subjects) in face recognition task.

FAMOUS		UNKNOWN	
hits	false alarms	hits	false alarms
85	10	77	14.5
corrected hit rate		corrected hit rate	
87		77	

The fact that repeating an item has a much different effect on recognition memory than on a semantic task has been pointed out before, but in these cases, the repetition effect has been found to persist for lengthy periods in semantic tasks, while recognition memory for the same materials deteriorates over comparatively short periods of time (Jacoby and Dallas 1981, Jacoby and Witherspoon 1982, Scarborough et al 1977, Scarborough et al 1979, Tulving et al 1982). In the light of these previous findings, it has been suggested that two independent memory systems are being tapped by the two types of task - those memory systems being semantic and episodic. The recognition task would depend on an episodic trace which would not persist to a long delay. This however has not been the case in this experiment. The memory trace for previously unknown material has been shown to persist, but this trace does not facilitate response time on the next presentation. It appears then that a memory trace is laid down at the first presentation of an unknown stimulus but a previously existing representation of some sort is required for the priming effect to be observed. This obviously supports an explanation of repetition effects in terms of the modification of some kind of semantic information. The episodic information survives, but lack of access to semantic information results in the failure to observe a repetition effect.

9.13 GENERAL DISCUSSION

The repetition effect is most important to the distinction between episodic and semantic memory systems. The experiments reported here demonstrate a number of important points concerning repetition effects in face recognition. Supporting a semantic explanation like the face recognition unit theory are the large priming effects observed with familiar faces, which are independent of tasks employed in prime and test encounters. Also supporting a recognition unit explanation is the observed absence of a priming effect in reaction time from one instance of an unknown face to a later presentation. A purely episodic account of the repetition effect faces problems on the basis of this result, since the memory traces for the unknown stimuli were shown to be accessible to a much greater degree than indicated by the difference in reaction times between prime and test encounters. The interaction of the factors of pre-exposure and repetition on the processing of famous faces demonstrates the important fact that despite the large semantic contribution to repetition effects, these are not dissociable from episodic traces. It is possible then to suggest that the processing of faces in the long and short term is mediated by one system - in this case it would seem to be a semantic system with a subsystem incorporating an episodic component, like pictorial memory or visually derived semantic codes. Frequent encounters with the unknown stimulus could then lead to the establishment of a semantic recognition unit when the necessary links between the episodic and semantic codes are established, while no further encounters will lead to the ultimate decay of the trace. There would thus be no need to postulate any kind of separate systems of processing for familiar and unfamiliar faces, but rather a shared system with episodic and semantic components making relative contributions. The availability of some sort of unitised code in the case of the famous faces is an appealing explanation for the results obtained in this series of experiments.

When dealing with questions of how unfamiliar faces are processed and become familiar in time, it is important to note the differences between real-life encounters with individuals and the experimental situation using photographic stimuli. Almost inevitably, our first encounter with any individual will include seeing them from a few different angles. We will also have access to dynamic information about the face from varying expression and facial speech. In experimental situations like that reported here, there is but one single static encounter with the previously unknown faces. It is possible therefore to contend that what is being investigated is memory for pictures rather than face memory. In order to clarify the way in which faces are remembered and stored, it would be useful to provide more information at the priming stage, either by real-life or video encounters. This would not only increase the amount of visual information available, but would possibly contribute to the establishment of semantic information. The use of different photographs of the same individual for prime and test stimuli will also be useful in the context of this experiment. Effects of contextual change have been found for faces whose pose and expression were changed between prime and test (eg. Davies and Milne 1982). This would again be more indicative of a "facial" as opposed to "pictorial" memory. It is interesting to note that Davies and Milne found additive effects of pose and context change - consistent with independent effects at the level of pictorial and semantic codes. Perhaps the question that needs most addressing in the light of such results and those reported here, is that of the nature of the "transition" from the pictorial to the semantic in memory or the connections that necessarily need to be established between episodic traces and semantic information. While it is possible to propose that the two need not be distinct but interact at some stage of processing, it is still necessary to determine how a semantic system can be emergent from many pictorial or episodic instances.

SUMMARY AND CONCLUSIONS

There follows a brief overview of the experiments described in this thesis and the implications of their results.

Experiments involving the recording of event-related potentials (E.R.P.s) from the scalps of human subjects have demonstrated that when a stimulus word is repeated, this causes a modulation in the E.R.P. This modulation takes the form of a negativity associated with the first presentation of a stimulus, occurring at around 400 msec post stimulus onset. This 'N400' is attenuated when the stimulus is repeated. In EXPERIMENT ONE, evoked potential recordings were taken from two monkey subjects in order to explore whether this modulation of the N400 is related to basic memory processes, or is associated with processes not available to monkeys, such as verbal encoding of a stimulus. A series of familiar pictures were repeatedly used as stimuli, and the monkey's task was to respond to immediately repeated items. The waveforms elicited by non-immediate repeats were compared to those elicited by novel stimuli. No difference emerged between the compared waveforms. It was reasoned that the familiarity of the stimulus pictures to the monkey may have confounded any potential experimental effect. EXPERIMENT TWO replicated experiment one using sets of pictures which were unfamiliar to the two monkeys. In the case of one monkey, an effect of repetition was observed which took the form of an increased negativity peaking at around 400 msec post-stimulus in the E.R.P. elicited by the first presentation of a picture. There was no effect of repetition observed in the E.R.P. recorded from the other experimental subject. The finding of an effect in one monkey was hopeful, and implied that monkey evoked potentials can be sensitive to at least some aspects of repetition. The effect was not constant across monkeys or familiar/unfamiliar pictures. It was reasoned that this could be due to the nature of the stimuli used in experiments one and two. The pictures were of objects and scenes which would have been relatively meaningless to the monkeys.

EXPERIMENT THREE sought to investigate whether rendering pictures meaningless for human subjects would obliterate any effects of repetition, such as the modulation of the N400 component, on the E.R.P. Sixteen subjects were presented with two series of pictures; one series consisted of portrayals of a wide variety of complex objects and scenes, while the other series was rendered 'meaningless' by a process of pixellation. The subjects' task was to respond to immediately repeated stimuli. The waveforms elicited by non-immediate repeats (non-targets) were compared to those elicited by novel stimuli. With normal pictures, a reliable effect of repetition was observed, taking the from of a widespread increased negativity peaking at around 400 msec post-stimulus. This negativity was highly similar to that observed in studies employing words as stimuli. In the case of the 'pixellated' pictures, there was no effect of repetition. This result was interpreted as evidence that on stimulus presentation, some access to a meaningful code is necessary in order for repetition effects to emerge in evoked potentials.

Following on from this result, EXPERIMENT FOUR returned to monkey E.R.Ps, in the hope that presenting a more meaningful set of stimulus pictures would elicit repetition effects. For this experiment, only one experimental monkey was available. The monkey from which the repetition effect was recorded in experiment two could not be used due to the development of an epileptic condition.

The stimuli used in experiment four were a series of faces. Faces have been shown to be highly salient stimuli for monkeys and there is evidence for the existence of cells in the monkey brain which respond selectively to facial stimuli. The pictures were a series of photographic and line drawn faces, unfamiliar to the monkey. The experimental design was the same as that used in experiments one and two. Again, no effect of repetition was observed in the E.R.P. What did emerge in this case however was that on comparison of the E.R.P with that observed in experiments one and two, a positive peak (around 70ms) was evident, maximal at the posterior electrode site, which was greater in amplitude for facial stimuli. There was also a negative peak (118 msec), maximal at the frontal site which was also larger for the facial stimuli. Recordings from humans presented with facial stimuli have demonstrated a positive peak at around 150 msec. There is also some previous evidence of a face responsive peak in monkey brains. In order to further explore the existence of face-responsive evoked potentials in the monkey brain, EXPERIMENT FIVE involved the presentation of a series of faces, some of which were highly familiar to the monkey and the rest of which were unfamiliar. These were interspersed with pictures of objects. The faces were also repeated at times during the experiment in order to have another attempt at generating a repetition effect.

Again, no effect of repetition was evident in the E.R.P with either familiar or unfamiliar faces. There was however a positive peak (85-100 msec) which was selective for facial stimuli. This peak was maximal at the frontal site. The posterior recording site had developed faults so it was not possible to observe whether the effect was present in this area. The finding of a face-responsive peak was highly interesting, as it was present in both experiments four and five using very diverse facial stimuli. The failure to observe a repetition effect in the same experimental subject, even using familiar face pictures, points to the possibility that, at least in this case, some if not all of the factors that contribute to E.R.P repetition effects are denied to monkey subjects. It is possible that the ability to verbalize a stimulus is a necessary factor in order for consistent repetition effects to emerge.

Repetition effects are evident in behavioural as well as E.R.P measures. EXPERIMENTS SIX, SEVEN AND EIGHT sought to determine how behavioural indices of processing could be manipulated when familiar and unfamiliar faces are used as stimuli. In the first phase of experiment six, subjects were presented with a series of famous and non-famous face pictures, and were asked to rate them for attractiveness. Twenty minutes later they were shown another series of faces, some of which were repeats from phase one. Some of the faces were also repeated in this phase. Subjects made a famous/nonfamous decision about each face as it was presented. In the case of the famous faces, reaction time and accuracy were facilitated in phase two if the face had been previously seen in phase one. Faces seen twice in phase two were also associated with faster reaction time and accuracy. In the case of the non-famous faces, there was no effect of facilitation from phase one to phase two. There was however, a facilitation on repetition within phase two. This would seem to imply that in order for long lasting repetition effects to emerge, there needs to be some kind of pre-existing representation in memory for a stimulus.

EXPERIMENT SEVEN replicated experiment six, but the same task was used in both phases - that of a famous/nonfamous decision. This was carried out in order to determine that the results of experiment six were not due to a different task context from one phase to the next. The results were identical to those observed in experiment six. It was possible that repetition effects were not evident in the case of the unfamiliar faces due to an inability to remember a large set of unfamiliar new faces. Experiment eight demonstrated that subjects could in face remember up to 80% of the new faces. This ability however, did not manifest itself in a repetition effect. In conclusion, it is suggested that access to some meaningful memory code is necessary in order for behavioural repetition effects to be observed.

All the experimental evidence with regard to repetition effects in this thesis point to the necessity of access to some meaningful memory code. This is in contradiction with those explanations which see repetition effects as being purely episodic phenomena. The favoured candidate for explaining the results is that suggested by Feustel et al (1987) who proposed that differences in response facilitation across meaningful and non-meaningful stimuli may be due to an automatic generation of a 'unitized code` for meaningful/familiar stimuli that is not available for meaningless/unfamiliar stimuli. In essence, the repetition effect is due to *support* from episodic memory images but the main difference is due to the availability of a unitized code for familiar or meaningful stimuli. Newly created representations for unfamiliar or meaningless stimuli are not capable of producing a unitized identification response.

The pilot studies investigating repetition effects in monkey E.R.P.s , despite showing negative results in the main, point to the possibility of further investigation in this field. The use of some other kinds of stimulus material may lead to the emergence of a repetition effect. It may be however, that repetition effects are highly dependent on the ability to verbalize stimuli.

The positive and interesting result of the face-responsive peak in the monkey E.R.P. also points to potential future investigations. The combination of results from single-cell recordings and human E.R.P studies with monkey E.R.P results can make a powerful package in understanding how faces are processed.

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FIGURE LEGENDS

FIGURE 1.1. Crossing of two memory systems with types of processing.Most studies have investigated only the lower left and upper right cell combinations. From Roediger and Blaxton 1987.

FIGURE 1.2. Test conditions used in Blaxton (1985, experiment one).

FIGURE 1.3. Bruce and Young's (1986) functional model for face recognition.

FIGURE 2.1. Figure showing all standard positions of the ten-twenty electrode placement system. The figure represents the head drawn in one plane seen from above. The location of the Rolandic and Sylvian fissures are indicated. The outer circle was drawn to the level of the nasion and inion. The inner circle represents the temporal line of all electrodes. From Picton (1978)

FIGURE 2.2. From Rugg (1987). Effects of repetition on evoked potentials.

FIGURE 2.3. From Rugg and Nagy (1987). Waveforms elicited by legal and illegal non-words.

FIGURE 3.1. Typical experimental set-up for study of pattern-onset V.E.Ps. From Jeffreys (1989).

FIGURE 3.2. V.E.Ps recorded to half and full-field stimuli. From Jeffreys (1989).

FIGURE 3.3. Evoked potentials in response to known and unknown faces, geometric designs and pattern reversal. From Small (1983).

FIGURE 3.4. Laplacian responses associated with correct shape identification and the report 'no shape'. From Srebro (1985b).

FIGURE 3.5. Laplacian responses associated with reports 'a face', 'the face' and 'no face'. From Srebro (1985b).

FIGURE 3.6. V.E.Ps recorded from Cz electrode to the illustrated figures (a-g). From Jeffreys (1989).

FIGURE 3.7. Evoked responses to 'good face', 'poor face' and 'non-face' schematic line drawings. From Botzel et al (1989).

FIGURE 3.8. Evoked responses to face, chair and tree stimuli. From Grusser et al (1990), originally reported in Botzel and Grusser (1989).

FIGURE 3.9. Evoked responses to pictures of vases, faces, shoes and flowers. From Grusser et al (1990).

FIGURE 3.10. Evoked responses to previously seen and unseen faces. From Grusser et al (1990).

FIGURE 3.11. Evoked responses to learned and unknown flowers. From Grusser et al (1990).

FIGURE 3.12. Evoked responses to silhouettes of hands, face profiles and abstract figures. From Seeck et al (1989).

FIGURE 3.13. Evoked responses to animate and inanimate silhouettes. From Seeck et al (1989).

FIGURE 3.14. Evoked responses recorded from a Java monkey. Stimuli are rewarded and unrewarded monkey and human face stimuli. From Grusser and Fuhry (1989).

FIGURE 3.15. Evoked responses recorded from a Java monkey. Stimuli are rewarded and unrewarded monkey face and non-face stimuli. From Grusser and Fuhry (1990).

FIGURE 3.16. Populations of cells responsive to facial stimuli and associated authors. From Perrett et al 1990.

FIGURE 4.1. Examples of stimulus pictures stored on video disk used as stimuli in experiments one and two.

FIGURE 4.2. Example of stimulus sequence in matching-to-sample task. Task used in experiments one, two, three, four and five.

FIGURE 4.3. Experiments one and two. Accuracy scores for repeat non-target stimuli. Female (F) and male (M) monkeys.

FIGURE 4.4. Experiments one and two. Accuracy scores for novel non-target stimuli. Female (F) and male (M) monkeys.

FIGURE 4.5. Experiments one and two. Accuracy scores for repeat target stimuli. Female (F) and male (M) monkeys.

FIGURE 4.6. Experiments one and two. Average reaction time (RT) in milliseconds for target pictures. Female (F) and male (M) monkeys.

FIGURE 4.7. Experiment one. Grand-average evoked responses to novel non-target and repeat non-target familiar pictures. Female monkey.
No. of trials per condition: Novel non-target = 555, Repeat non-target = 401.

FIGURE 4.8. Experiment one. Grand-average evoked responses to novel non-target and repeat non-target familiar pictures. Male monkey.
No. of trials per condition: Novel non-target = 226, Repeat non-target = 164.

FIGURE 5.1. Experiment two. Grand-average evoked responses to novel non-target and repeat non-target unfamiliar pictures. Female monkey.
No. of trials per condition: Novel non-target = 356, Repeat non-target = 274.

FIGURE 5.2. Experiment two. Grand-average evoked responses to novel non-target and repeat non-target unfamiliar pictures. Male monkey.
No. of trials per condition: Novel non-target = 405, Repeat non-target = 316.

FIGURE 6.1. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat non-target normal pictures.
No. of trials per condition: Novel non-target = 417, Repeat non-target = 382.

FIGURE 6.2. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat non-target pixellated pictures.
No. of trials per condition: Novel non-target = 421, Repeat non-target = 370.

FIGURE 6.3. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat target normal pictures.
No. of trials per condition: Novel non-target = 417, Repeat target = 649.

FIGURE 6.4. Experiment three. Grand-average of evoked responses from sixteen subjects to novel non-target and repeat target normal pictures.
No. of trials per condition: Novel non-target = 417, Repeat target = 617.

FIGURE 7.1. Evoked responses to repeated presentations of known and unknown faces. From Debruille et al (1991).

FIGURE 7.2. Experiment four. Grand-averaged evoked responses to novel non-target and repeat non-target face pictures. Female monkey.
No. of trials per condition: Novel non-target = 326, Repeat non-target = 241.

FIGURE 7.3. Comparison of grand-averaged evoked responses to novel non-target face (experiment four) and non-face stimuli (experiment two).
No. of trials per condition: Novel non-target faces = 326, Novel non-target non-faces = 356.

FIGURE 8.1. Experiment five. Grand-averaged evoked responses to novel non-target and repeat non-target faces. Female monkey.
No. of trials per condition: Novel non-target = 143, Repeat non-target = 114.

FIGURE 8.2. Experiment five. Average reaction time (RT) in milliseconds for repeat target object and face pictures. Female monkey.

FIGURE 8.3. Experiment five. Grand-averaged evoked responses to novel non-target face and object stimuli.
No. of trials per condition: Novel non-target face = 143,
Novel non-target object = 181.

FIGURE 9.1. Experiment six. Average reaction times (RT) in milliseconds for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

FIGURE 9.2. Experiment six. Average error scores (maximum possible 25) sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

FIGURE 9.3. Experiment seven. Average reaction times (RT) in milliseconds for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

FIGURE 9.4. Experiment seven. Average error scores (maximum possible 25) sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

TABLE 4.1. Stereotaxic co-ordinates of electrode sites relative to saggital and interaural planes.

TABLE 4.2. Experiment one. Mean amplitude (v) at each electrode site for selected latency ranges of E.R.Ps from each picture condition. Female monkey viewing familiar pictures.

TABLE 4.3. Experiment one. Mean amplitude (v) at each electrode site for selected latency ranges of E.R.Ps from each picture condition. Male monkey viewing familiar pictures.

TABLE 4.4. Experiment two. Mean amplitude (v) at each electrode site for selected latency ranges of E.R.Ps from each picture condition. Male monkey viewing unfamiliar pictures.

TABLE 6.1. Experiment three (a). Reaction times (rt) in milliseconds and accuracy scores (% correct) for eight subjects in normal and pixellated picture recognition test. Immediate repeat scores and later repeat scores. Fa= false alarms.

TABLE 8.2. Experiment five. Average reaction time (rt) in milliseconds for repeat target face and object picture stimuli. Accuracy (% correct) across stimulus condition. Female monkey.

TABLE 9.1. Experiment six. Stimulus presentation conditions. ITEM = First presentation. R1 = First appearance in the test phase. R2 = Second appearance in the test phase.

TABLE 9.2. Experiment six. Mean reaction times in milliseconds of sixteen subjects across condition. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase after a twelve item lag.

TABLE 9.2(a). Experiment six. Median reaction times in milliseconds of sixteen subjects across condition. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase after a twelve item lag.

TABLE 9.3. Experiment six. Average error scores (maximum errors 25) for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

TABLE 9.4. Experiment seven. Mean reaction times in milliseconds of sixteen subjects across condition. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase after a twelve item lag.

TABLE 9.4(a). Experiment seven. Median reaction times in milliseconds of sixteen subjects across condition. Standard error in italics.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase after a twelve item lag.

TABLE 9.5. Experiment seven. Average error scores (maximum errors 25) for sixteen subjects in a famous/non-famous decision task.
R1 = First presentation in the test phase.
R2 = Second presentation in the test phase.

TABLE 9.6. Experiment eight. Raw and corrected hit rates (mean % across eight subjects) in face recognition task.