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The Visual-Paired Comparison Task; limitations of the novelty preference as an index of memory

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Abstract

The Visual Paired Comparison task (VPC) is an established methodology for measuring infant recognition memory. The standard index of memory in this task is the novelty preference - longer looking at a new stimulus. However, a growing number of studies report a preference for the familiar stimulus. This thesis explores the parameters within which the VPC task produces a novelty preference, examining the variables of movement, interaction and emotion at learning.

In Experiment 1, infants were habituated to a moving, colourful puppet held by an experimenter. Six-, 9- and 12-month-olds demonstrated an attenuated novelty preference; 18- and 24-months demonstrated a familiarity preference. Removing the human experimenter from view attenuated the novelty preference at 6-, 12- and 18-months when the habituation was live, and attenuated the novelty preference at 6- and 18-months when the habituation was on pre-recorded video.

In experiments 2-4, adults exhibited a novelty preference in the traditional VPC procedure and an attenuated novelty preference when there was social interaction with the stimulus. A static habituation face displaying emotion attenuated the novelty preference; a neutral habituation face and emotion displaying test stimulus resulted in a novelty preference.

Experiment 6 introduced the importance of accounting for cortisol levels in infant memory research. The relationship between cortisol, emotion and memory was examined, with emphasis on the regulatory role of the amygdala in the developing memory system.

This body of research demonstrates that conventional models of the medial-temporal lobe (MTL) memory system's involvement in the VPC are insufficient for explaining recognition memory performance in response to complex social or emotional stimuli. It is contended that the involvement of the amygdala in the non-typical VPC paradigms can account for the preferences reported here. A model integrating the amygdala with the MTL system is proposed for understanding recognition memory performance and the VPC.

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Chapter 1 – Introducing Visual Recognition Memory

The VPC – A Tool for Exploring the Abyss

In 1927, Piaget remarked that “The mental life of the infant is unhappily a mysterious abyss for the psychologist.” This is no longer true. Aspects of infant cognition, and the neurobiological substrates underlying it, can now be evaluated with confidence. Memory – the focus of this thesis – can be considered in terms of different memory typologies, the implicated neuroanatomical circuitry, the ontological pace and sequencing of such circuitry, and performance on a range of tasks over the first years of life. There is still, of course, much to be explored, but such data, when combined with that from adult studies, cognitive neuropsychological case studies, and animal studies, allow a broader picture of memory systems to be painted.

The study of the ontogeny of memory is a multidisciplinary field of research. An understanding of the neurobiology of memory is best reached through a combination of human adult studies with brain-damaged subjects, animal research with both infant and mature subjects, imaging research, and the cognitive study of normal human infants. Human infant and animal research both present similar challenges to experimental designers; memory tasks must be completely independent of the ability to understand language, and must also seek to minimise additional requirements on the part of the subject, both cognitive and motor. For example, the attentional demands of tasks designed for infants must not be too great; similarly, motor skills such as reaching for and

picking up objects must also be kept to a minimum, especially in methodologies intended for use with the youngest infants. Human adult studies, in contrast, are not limited by such factors, and often depend on relatively complex verbal instructions, for example concerning which of an array of stimuli the subject is required to select. For these reasons, typical adult studies are limited in how generalizable to infants the findings might be (Nelson, 1995)

Developmental cognitive research, then, must rely on ostensibly simple experimental design to measure the abilities of infants.

The type of memory examined most often in human infant research is *recognition* memory; in most research, *visual* recognition memory (VRM). VRM reflects the ability to visually discriminate between stimuli, enabled by prior exposure to one of these. It is VRM that will be the focus of this thesis. There are a number of methodologies employed in the measurement of VRM. Of these, one of the most basic and enduring methodologies is the Visual Paired Comparison task (VPC). The VPC task now constitutes a substantial proportion of cognitive developmental research with human infants; it was one of the first empirical tools developed to assess memory in infancy and its use is still widespread (for reviews see Pascalis & deHaan, 2004; Rose et al., 2004). It is a test of visual discrimination and in its most common form begins with a period in which the infant is habituated to a specific stimulus: after a specified delay, this stimulus is then re-presented at the same time as a novel stimulus. The infant exhibits memory by visually discriminating between the previously seen stimulus and the novel stimulus.

The VPC is one of the simplest possible memory tests, as befits a paradigm intended for use with extremely young infants, and is considered by many researchers to measure a

precursor to more complex explicit memory abilities, which develop over the first two years of life. Explicit memory is considered in detail below; put simply, it is conscious memory for prior experiences and is dependent on the function of a neuronal system centring around the medial temporal lobe. There is, however, some theoretical debate concerning the precise nature of the memory processes being measured in pre-linguistic humans. The consensus is that such tasks measure an early, developing form of *explicit* memory in the infant (Rose et al., 2004; Nelson, 1995; although see Snyder, 2002); this will be considered in detail later in the chapter.

The purpose of this thesis is threefold:

- To consider the extent to which the VPC can shed light on memory development
- To examine the utility of the VPC as a task to measure memory right across the human lifespan, and
- To evaluate the degree to which altering the parameters of the VPC can affect task performance and to consider the implications this has for understanding the memory systems necessitated by the task.

To fully consider the VPC as it is used today in infant research (and also in animal and human adult research) and what it can and can't tell us about memory development, it is first necessary to examine the origins of the VPC itself. It is also necessary to demonstrate how developments in memory research with adults and animals continue to inform infant research in providing a picture of the mature memory system, its ontogeny and sequence and pace of development. The VPC will also be briefly contrasted with other procedures commonly used to assess memory in infants. Before the current state of

such research is outlined, however, it is first necessary to review the different methodologies employed in the field, and the associated, dissociable forms of memory that can be observed in adult, infant and animal research.

Methods of testing human infants

The VPC

In a typical, modern VPC task (see Pascalis & deHaan, 2003) the subject is presented with a static image on a computer screen for a set period until habituation occurs. The same image is then presented simultaneously with a new static image. In the absence of prior exposure to either of the images, subjects spend an equal amount of time looking at the two images during the test. An attentional bias towards one of the images at test is taken to indicate memory for a previously seen image. The most commonly observed response that indicates recognition memory is a novelty preference. That is, if a subject remembers the habituation image they spend proportionally more time attending to the novel image. Indeed, the assumption of an intrinsic preference for novelty is central to the rationale of the VPC. One model upon which this rationale is based was developed by Sokolov (1963). Sokolov postulated that an *engram* is formed when a stimulus is attended to, which is strengthened with sustained or repeated exposure. Once sufficient exposure has occurred to develop a strong engram, the stimulus no longer attracts the subject's attention. A novelty preference in the VPC is thus evidence of encoding of the original stimulus to the extent that it is afforded less attention than the novel stimulus. Conversely, as the original stimulus is forgotten the engram will dissipate and the participant will attend to the previously familiar stimulus as novel.

Further more recent models seek to account for infant's attentional patterns when tested with the VPC. Hunter and Ames (1988) proposed a multifactorial model to account for infant preferences, based on 'optimal-level' theories which hypothesise that an organism intrinsically seeks an optimal level of stimulation and shows less attention to any stimulus that falls significantly above or below this optimum. Their model sought to account for the familiarity preference demonstrated by infants following less than complete stimulus familiarization. Thus, the process of familiarization is viewed as a continuum; as a stimulus is partially familiarized, infants will be motivated to attend to this stimulus if given the opportunity. When greater familiarization has occurred, the infant will instead be motivated to attend to the novel stimulus. Crucially, they argue that in the middle of this process is a null preference marking a transition in responding. Furthermore, Hunter and Ames (1988) argue that familiarization time, participant age and task difficulty can all impact on the duration required for each stage and the overall process, and that all three need to be taken into account in appropriately interpreting infant looking data.

McCall and McGhee (1977) forward the 'discrepancy hypothesis', which provides a similar but earlier account for infant looking preferences than Hunter and Ames (1988). They contend that the infant attends and affectively responds to new stimuli in an inverted-U pattern relating to the stimulus' 'physical or conceptual' discrepancy from a well-familiarized stimulus. Thus, stimuli eliciting the greatest attention are those that are moderately discrepant when compared to what the infant has previously experienced.

The final account of infant preferences was advanced by Wagner and Sakovits (1986), the *amodal code hypothesis*. This hypothesis was developed to account for the results of cross-modal VPC methodologies, in which infants demonstrate recognition of a stimulus when tested in a different modality to the familiarization period of the test. In essence, Wagner and Sakovits (1986) contend that infants' knowledge is stored in a modality-independent fashion. In other respects, their model is similar to Hunter and Ames, and makes similar predictions, such as; as stimulus complexity / salience increases, the probability of a familiarity preference will increase.

Despite debate regarding the type of visual preference which might be observed and the reasons behind this, VPC research now has a fifty year history, and initially grew from observations made by Robert Fantz. Firstly, in a 1956 study on chimpanzees, Fantz demonstrated that, when presented with paired stimuli, chimpanzees reliably fixated for different amounts of time on each depending on whether or not they had previously been exposed to them. Chimpanzees spent longer fixated on novel than on previously viewed stimuli. Secondly, in 1964 Fantz demonstrated that such a preference for novelty was also observable in human infants, and that furthermore the preference for a stimulus could be observed to diminish as images became less novel. Two photographs were simultaneously presented to infants for 60 seconds. One of these images was then presented again for a further 60 seconds, this time paired with a new image. A further eight 60 second presentations were made of the same image, paired each time with an image the infant had not encountered previously. Infants over 2 months old attended increasingly to the new image as the original image became less novel.

Fagan and the development of the VPC

Over the course of the 1970s, Fagan systematically unpacked the variables encapsulated within the VPC, exploring the ontogeny and development of recognition memory in the first year of life. He established that by 2 ½ months of age the novelty preference could be reliably observed when infants were tested with images of widely contrasting patterns (Fagan, 1970); stimuli differing only in the arrangement of subcomponents of a pattern were not distinguishable before 4 months. Similarly, infants were unable to distinguish between achromatic photos of faces at 4 months but were able to express a novelty preference by 5-6 months. Distinguishing between line drawings of faces was not possible even by 5-6 months (Fagan, 1972). Such findings illustrate the developmental trajectory of discrimination abilities and demonstrate that in the first half of the first year of life stimulus complexity is of paramount concern in experimental design.

When investigating the longevity of the recognition effect, Fagan observed that 5-6 month-old infants were capable of recognizing a photo of a face for up to two weeks. This could, however, be disrupted by presenting other similar stimuli in the interim, even after 1 minute delay in some cases (Fagan, 1973).

After establishing the presence of impressive (though fragile) recognition memory abilities in the VPC, Fagan began to address the variables that impacted on infant VPC performance. In initial recognition memory studies, 30-60 seconds fixation time to the habituation image was used to elicit a novelty preference in the test phase. Fagan (1976) tested infants with shapes, line drawings and achromatic photos at familiarization periods from five to 30 seconds and observed that necessary fixation time varied by stimulus type. For geometric shapes which can be easily discriminated, only 3.4 seconds of

fixation time was required; achromatic photos required at least 22 seconds, whilst face line drawings required at least 35 seconds.

A further variable concerned the degree of similarity required between the familiarization and test stimuli. In initial VPC studies, the two stimuli had almost always been identical. That is, what the infant saw at familiarization was an exact physical match with what would be presented at the test. Fagan (1976) demonstrated, however, that by 7 months infants can show recognition of a photograph of a man even though he had appeared in a different pose in the familiarisation stimulus. In a further series of experiments (Fagan, 1978), this variable was explored in greater detail. Seven month-old infants were shown a full-face photograph of a man paired with a $\frac{3}{4}$ profile of the same individual. When tested for recognition of this man paired with a novel man, a novelty preference was elicited. These findings indicate that by 7 months of age, infants are not just demonstrating picture recognition but have encoded a detailed representation of the stimulus experienced during familiarisation and can demonstrate some form of categorisation representation.

In an investigation of the types of stimuli suitable for eliciting recognition, Fagan (1977) compared photographs of faces and line drawings with very similar stimuli or with stimuli rotated by 180°. Six month-old infants experienced difficulty in recognition when the stimuli were most similar, and showed few memory problems when inverted stimuli were used as comparators. Furthermore, Fagan observed that, even with familiarization periods of 120 seconds, recognition could be disrupted immediately prior to test by even a 20 second presentation of distractor stimuli that were visually similar to

the familiarization and test materials. Recovery of the recognition effect could be observed, however, when a 60 second rest period was introduced before the test period.

Courage and Howe (2004) observe that Fagan's work produced three key findings that are still relevant today. First, it was possible to measure objectively the cognitive processes underpinning memory in young infants. Second, even very young infants were capable of visually attending to two stimuli and, crucially, of discriminating between these. Third, several of the variables that could be seen to impact on performance in adult memory tests, such as the role of stimulus complexity and familiarization time, are similarly important in infant methodologies (see Fagan, 1970, 1972, 1973, 1976).

It is inevitable that, over the past thirty years, some of Fagan's findings have been challenged and aspects of his methodology refined. For instance, less familiarization time is required to elicit recognition as infants increase in age. Rose (1983) demonstrated that 12 month-old infants required 50% less familiarization time than 6 month-old infants to produce a novelty preference (10 seconds versus 20 seconds.) Furthermore, the role of stimulus complexity alters with age; older infants prefer to look at more complex stimuli – for example patterns - than do younger infants (see Rose, 2004). The ability to recognise images that are degraded or altered versions of the familiarization stimulus (as evidenced by a novelty preference) also increases with age – by 12 months, infants were capable of passing tasks comprising line drawings missing up to 66% of their contour (Rose, Jankowski & Senior, 1997).

Many researchers have found that the familiarisation periods required even by infants of three months or younger are more in the order of 10 seconds than the 30 seconds or more previously adopted. Similarly, infants far younger than 5-6 months have

now been shown to reliably demonstrate a preference for novelty when presented with photographs of faces. Indeed, under the right conditions, the VPC is suitable for use with infants as young as three days old (Pascalis & de Schonen, 1994); a simplified Visual Preference task in which subjects are presented simultaneously with two images in the absence of a familiarization component is suitable for use with newborn infants (Kelly et al., 2005). Nevertheless, the fundamentals of Fagan's research programme have been demonstrated to be sound and form the bedrock of what is now a substantial research area.

Research has continued to explore further manipulations of the variables contained within the VPC (for reviews see Pascalis & de Haan, 2003; Nelson, 1995; Rovee-Collier, 1997; Rose & Feldman, 2004). Building on Fagan's work, several observations concerning performance on the VPC by infants of different ages have now been firmly established.

The VPC, then, demonstrates that infants are capable of visual discrimination from birth, and are capable of demonstrating memory from very early in life. Infant's abilities to remember more complex stimuli over longer periods of time and with shorter periods of initial exposure increase with age, such that by 18 months of age memories can be recalled after a duration of over two months (e.g. Hartshorn et al., 1998)

In addition to shedding light on the developing mnemonic capacities of infants, the VPC has also been employed to research category perception (Ross-Sheehy, Oakes & Luck, 2003; Quinn, 2002), to explore correlation between looking and attentional style and future intelligence (e.g. Rose, 1997), to investigate processing of three-dimensional

and/or moving stimuli (e.g. Hollich, 1998; Diamond, 1990; Courage & Howe, 2004), and to examine face recognition (e.g. Kelly et al., 2005; Walton, 1997).

With few exceptions, the findings of such research are in line with the original underlying rationale of the methodology. A novelty preference is regarded as evidence of memory; an absence of a novelty preference (or indeed the occurrence of a familiarity preference (i.e. preferentially looking towards the familiar stimulus at test) that *was* observed would be indicative of insufficient familiarization time. That is, if the infant fails to show a novelty preference it is usually assumed that they do not remember the familiarisation stimulus or that they failed to initially encode sufficient information about the stimulus. Such consistent findings have fuelled theorising about the putative automaticity of the mechanisms of pre-explicit memory. Whether or not such assumptions can go unchallenged is the subject of this thesis.

Before focusing exclusively on the VPC, it is important to place this paradigm within the context of other infant memory paradigms. Three paradigms used in visual recognition memory research are reviewed below before a summary of the current status of infant memory is considered.

The Delayed Non-Match to Sample (DNMS) Task

The DNMS task is a further tool for measuring explicit memory in human infants and has its origins in research with monkeys (e.g. Mishkin and Delacour, 1975). Due to the difficulties the task presents to human infants, the majority of its utility in elucidating the neurobiological basis of memory still comes from monkey research; human infants are unable to learn the task until 2 years (Diamond, 1990; Overman et al., 1990). In a

typical DNMS task, the monkey is habituated to an object, under which is a food reward. Then, after a short delay, the same object and a novel object are simultaneously presented. A food reward is now hidden under the *new* object; the familiar object is not baited with food. Over a series of training trials, monkeys are then trained to associate novelty with reward; memory ability is therefore demonstrated by obtaining the reward by successfully discriminating between the two stimuli and selecting the novel one.

Successfully retrieving food from the novel object in the test period is a skill that infant monkeys find difficult to acquire. 3-month-old monkeys cannot master the task even when delays are as short as 10 seconds (Bachevalier & Mishkin, 1984).

Performance of the task at adult levels is not observed until 1 to 2 years old (Bachevalier, 1990). This demonstrates that the DNMS task is a far harder task than the VPC. The most obvious difference between methodologies is that the DNMS, in addition to the visual recognition demands required by the VPC, places problem-solving demands on the subject (Alvadaro & Bachevalier, 2000). It is seemingly this task component – learning to use novelty as a cue for behaviour – that makes the task hard. Interestingly, however, Diamond, Churchland, Cruess and Kirkham (1999) demonstrated that 9 and 12-month-old infants *succeeded* in versions of the task in which tool use and motoric demands were minimised. When the reward object was attached by Velcro to the base of the stimulus itself rather than being hidden near or inside the stimulus, infants passed the test.

Similarly, when the reward was not an object at all, but praise and applause, infants passed. In a more typical version of the task, in which a reward object was located in a well beneath the stimulus, infants failed. Such findings suggest that the additional problem-solving demands of the standard task contribute to young infants' failure.

Mobile Conjugate Reinforcement

The mobile conjugate reinforcement task is a further methodology that has been used for over thirty years to measure memory in young infants (Rovee & Rovee, 1969; for review, see Rovee-Collier, 1997). In essence, the task works by exposing infants to a visual display and then allowing them the opportunity to demonstrate recognition of the same stimuli at a later stage. The dependent variable in this task is a motor behaviour; the leg-kicking response of infants. In a relatively complex procedure, infants are presented with a visual display (usually presented above them in the form of a mobile while they are lying face-up in an adapted cot) for a period during which their leg is attached by a ribbon to an empty hook on the cot that allows measurement of baseline kick rate and vigour. The infant is then afforded the opportunity, over several minutes across two days, to move the display by kicking (the infant's leg is now attached via the ribbon to the mobile apparatus). After a delay period, the recognition component of the test is conducted; depending on the exact methodology of a task, the infant is either again presented with exactly the same mobile they encountered during the habituation phase, or is presented with a mobile that is in some manner different from the mobile presented at habituation (usually number, type or colour of the stimuli on the mobile). Infants display recognition by kicking at a rate higher than baseline when presented with the experimental stimulus; if they fail to recognize the stimulus, kicking does not occur at a rate above baseline (Rovee-Collier, 1997).

The mobile conjugate reinforcement task has been used extensively to investigate the development of memory in early infancy and how altering the many different task parameters impacts on the expression of memory. Successful demonstration of memory

with this task is again a skill that improves with age. In a series of experiments with infants aged from 2 to 6 months, for example, Rovee-Collier and colleagues demonstrated that the maximum length of retention interval positively correlated with infant age (for review see Rovee-Collier, 1997).

Further variables explored in this manner include the role of interference. For example, when 3 month-old infants were habituated with mobile A and then tested with mobile B, in a 24-hour delayed recognition test of mobile A they failed to show recognition (Fagen, Morrongiello, Rovee-Collier & Gekoski, 1984). Such interference also occurs when the altered mobile causing the interference is displayed only briefly. When 3 month-old infants have been trained over two days on recognising mobile A, the mere exposure of mobile B for 3 minutes is sufficient to disrupt subsequent recognition of mobile A (Rovee-Collier, Borza, Adler & Boller, 1993). Such a striking effect of interference has also been demonstrated in 6 month-old infants (Muzzio & Rovee-Collier, 1996).

The number of training trials used has also been shown to have a substantial effect on recognition. With 3 month-old infants, each additional training session increased the period over which recognition could be discerned by 1 week; however, the magnitude of reactivation observed three weeks after training finished was unaffected (Ohr, Fagan, Rovee-Collier, Hayne & Vander Linde, 1989; Rovee-Collier, 1997).

Similarly, spacing effects have an impact; both 2 and 3 month-old infants show greater recognition 8 days after testing when the interval between training sessions was 2 days than when it was only one day (Rovee-Collier, Evancio, & Earley, 1995; Vander Linde, Morrongiello & Rovee-Collier, 1985).

Further variables examined and found to affect infant performance include: the amount of overall stimulus exposure time, the number of items in the visual array to be studied, the role of context, and the role of affect (see Rovee-Collier, 1997).

Deferred Imitation

A similarly well-established but more recent infant research methodology is the deferred imitation paradigm. Capitalising on the tendency of infants to repeat actions they observe, deferred imitation seeks to elucidate the characteristics of infant memory by observing how well infants imitate over time as various task parameters are manipulated. In a typical deferred imitation paradigm, the infant is shown a series of simple motor tasks involving a novel object; often some sort of toy that can be disassembled or reassembled in a discrete number of simple steps. Meltzoff (1985), for example, demonstrated to 24-month-old infants that a dumbbell-shaped toy could be dismantled. He found that 80% of the sample tested immediately could replicate what they had been shown; 70% of those required to wait 24 hours before demonstrating the behaviour could also replicate what they had been shown. At 14-months of age 45% of tested infants were able to replicate the modelled action following a 24 hour delay (compared to a control baseline of 7 %).

In further studies, Meltzoff demonstrated that even younger children had some capacity for deferred imitation, and that the capacity in older children was surprisingly advanced. Nine-month-olds were able to demonstrate deferred imitation over 24 hours (Meltzoff, 1988a), whilst 14-month-olds proved able to retain memory for 6 different novel actions for one week when they had observed them being modelled live by an

experimenter (1988b), and for 24 hours when they instead observed the actions demonstrated on television (1988c). Meltzoff also established the comparatively long-lasting nature of some to-be-imitated sequences; 14- and 16-month infants were shown to be able to retain memory for a sequence over 2- and 4-month retention intervals respectively (Meltzoff, 1995). In addition, Meltzoff demonstrated just how early the precursors of imitative behaviour are observable; 6 week-old infants, under certain circumstances, will imitate facial expressions and head movements and can retain these for 24 hours (Meltzoff & Moore, 1994).

Hayne and colleagues (Collie & Hayne, 1999; Hayne, MacDonald, & Barr, 1997; Herbert & Hayne, 2000a, 2000b) have conducted more systematic investigation of the developmental trajectories of imitative abilities between 6- and 30-months of age. Whilst even the youngest infants demonstrated some capacity for deferred imitation with a 24 hour delay, 6-month-olds required twice as much initial exposure as older infants, and even so were less accurate in demonstrating actions than were older infants (for review see Hayne, 2004). Furthermore, generalizing modelled actions to a visually distinct but functionally comparable object was not an ability that infants younger than 18 months demonstrated robustly. The period over which sequences could be retained similarly increased as a function of age; 18-month-olds were able to recollect a three-step sequence for 14 days, whereas 24-month-olds could demonstrate retention over 3 months (Herbert & Hayne, 2000b).

In summary, then, what has been learned from infant memory procedures is that, across paradigms, there is an increase in the rate of learning and the duration of retention as age increases. There is a need, however, for more substantive comparison across ages, and

greater consideration of exactly what sort of memory the different paradigms are measuring. Central to such concerns is the terminology of memory research; this will now be explored.

Explicit, Declarative, Implicit, Nondeclarative and Procedural – the Terminology of Modern Memory Research

One of the most important distinctions in current memory research is drawn between two separate memory systems. A dissociability between two different memory systems was first demonstrated in research with amnesic patients, which demonstrated that some learning *could* still occur in patients who were ostensibly unable to acquire new knowledge (most famously, patient HM – see Manns, 2004; Postle & Corkin, 1998; Smith, 1988).

One of these systems is associated with conscious recollection and relies on a circuitry of neural areas including several components of the medial temporal lobe; the other is more of an umbrella term, categorising a variety of nonconscious types of memory relying on subcortical pathways. Two different terminologies describe this distinction. The two systems are described either as *explicit* and *implicit* memory, or as *declarative* and *nondeclarative* (or sometimes *procedural*) memory. The former pair of terms originate with Graf and Schacter (1985); the latter with Cohen and Squire (1980). To most researchers, however, the pairs of terms are interchangeable (although see Hayne, 2004). For sake of ease, the terms *explicit* and *implicit* will be used here.

Implicit memory is a somewhat nebulously defined phenomenon. Schacter, Chiu and Ochsner (1993) define ‘implicit memory’ as a descriptive label intended to refer to

one way in which the influence of past experiences can be expressed unintentionally and without conscious recollection during subsequent task performance. The defining feature of implicit memories is that they are not accessible to consciousness (i.e. the act of learning itself cannot be remembered). Skill and habit learning, conditioning and priming are all examples of implicit learning. Implicit memory is thus assessed through performance rather than by overt questioning about knowledge (for reviews, see Gabrieli, 1998; McKee and Squire, 1993; Rose et al., 2004).

Explicit memory, on the other hand, constitutes conscious recollection of previous experiences; the individual consciously retrieves memories and is aware of doing this. In adults, it is most often assessed with tests employing recall and / or recognition methodologies (i.e. explicitly asking the subject to make a response based on what they remember). Furthermore, it has been robustly demonstrated to be dependent on neural circuitry within the medial temporal lobe (MTL) (for reviews, see Bauer, 2004; McKee & Squire, 1993; Nelson, 1995; Squire & Zola, 1997) (see figure 1)

An important distinction between the two systems is that, in implicit memory, learning is more likely to occur gradually over many trials; explicit memory, on the other hand, is specialized for very rapid learning (Bauer, 2004). It is this specialization that allows for the methodologies such as the VPC and the DNMS to be employed in assessing such processes. It is the declarative memory system, then, that is the system of interest here. Whilst implicit memory is a more varied research topic than explicit memory, there is a body of evidence that strongly supports the assertion that the two memory systems are distinct. Manns, Stark and Squire (2000) found that VPC performance was predictive of subsequent performance on a recognition task in healthy

adults, whereas performance on a priming task was uncorrelated. This suggests that the mnemonic processes required by the VPC have a commonality with those demanded by explicit memory tasks, and not by implicit memory tasks. Further evidence for this dissociation is provided by bodies of literature obtained from animals and from stroke patients. This literature demonstrates that whilst explicit memory is dependent on hippocampal and diencephalic structures, implicit memory tasks can still be passed in patients with explicit memory problems and lesioned animals (for a review, see Zola-Morgan and Squire, 1993). Schott et al. (2005) recently demonstrated this dissociability in an fMRI study with adults. In word completion tasks, priming was associated with decreases in activity in the left fusiform gyrus and frontal and occipital regions bilaterally; explicit memory tasks, however, were associated with increases in left frontal areas and in parietal and temporal areas bilaterally. Schott et al. (2005) concluded that implicit and explicit memory systems have distinct functional neuroanatomies. The extent to which the VPC can be seen to be a measure of explicit memory per se is, however, the cause of some debate (see Nelson, 1995). It is necessary, therefore to consider explicit memory in greater detail.

Neurobiological Development – Just How Explicit is Explicit Memory?

Infant memory research seeks to elucidate how cognitive mnemonic abilities develop from birth to maturity in the human. To this end, it is important to be aware of the sequencing, pace and development of the neurobiological development underpinning such abilities. Such awareness also informs the sort of tests suitable to use with an infant

population, and the degree to which infant findings are generalisable to adults (and vice versa). Whilst lesion case studies with adults have provided a degree of insight into the neurobiology of memory, there is a limit to how far it is sensible to assume that this will represent how the intact, developing system works. Carver and Bauer (2001) observe that “infants are not lesioned adults,”; as a developing brain is qualitatively different to a grown and subsequently injured brain, behavioural studies with infants are also critically important in understanding the development of the neural structures involved in memory.

The structures held to be necessary for recognition memory in humans are summarised in figure 1, and include the hippocampal region and the entorhinal, perirhinal and parahippocampal cortices.

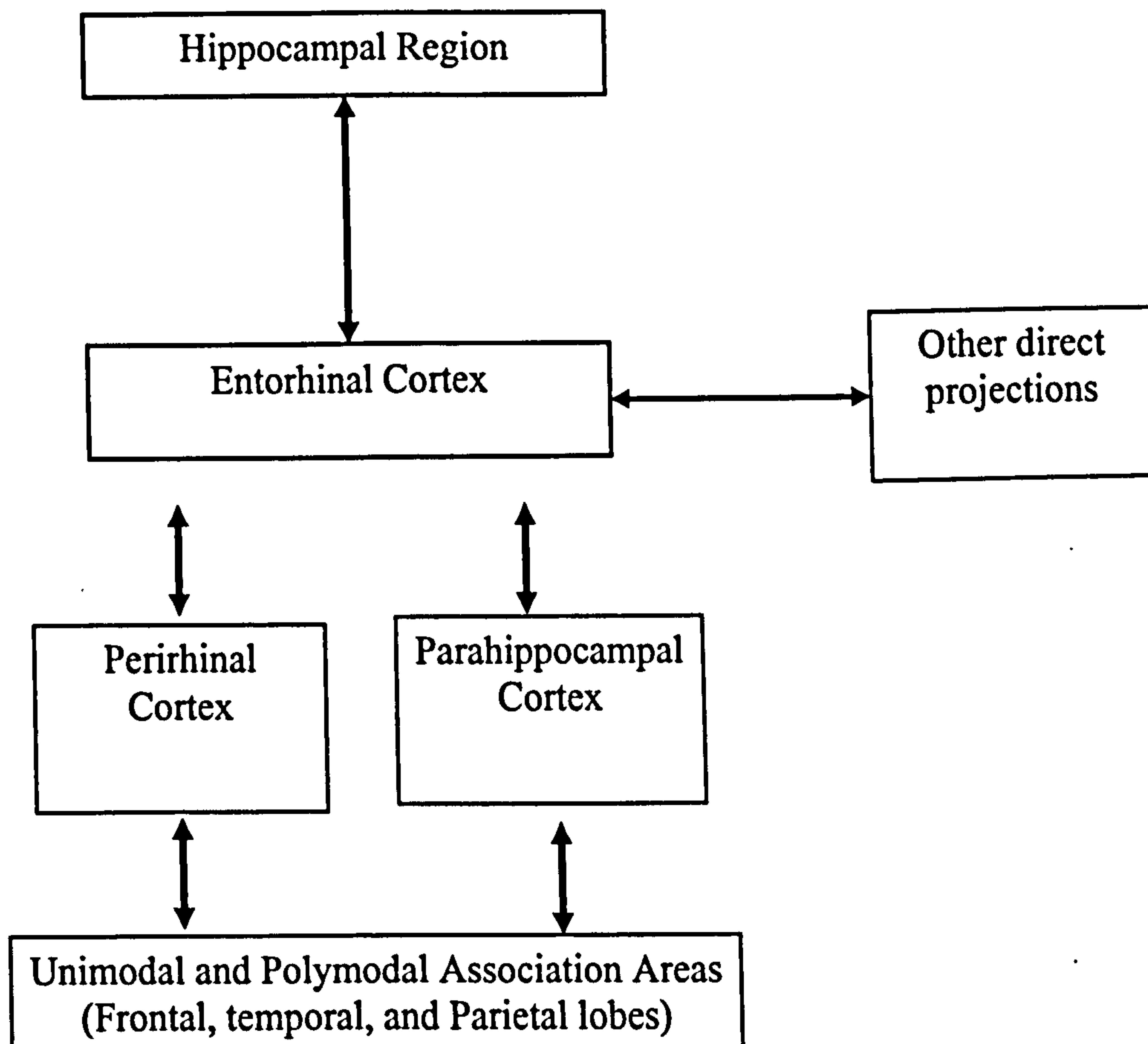


Figure 1: schematic diagram of the principal neural structures and pathways necessary for visual recognition memory in humans and nonhuman primates (Herbert & Pascalis, 2007)

It is clear that the structures that will comprise the MTL memory circuitry in adults develop at substantially different rates during infancy. In a review of the literature, Bauer (2004) observes that a large proportion of the MTL system develops early in life. For example, the majority of the cells comprising the hippocampus are formed in the first half of gestation; by birth, almost all of these are in the location in which they can be found in

the adult brain (Seress et al., 2001). Neuronal hippocampal synapses begin to form by 15 weeks gestational age. However, the number and density of synapses, as well as the size of surrounding limbic structures, do not reach adult levels until approximately 6 months postnatally (Seress et al., 2001; Kretschmann, Kammradt, Krauthausen, Sauer & Wingert, 1986).

Whilst the majority of the hippocampus reaches maturity at a young age, the dentate gyrus of the hippocampus takes longer to develop. Approximately 30% of the dentate gyrus' cells are produced postnatally, and it is not until 12-15 months of age that the morphology of the structure resembles that found in adults (Seress et al., 2001).

The thalamus is another structure that matures quite early (Carver & Bauer, 2001). At least some functionality must be present in the thalamus from birth; infants with bilateral thalamic lesions are severely impaired in terms of motor skills and die very early in life (Eicke, Briner, Willi, Uehlinger & Boltshauser, 1992). Similarly, the entorhinal cortex (the structure connecting the hippocampus and the cortex in which memories are ultimately stored) has already begun to form synapses by mid-gestation in the monkey (Nelson, 1995; Berger & Alvarez, 1994).

In contrast to such subcortical structures, cortical areas of the infant brain are slow to develop. Association areas of the frontal cortex are held to be where long term information is ultimately stored. It is argued that the role of the hippocampus is to bind together aspects of multimodal information and consolidate them (see Manns & Eichenbaum, 2006; Eichenbaum, 2001, 2003); as projections to association areas are strengthened over a period of time (sometimes months or longer), memories can initially be recalled independently of the MTL system (therefore accounting for amnesia caused

by MTL damage not effecting previously well-stored memories). Infantile amnesia – the phenomenon whereby memories of the first few years of life are characterised by their absence – can be argued to be caused by such cortical immaturity. All six neuronal cortical layers are not discernible until the 7th month of life (Bauer, 2004). Synapse density does not peak until 15-24 months whilst pruning to adult levels does not occur until puberty (Huttenlocher & Dabholkar, 2001). Myelination in the frontal cortex continues into adolescence (Benes, 2001).

It is clear, then, that the structures necessary for fully-fledged explicit memory ability are not fully functioning from birth. Such findings provide an explanation for the increase in memory ability as measured by the VPC over the first few months of life.

The neurological substrates of other memory tasks are less clear; they will now be summarised.

Functional Maturity Differs Between Infant Memory Methodologies: Substrates of the Delayed Non-Match to Sample Task

There is little doubt that the neurobiological underpinnings of the DNMS task are the same MTL, declarative memory circuitry underpinning successful performance on other memory tasks. Monkey lesion studies demonstrate that damage to the MTL system disrupts task performance on a sliding scale of severity dependent on the neural locus of lesioning. Damage to areas TE, and to the entorhinal and perirhinal cortices, and solely to the perirhinal cortex, severely impair DNMS performance (Alavadro & Bachevalier, 2000; Bachevalier & Mishkin, 1994; Horel et al., 1987; Suzuki et al., 1993; Zola-Morgan et al., 1989). Parahippocampal lesions to area TH and TF damage performance in a

limited manner (Nemanic et al., 1998). Alvarado and Bachevalier (2000) conclude that, for the DNMS as for the VPC, “the MTL cortical areas play a key role in both the acquisition and performance of the task.” DNMS performance is equally poor in human amnesic subjects (Squire, Zola-Morgan & Chen, 1988).

Reviewing the evidence, Nelson (1995) observes that human infants fail the DNMS task until they are 12-15 months old. At this age, they require extensive training to perform the task (Overman, Bachevalier, Turner & Peuster, 1992). By 18-32 months, less training is necessary, although performance still falls well short of adult levels. Similar developmental changes are observed in the monkey. Monkeys only begin to perform the task at 4 months, and do not reach adult levels of performance until 1 year (Bachevalier & Mishkin, 1994). Nelson (1995) observes that when a ratio of 4 monkey years to one human year is observed, the monkey and human data correspond well regarding the age of onset of ability. Interestingly, infants *look* appropriately at the novel stimulus in the DNMS by 6-12 months (Diamond, 1992); this strongly suggests that the motor requirements of the task preclude it from being used to study VRM early in human development.

Substrates of the Mobile Conjugate Reinforcement Task

The mobile conjugate reinforcement task has been used to great effect to explore the nature of early memory. There is ongoing debate, however, concerning the type of memory that is being measured with this paradigm. Some researchers contend that, along with the VPC, the mobile conjugate reinforcement task measures the developmental beginnings of explicit memory (Gerhardstein, Adler & Rovee-Collier, 2000; Adler,

Gerhardstein & Rovee-Collier, 1998). Rovee-Collier herself (1997) argues that separate components of the mobile conjugate reinforcement paradigm measure implicit *and* explicit memory. The version of the task employing *reactivation*, is proposed as a measure of implicit memory. The reactivation task briefly re-exposes the infant to the same mobile following a relatively short delay, in essence reactivating the memory as forgetting begins to occur. Rovee-Collier argues that this in essence analogous to a priming methodology in which adult subjects show greater memory for stimuli following a brief re-exposure. The longer-term, full re-exposure that forms the delayed recognition component of the task, however, is held to be a measure of explicit or declarative memory due to its similarity to other explicit paradigms (Rovee-Collier, 1997).

A corollary of task complexity is that it is currently impossible to determine the neural substrates of the mobile conjugate reinforcement task, given the strong motor component and the comparatively large amounts of physical training inherent in the methodology.

Substrates of the deferred imitation task

It perhaps seems intuitive, given the nature of what infants are required to do, that the most consistent claim made for the deferred imitation paradigm is that it measures explicit or declarative memory capabilities (Nelson, 1995, 1997; Schacter & Moscovitch, 1984). Infants are clearly required to remember a series of visual memories, and after a delay to translate these memories into motor behaviour. It would be difficult to postulate that such a set of requirements could be met by any sort of implicit memory system.

Gross et al. (2002) argue that not only is the deferred imitation paradigm a nonverbal test

of fully-fledged explicit memory, but that given the equivalent performance infants in their series of studies demonstrated on the mobile conjugate reinforcement task, both tasks can in some manner be viewed as functionally equivalent measures of explicit memory capacities.

Tests of deferred imitation are measures of explicit memory that become passable in the second half of the first year of life. In essence, such tasks involve a researcher demonstrating a series of actions to an infant - typically three actions in a row, such as removing a glove containing a bell from a hand puppet, shaking the glove, and then replacing it on the puppet (Barr, Dowden & Hayne, 1996). The infant is then 'invited', following a delay, to replicate the actions – they are presented with the same objects, typically in the same location. Task variations include changing the context between demonstration and test in some manner, and changing aspects of the props themselves in order to infer the degree of generalisability possible with such learning. It is well established that by 12 months of age, infants can robustly demonstrate learning through the deferred imitation paradigm. The temporal period over which infants are able to correctly recall the sequence of actions they have been shown changes as a function of age. Bauer, Hertsgaard and Dow (1994) demonstrated that 16 – 18 month infants are able to remember a sequence of events in a deferred imitation paradigm (in addition to the events themselves) for as long as 8 months. In a further study, Bauer, Wenner, Dropik and Wewerka (2000) tested infants aged 13, 16 and 20 months of age. The eldest group remembered both the actions themselves and the temporal sequencing of events after a delay of 12 months (the longest tested). In contrast, the youngest age group only remembered the sequencing of actions for 3 months.

Deferred imitation research with infants in the first year of life demonstrates that the ability to recall actions themselves, and particularly the temporal sequencing of such actions, is markedly impaired. Carver and Bauer (1999) tested 9 month-old infants, and found that whilst they were able to recall the actions of a two-step sequence over a one-month delay, the majority were unable to recall the order in which the actions occurred.

Research with 6 month infants shows poorer performance still. Barr et al. (1996) tested such an age group on a three-step sequence with a 24-hour delay, and found that whilst 75% of those tested could recall one step of the sequence, only a quarter could recall more than one.

In a series of adult studies, McDonough, Mandler, McKee and Squire (1995) demonstrated that passing the deferred imitation task relies on declarative memory structures. Amnesic patients with damage to the hippocampal formation performed at chance when presented with the objects from a deferred imitation task they had been shown the previous day. In contrast, frontal lobe patients and healthy controls both succeeded on replicating on day 2 what they had previously been shown. Such a finding clearly demonstrates that successful completion of the deferred imitation task relies on MTL structures.

Is the VPC a Qualitatively Different Task to Other Human Infant

Methodologies?

It is clear, then, that whilst the human infant is far from being the *tabula rasa* s/he was considered to be by the first empirical investigators (e.g., Piaget, 1927), at birth the explicit memory system found in the adult is not fully functional; furthermore, it cannot

be expected to perform in an adult-like manner until each of the system's components, and the neuronal connectivity between these components, is functionally mature – towards the end of the first year of life at the earliest (Bauer, 2004).

McKee and Squire (1993) also suggest that immaturity of the limbic-diencephalic structures (Bachevalier & Mishkin, 1994) involved in the MTL circuitry in the normal adult is the reason why infants fail on tests of declarative memory such as the DNMS until at least two years of age. Damage to such structures in the adult leads to amnesia and failure on tests of declarative memory (McKee & Squire, 1993; Pascalis et al., 2004). The neurobiological data, then, would predict that tests of explicit memory would only be passed by infants that were, at the youngest, several months old. This prediction is borne out by the several strands of behavioural data elucidated above.

Gross, Hayne, Herbert and Sowerby (2001) have demonstrated the non-equivalence of both the conjugate mobile reinforcement task and the deferred imitation paradigm when compared to the VPC. Six-month-old infants, despite showing no recognition for stimuli in a version of the VPC, did however show memory in both the mobile conjugate reinforcement paradigm and in the deferred imitation paradigm. It is clear, then, that the conjugate mobile reinforcement task is *not* an equivalent test of preexplicit memory to the VPC. This finding does, however, suggest that the most appropriate use of the task is a topic of ongoing theoretical concern.

What emerges in the DNMS and deferred imitation literature, then, is a picture of infants only able to perform reliably on tasks by the end of the first year of life. The visual-paired comparison task (along with the mobile conjugate reinforcement task), however, is suitable for use with infants from birth and robustly demonstrates evidence of

memory under normal conditions from this time. There is clearly a difference in task complexity between the VPC, which relies in simple looking behaviour, and most other tests of explicit memory which require complex motor behaviours such as reaching, kicking and reproducing actions. A task for researchers in the area is to discern the precise nature of this difference. In short, if the VPC does indeed measure explicit memory, why are other tests of explicit memory not passed until at least several months after the VPC?

It is possible, of course, that what differentiates the VPC from other tests of explicit memory is the degree to which all other tests rely on motor control on the part of the subject. Such a theoretically uninteresting account can be ruled out as the sole cause of the difficulty experienced by younger infants, though; adult lesion studies and animal studies demonstrate that damage to the MTL compromises task performance. In the case of deferred imitation, McDonough, Mandler, McKee and Squire (1995) tested amnesic adults and found that they fared no better at replicating a temporal sequence of actions than control patients who had never observed the actions. The DNMS has also been demonstrated to rely on the MTL in the animal literature; lesioning the MTL in adult monkeys and in rats impairs DNMS performance (Mishkin, Malamut & Bachevalier, 1984; Mumby & Pinel, 1994). As has already been noted, infant monkeys also fail the DNMS until 1 year of age, despite having motor control far superior to that of human infants at a comparable age (Bachevalier & Mishkin, 1984).

If motor control is not the only reason that successful VPC performance occurs much earlier than successful performance on other tests of explicit memory, another explanation must be found.

One possibility is that, whatever the VPC is measuring, it is not an aspect of explicit memory. Given that other explicit tasks are not passed until the latter half of the first year of life, and that successful performance on these is dependent upon MTL circuitry that is still very much developing in the first few months of life, there might on first consideration seem to be a degree of justification for positing that the VPC does not tap explicit memory. Such an argument might also be thought to find support in the fact that the VPC is quite obviously on some levels an *implicit* task. This, of course, is necessitated by the experimental populations with which the VPC is used. A typical declarative memory task used with adults involves verbal instruction, for example to press a certain keyboard key if a presented stimulus has been seen before during the test. Such instruction cannot be given to pre-linguistic infants or to animals, and as such the test is an implicit one. It is not logical, however, to conclude that because a test is not itself explicit, it cannot be measuring explicit memory. Most obviously, none of the other infant methodologies outlined above are truly explicit in design, but the supporting animal, imaging and lesion studies provide evidence beyond reasonable doubt that the structures subserving the cognitive abilities required to pass such tasks are dependent on the same structures that comprise the declarative memory system (and, crucially, *do not* comprise the implicit memory system). The same is true of the VPC. Adults with damage to the MTL experience difficulty with the VPC (McKee & Squire, 1993), as do animals with MTL lesions (Bachevalier, Brickson & Hagger, 1993; Pascalis & Bachevalier, 1999; Zola et al., 2000; Nemanic et al., 2004). Such findings have led some researchers to question the appropriateness of stipulating demonstrable conscious recall as the principle criterion of explicit memory (Courage & Howe, 2004).

An alternative account of the cognitive processes tapped by VPC in young infants is offered by Nelson (1995). He suggests that one way to theoretically account for the difference in age at which different memory tasks are passed is to postulate that memory processes that are present from birth are dependent on the hippocampus and differ qualitatively from those that emerge towards the end of the first year of life.

Other researchers have considered the possibility of a qualitative difference between the abilities required for the VPC and for more complex tasks. Alvarado and Bachevalier (2000) argue that the hippocampal memory may in fact be comprised of a number of functional mnemonic modules which mature at different rates.

One of these distinct components, it is argued, is the necessary component for passing the VPC; this component is dependent on 'reflexlike' abilities controlled by the hippocampus (Nelson, 1995). Citing Event Related Potential (ERP) results demonstrating that before 6 months the infant brain appears unable to differentiate between visual stimuli presented frequently, stimuli presented infrequently and novel stimuli (Nelson & Collins, 1991, 1992), Nelson argues for the existence of two types of memory processes observable in the infant. The ontogenetically earlier of these depends on hippocampal and other MTL structures, and produces novelty preferences that are reflexive in nature. During the later months of the first year of life, a second process develops and supplants the former. This form is explicit memory proper, and relies on additional cortical areas as well as on the increasingly mature MTL regions. The earlier form, Nelson proposes, is more 'primitive'; he terms this *preexplicit* memory.

Nelson's preexplicit model seems, then, to be a way of accounting for the different abilities required for different memory tasks, and the neuronal architecture available at different stages of the first year of life.

Central to the theory of pre-explicit memory is the novelty preference as a sign of recognition memory. There exist, however, a number of studies that demonstrate a familiarity preference rather than a novelty preference in young infants. Such findings are potentially challenging for the preexplicit model in that they can be argued to cast doubt on the 'reflexlike' performance of this system. At the least, such findings require greater clarity of the preexplicit memory model concerning exactly how a reflexlike system can be expected to behave and under what conditions this might hold true. These findings will now be considered.

VPC data analysis

VPC data are typically simplistic and require no more than a t-test to be analysed. The task's limitations lie in the fact that the number of trial each participant is limited by the age of infants tested and also by the fact that, when testing adults, it is not feasible to have adults doing too many trials of visual search without instructions. Typical sample sizes in the field, however are between ten to thirty participants (although experiments in which over 100 infants have been tested have shown similar results; see e.g. Jacobson, Fein, Jacobson, Schwartz, & Dowler, 1985). As several of the studies conducted in this thesis will involve age group or condition comparison, a conservative approach to the analysis would be to enter both condition and stimulus as variables in a factorial ANOVA. In this case evidence that the effect of stimulus varied across condition would be indexed by a significant interaction. Given the low statistical power afforded by the

sample sizes achievable in this type of research, however, a common approach is to explore the data with separate analyses of the effect of one variable at a time (see Bahrick, Moss & Fadil (1996); Cassia, Simion & Umilta (2001); Fagan (1974); Fagan (1978); Gross, Hayne, Herbert & Sowerby (2002); Kelly, Liu, Ge, Quinn, Slater, Lee, Liu & Pascalis (2007); Kelly, Quinn, Slater, Lee, Gibson, Smith, Ge & Pascalis (2005); Morales, Mundy & Rojas (1998); Pascalis, deHaan, & Nelson (2002); Pascalis, Hunkin, Holdstock, Issac, & Mayes (2004); Quinn, Yahr, Kuhn, Slater, & Pascalis (2002); Quinn, Uttley, Lee, Gibson, Smith, Slater, & Pascalis (in press); Rose, Gottfried, Melloy-Carminar, & Bridger (1982); Simion, Farroni, Cassia, Turati, & Barba, (2002); Walton, Bower, & Bower, (1992)). Although this approach leaves the analysis more vulnerable to Type I errors, it provides more power to identify effects of theoretical interest, the replicability of which may be tested in future research. Thus, the experiments reported in this thesis will employ t-test analysis.

The Cornerstone of the VPC – the Novelty Preference – Reconsidered

It would seem, then, that much of the evidence from the human infant literature supports several of the theoretical claims that have been expounded here. The VPC elicits novelty preferences from infants as young as a few days old (Slater, Morrison & Rose, 1983; Pascalis & de Schonen, 1994) and in a simplified form is suitable for use with newborns (Kelly et al., 2005). In turn, the VPC seems to be dependent on aspects of the MTL memory system found in adults. The hippocampus, thalamus, and entorhinal cortex *are* well-formed at birth; the dentate gyrus, limbic-diencephalic structures, and the frontal association cortex are not. Tests such as the DNMS, and arguably deferred imitation,

cannot be passed in the first few months of life, thereby indicating that the ability to perform such tasks depends, at least in part, on the development of other components of the adult explicit memory system and the connectivity between these.

Such observations have led to the suggestion that what is measurable in infants in the first few months of life is a memory system that is a precursor to the fully-fledged MTL system. It is suggested that this *preexplicit* memory system has certain properties that render it distinct from later-developing systems (Nelson, 1995). Crucially, it is contended that “novelty preferences early in life *may be reflexive or obligatory in nature* ... memory inferred from novelty preferences, despite being dependent on hippocampal or related structures, may thus differ quantitatively from memory as evaluated in the DNMS task” (Nelson, 1995; italics added). The preexplicit system, according to this view, is critically dependent on the hippocampus and rhinal cortex, and becomes more functionally mature as the cortical structures necessary for explicit memory proper, such as the inferior temporal cortex, develop (Nelson, 1998.)

It is, of course, the case that the assumption of an intrinsic preference for novelty in infants has been part of the rationale of the VPC since its inception. Indeed, it is argued that the ‘defining feature’ of visual recognition memory is a biologically adaptive preference to novelty (Rose et al., 2004). A full account of infant attention during visual recognition tasks is, however, rather more complex than this. Hunter and Ames (1988) multifactor model, for instance, which was described earlier proposed that the timing of the observed shift from familiarity to novelty preference is dependent on infant age and on stimulus complexity as well as on familiarization time.

An important aspect of the preexplicit model, however, is the concept of hippocampal-driven automaticity.

If an ability is 'reflex-like', it should be expected to be extremely robust. However, findings of familiarity preference are now not uncommon in the field. Task parameters, even when changed slightly, are capable of disrupting the novelty preference. If it *is* a reflex like ability, then it is perhaps a surprisingly fragile one.

A number of different studies have consistently shown that the reality is more complex than an inevitable finding of a novelty preference in human infants. Some of these findings gel well with the traditional theoretical account propounded in the literature. For example, full encoding appears to be a prerequisite for novelty preferences; shorter familiarisation periods are more likely to result in a familiarity preference being expressed (Slater, 1995). Furthermore, younger infants habituated with complex stimuli show a similar familiarity preference (Sophian, 1980). Similarly, Rose (1982) demonstrated that the switch from familiarity preferences (caused by limited habituation) to novelty preferences is a function of the length of habituation period, and not of age per se. In a study employing a 30 second familiarization period followed by a 20 second test period, 3 ½ month-old infants demonstrated a familiarity preference, whilst 4 ½ and 6 ½ month-olds displayed a novelty preference. In a further experiment in which the familiarization period was manipulated, both 3 ½ month-olds and 6 ½ month-olds showed a familiarity preference following limited exposure (10 and five seconds respectively), switching to a novelty preference at 30 and 15 seconds respectively.

Such findings are supported by Sokolov's initial theorising and Fagan's observations; infants require a certain amount of time to fully habituate to a stimulus.

This period increases with stimulus complexity in babies of the same age; overall time decreases as infants get older. Thus, the failure to elicit a novelty preference can be explained in terms of insufficient habituation.

One series of research findings that suggest greater complexity in the VPC that is consequently more difficult to explain with a traditional model concerns the apparent oscillation from a novelty preference to a null preference and then finally to a familiarity preference, as a function of the time of delay between habituation and test (Bahrick & Pickens, 1995; Bahrick, Hernandez-Reif & Pickens, 1997; Courage & Howe 1998).

Bahrick and Pickens (1995) first investigated this relationship with three-month-old infants. When habituated to a shape stimulus, infants showed the expected novelty preference when tested after a one-minute delay. When infants were instead tested after delays of one day or two weeks, a null preference was observed. In test periods of one or three months, however, a familiarity preference was seen which suggests that initial learning continued to have an impact on responding, but that the expression of the response had altered. These fluctuations in responding as a function of delay lead the researchers to postulate the existence of a 'four-phase' model of VPC response. In further experiments, it was established that presenting infants with short periods of retrieval cues prior to test boosted performance at each delay interval; thus, whilst the novelty preference at a one day interval was stronger; one-month and three-month delay periods yielded nonsignificant results increasingly in the direction of a familiarity preference (Bahrick, Hernandez-Reif & Pickens, 1997).

Courage and Howe (1998) report similar findings. When 3 month-olds were habituated to shape stimuli and varying delays, novelty preferences were evidenced at 1

minute and 1 day, and null preferences at 1 week, both for infants that viewed the test stimuli only at one delay point and for those that viewed them at all delay points. At one month delay, however, infants who observed the test stimuli at each delay point showed a novelty preference; those who saw the stimuli only at the longest delay also looked longest at the familiar stimulus.

The findings that support the existence of a four-phase attentional model differ from much of the VPC literature in a number of important ways. Each study employed as habituation stimuli complex, moving, abstract shapes. Two of the experiments (Bahrick & Pickens, 1995; Bahrick, Hernandez-Reif & Pickens, 1997) also employed a soundtrack of the natural noises made by the moving stimuli. In all cases, habituation times were well in excess of those usually employed (four 40-second periods in each study). In addition, one of the measures taken as an index of preference – the longest look given by the infant to one of the stimuli in the test phase (Courage & Howe, 2004) is similarly nonstandard. Nevertheless, the findings do raise the possibility that the traditional model of infant visual recognition memory preference – i.e. given sufficient habituation time, a novel preference is observed which, given a sufficient delay will produce a null preference taken as an indicator of a loss of memory – does not provide a complete picture of infant preference. In the atypical circumstances employed in these studies, at least, the null preference does *not* appear to be the end-point of useful measurement. Bahrick et al. (1997) instead suggest that infant visual recognition memory, in terms of the null preference, entails a transitional period, during which infant memory is still intact despite the failure of the VPC to measure such memory. Such a contention is compatible with Hunter and Ames' (1988) model described above, and demonstrates that infants'

attentional processes are dynamic. As such, researchers must be careful of attempting to claim too much theoretical ground on the basis of null preferences. For example, Houston-Price and Nakai (2004) argue that random looking behaviour (i.e. null preferences) is not necessarily an indication of failure to remember. Rather they propose that the looking behaviours such as null preferences may be part of an expected transition between preference for the (relatively) familiar stimulus and preference for the novel stimulus. Houston-Price and Nakai (2004) also make the point that individual differences in progression through these stages is a neglected variable in the classic VPC paradigm, where the looking data from a group of infants is typically averaged to produce group means. Previously Wagner and Sakovits (1986) had also described this use of averaged group data as an intrinsic problem within the paradigm.

In addition to the questions raised by advocates of the four-phase model, there have, over the past 20 years, been a small but consistent number of studies in the infant VPC literature reporting familiarity preferences (Nachman, Stern & Best, 1986; Pascalis & de Haan, 2003; Rose, Futterweit, and Janowski, 1999). This changing expression of visual recognition memory complicates the interpretation of results from a relatively simple looking task. Rather than having a single behaviour that demonstrates evidence of memory (a novelty preference), there are now two apparently contradictory behaviours (a novelty preference and a familiarity preference) that can both be claimed to provide evidence of recognition memory. Such studies suggest that when the VPC is adapted to include social and emotional demands placed on the infant, the usual novelty preference is not observed. Rose, Futterweit, and Janowski (1999) took a baseline measure of affect in 5-, 7- and 10-month-old infants prior to administering a variant of a VPC task. Infants

who displayed positive affect prior to the experimental task, defined by smiling or laughing at a photo of a baby, tended to make longer and less frequent looks to the test images, and were also slower to display learning than infants displaying neutral affect (this is analogous to showing a null rather than a novelty preference in the standard VPC task).

The interplay between infant affect and learning was also observed by Nachman, Stern, and Best (1986). Seven-month-old infants were habituated to a puppet presented in a window in front of them. The presentation of the puppet was intended to engender either positive or neutral affect. In the positive condition, the puppet played 'peek-a-boo' with the child, and the experimenter brightly intoned 'peek-a-boo!' at every presentation. In the neutral condition, the puppet was moved slowly from side to side and remained in the child's view. At each return to the centre position in the neutral condition, the experimenter monotonously intoned 'peek-a-boo'. The positive affect group showed a familiarity preference that increased in strength between the 2 minute and 1 week tests. In contrast, the neutral affect group showed a novelty preference that again increased in strength over the 2 minute and 1 week test. Taken together, the findings from Rose et al. (1999) and Nachman et al. (1986) suggest that positive affect prior to or during learning may be an important factor in how memory is subsequently expressed in a standard VPC task.

Gross et al. (2002) demonstrated that interactive stimuli, rather than affect per se, may alter the expression of memory. Six-month-old infants experienced a habituation period comprising of a 60 second interaction with a large puppet held by an experimenter. Unlike the Nachman et al. (1986) study, the experimenter was in full view

of the infant during the habituation phase. The VPC task was then conducted with “live” puppets rather than more traditional static images. A null preference was observed.

Interestingly, however, when a subsequent deferred imitation test was conducted infants were seen to have remembered the actions they saw the puppet perform.

Why, when infants can obviously remember the puppet they have seen previously as in the Gross et al. (2002) study, did they fail to demonstrate the expected novelty preference? In both Gross et al. (2002) and Nachman et al. (1986), the interactive and somewhat social component of the habituation phase provided by a “live”, moving, puppet compared to a static visual image, would appear to attenuate the attentional bias for novelty that is usually observed.

It would seem, then, that there exist certain variables that attenuate the novelty preference in the VPC. Studies involving an element of live ‘interaction’, or eliciting emotion on the part of the subject, lead to performance that would not be predicted on the basis of much of the infant visual recognition literature. Such experience by infants at the time of encoding appears to impact on subsequent performance on the VPC task. However, the direction of the response, null preference or familiarity preference, is not well established.

These findings can also be argued to demand explanation from the perspective of any account of the VPC that contains the notion of automaticity in terms of novelty preference. Clearly, any automaticity engendered by the standard version of the task is at best overridden in some manner by experimental manipulation of the type of stimuli used during familiarization and test periods. A corollary of such an argument concerns what novelty preferences, familiarity preferences and null preferences actually mean. A robust

familiarity preference is as reliable a measure of infant visual discriminative abilities as is a novelty preference; whether it is thus a comparably effective index of memory is a topic that demands detailed consideration. Similarly, what can logically be deduced from a null preference requires close thought. Advocates of the four-phase model of attention are careful to argue that it does not necessarily demonstrate a lack of memory; it could equally be the result of competing mnemonic and novelty preference processing. Furthermore, Gross et al. (2002) demonstrated that other memory tests could be passed despite a null preference being observed. At any rate, Rose's 1982 contention that "the tendency of infants beyond the age of 2 ½ months to visually attend to novel stimuli is so pronounced and so consistent that it serves as the backbone of much of the research on visual memory" is outdated and requires revision. Furthermore, the preexplicit memory model needs to be given careful consideration in light of the literature demonstrating that the novelty preference can be attenuated.

The purpose of this thesis is to address key questions concerning the VPC:

- to afford greater consideration to the circumstances under which the novelty preference is *not* reliably elicited by the VPC task;
- to make explicit the ramifications of such for the model of preexplicit memory outlined above;
- to provide an account of how such findings can be understood in terms of neurobiological models of infant memory; and
- to explore the manipulation of task parameters in the VPC with human adult subjects, with the twin aims of testing the applicability of the visual recognition

comparison paradigm across the lifespan and considering how such findings illuminate the developing mnemonic processes in the infant.

Chapter 2 – Interaction during habituation alters the expression of visual recognition memory

It has been demonstrated in chapter one that the novelty preference is not the only potential expression of memory in the VPC. Familiarity preferences in particular cannot simply be accounted for by incomplete encoding and have instead been documented when the delay between familiarisation and test increases, but also when the stimulus itself varies from traditional static photos. For example, a familiarity preference has been observed in studies where the habituation period contains an element of interaction with a stimulus such as a puppet, or elicits positive emotion from the infant. Of particular relevance here, Nachman et al. (1986) observed that the visual preference demonstrated by seven month-olds who were habituated to a puppet depended on the emotion elicited in infants. In a condition where positive affect was elicited, a familiarity preference was observed. When affect was neutral, however, a novelty preference was observed.

A glove puppet, and the non-static habituation period that comes with it, is a relatively atypical stimulus in terms of the VPC, but a more common feature of procedures such as deferred imitation. It is possible that this type of interactive learning session might account, at least in part, for the disparity observed in the expression of memory in different infant paradigms (e.g., Gross et al., 2002). There is a clear need to examine the effect of interactive stimuli with a wide age-range of infant subjects to observe whether this effect alters over a developmental trajectory. The purpose of the experiments in this chapter is to systematically address whether there are developmental changes in the effect of non-traditional stimuli on recognition memory performance in the

VPC. The first experiment replicates the use of a puppet task as in previous studies conducted with 6- and 7-month-old infants (e.g., Nachman et al., 1986; Gross et al., 2002), but extends across the infancy period from 6 to 24 months of age.

Experiment 1: puppet task (the results of this experiment are reported in Brown, Robinson, Herbert & Pascalis, 2006)

Method

Participants

Eighty infants participated in this study. There were 16 infants in each age group. Independent groups of 6-month-old ($M=186$ days; $SD=8$ days), 9-month-old ($M=276$ days; $SD=6$ days), 12-month-old ($M=368$ days; $SD=6$ days), 18-month-old ($M=549$ days; $SD=5$ days), and 24-month-old ($M=731$ days; $SD=7$ days) infants were tested. Half of the infants at each age were female. A further 20 children were tested but excluded from the sample because of fussiness (6-month-old infants, $n=4$; 9-month-old infants, $n=1$; 12-month-old infants, $n=5$; 18-month-old infants, $n=3$; 24-month-old infants, $n=2$), side bias as defined by more than 90 % looking to one side (6-month-old infants, $n=3$; 12-month-old infants, $n=1$), and experimental error (6-month-old infants, $n=1$). None of the infants were born more than 3 weeks premature or had experienced birth complications. The infants were recruited through parent and baby groups in the local area which were either community based or run by Health Visitors, through posters in primary care settings, and through visits to a maternity hospital. The infants were all White British and from families of moderate to high socio-economic status.

Stimuli

The familiarisation stimuli were 4 commercially available fabric glove puppets; a sheep, a dog, a dragon, and a group of piglets. The puppets were all approximately 25cm in height but differed in shape and colour (see appendix A for examples). Stimuli were presented in a randomised and counterbalanced order over both familiarisation and test periods.

Colour photographs of the puppets were used as test stimuli. The test stimuli were back-projected onto a 45cm * 32 cm screen positioned approximately 60cm in front of the infant. A camera positioned centrally above the screen recorded the infant's eye movements between the two items.

Procedure

All infants were tested in the baby research laboratory at the University of Sheffield at a time of day that was defined by the caregiver as an alert/play period. The experimenter interacted with the caregiver and the infant in a reception room for approximately 5 minutes until the infant appeared comfortable with the experimenter. During this time informed consent was obtained from the caregiver.

Familiarisation session: During the familiarisation period the infant sat on their caregiver's lap on a chair in the experimental room and the experimenter knelt in front of them. The experimenter then revealed a puppet and proceeded to use the puppet in an interaction with the child and caregiver. The actions and language used were chosen to suit the age and mood of each child, and were intended, as far as possible, to constitute natural, interactive play. The total familiarisation period was approximately 60 seconds. Two criteria were used to define completed familiarisation. First, the infant had to have

fixated on the puppet for at least 20 seconds. It was important to stipulate minimum fixation on the puppet because infants often spent time looking at the experimenter. In addition, this fixation had to have occurred when the puppet was facing the infant and was an appropriate distance from the infant to be fully within his or her visual field (60cm approx). The puppet's position was important because many infants wanted to hug the puppet which meant that they were not seeing the same type of view as the one used in the test photographs. Second, the infant had to have been relaxed and to have enjoyed the interaction; this was quantified through laughter or smiles. Only one child (a 24-month-old female) failed to meet these two criteria because she appeared to be frightened of the puppet. In most cases infants fixated on the puppet for longer than 20 seconds. At the end of the familiarisation session, the puppet was removed from the infant's sight.

Test session: The test session occurred immediately after the familiarisation in the same room. The experimenter then turned the caregiver's chair so that the caregiver and the infant were facing the screen on which the test photographs would be presented. The test session began once the infant was looking towards the screen. During the test, a photograph of the familiar puppet was presented alongside a randomised photograph of a new puppet. There were two 5-second test trials separated by a delay of around 2 seconds. In the second test trial the lateral position of the puppets was reversed.

Results and Discussion

Videod looking data from the test session was coded using software specially developed in conjunction with Dr. Mike Coleman (human communications dept,

University College London). A sample of the data was coded by an additional postgraduate student to ensure reliability.

Preliminary analysis was conducted to determine whether there were effects of gender of the infant on proportional fixation times. A between-measures Analysis of Variance (ANOVA) revealed no effect of gender or interaction between gender and age, on proportional fixation times. The groups were therefore collapsed across gender.

The effect of interaction on the expression of recognition memory was then examined at each age. A series of one-tailed paired t-tests demonstrated that infants who were 6-, 9-, or 12-months of age at time of testing demonstrated a null preference. Of these age groups, 37.5%, 62.5% and 31.25% respectively showed a looking time in the direction of a novelty preference. 18-month-olds demonstrated a significant familiarity preference ($t(14) = 2.145, P < 0.05$) Of this age group, 37.5% showed a looking time in the direction of a novelty preference. Twenty-four-month-olds also demonstrated a familiarity preference ($t(15) = 4.519, P = < 0.01$; see table 2.1). Of this age group, 31.25% showed a looking time in the direction of a novelty preference.

Age group	Mean looking time to novel stimulus in milliseconds (standard error)	Mean looking time to familiar stimulus in milliseconds (standard error)	Mean % looking time to novel stimulus (standard error)	Two-tailed t-test (P)
6 month (N = 16)	4363 (338.71)	4105 (374.45)	50 (3.4)	0.637
9 month (N = 16)	4280 (291.78)	4150 (258.24)	50.548 (2.83)	0.787
12 month (N = 16)	3893 (335.61)	4193 (313.84)	48.054 (3.2)	0.603
18 months (N = 16)	3603 (288.48)	4882 (365.54)	42.84 (3.53)	0.048
24 months (N = 16)	3060 (363.09)	6180 (345.08)	32.923 (3.62)	0.0004

Table 2.1: the mean percentage looking time to the novel stimulus as a function of age

Consistent with previous research involving positive interaction in lieu of the traditional, emotionally neutral habituation procedure, 18 and 24-month-old infants in the present study displayed a familiarity preference when tested for recognition memory immediately after habituation. Younger infants also exhibited a disruption to the expected novelty preference, resulting in a null preference. Such a null preference is in line with the findings of Gross et al. with 6 month-old infants (2001), but contrasts with the finding of a familiarity preference in 7 month-old infants by Nachman et al (1986). A possible reason for this concerns the complexity of the current experimental stimulus. Nachmann et al (1986) employed a puppet presented without a visible experimenter; the habituation

period thus contained less for the infant to attend to than does the current experiment. Gross et al. (2001), however, employed mobiles as stimuli; furthermore, as the experimental design was mixed, infants were able to move the mobile by kicking during the habituation phase. Such a procedure is arguably *more* complex than the current experiment.

A number of alternative explanations could account for the present results. It is possible that disruption to the novelty preference is a reflection of insufficient encoding time when attending to a dynamic stimulus. Previous research suggests that a null preference or a familiarity preference may be obtained if the habituation period is insufficient in duration for full encoding of the stimulus to occur (e.g. Fagan, 1974). Although this provides a potential explanation for the results, the 20-second minimum habituation period employed here has been robustly demonstrated to be sufficient in even very young infants. By 6-months of age, a 20 second period is sufficient for a novelty preference to be observed (Pascalis, de Haan, & Nelson, 2002; Robinson & Pascalis, 2004). In the experiment conducted here, however, a null preference was observed until 18 months of age.

The representational nature of the test stimuli might also be a contributing factor in the changing preferences across age. In the present study the habituation stimuli were 'live', 3-dimensional puppets while the test stimuli were static photographs of these objects. It is possible that the representational nature of a photograph may place greater cognitive demands on younger infants, interfering with the recognition memory process. Although studies with older children reveal that they have difficulty using information presented in a 2-dimensional format to represent 3-dimensional reality (e.g. Barr &

Hayne, 1999; Troseth, 2003), several studies have employed this sort of change between habituation and test periods successfully. Neonates, for example, spend longer looking at an image of their mother's face than they do at the image of a stranger's face (Pascalis, De Schonen, Morton, Deruelle, & Febre-Grenet, 1995).

An alternative account for the lack of a novelty preference at younger ages and the familiarity preference at older ages is proposed here: the changing preference may be a reflection of the developing connectivity between emotion regulation and memory processing systems. Whilst the rationale of the VPC is based on the assumption of a preference for novelty, when emotional salience is attached to a stimulus this may also provide an equally important basis for attentional focus and subsequent affect memory performance. A growing body of research suggests that emotional events may be remembered for substantially longer than more neutral events. For example, 5-month-old infants who participated in a mildly emotionally negative interaction (a still face experiment) exhibited some evidence of memory for participation 16 months later (Bornstein, Arterberry, & Mash, 2004). The substantial retention interval for the interpersonal interaction suggests that there may be interplay between emotion and memory even at a very young age.

There are, however, aspects of the methodology employed here that are open to criticism. One such aspect is the practice of habituating the infant to the puppet while the experimenter is also in full view. This could be argued to compound the complexity of the task; in addition to gaining experience of the puppet, the infant is also experiencing an interaction with a human, and all the eye contact and attentional demands that this entails. In addition to increasing the complexity of the habituation phase, such a procedure also

has the potential to impact upon the test phase. If the experimenter and puppet have been encoded together, then the experience of seeing the puppet on its own during the test phase might in itself be a novel event. If this were the case, both stimuli presented at test would be 'novel' and a null preference would therefore be the expected result.

A further methodological criticism can be levelled at the nature of the interaction period itself. This period was designed to be relatively naturalistic and responsive to the individual child. Such a design, intended to fully engage the child, brings with it the possibility that there may have been uncontrolled individual differences in terms of the movement of the puppet and the emotional responses of the experimenter. In addition, they may have also been age group differences endangered by the altering attentional and interactional styles of participants of varying ages.

Such methodological considerations are addressed in experiment two, in which 6-, 12-, and 18-month-olds are tested with two different versions of a controlled puppet VPC task with presentation format matched at familiarisation and test.

Experiment 2: Puppet VPC with Additional Controls

Method

Participants

Twenty-five 6-month-olds (13 female), 26 12-month-olds (15 female), and 22 18-month-olds (16 female) were tested. All infants were tested within 5 days of being the required age. A further 11 children were tested but excluded due to fussiness (6-month-old infants, $n = 4$; 12-month-old infants, $n = 2$; 18-month-old infants, $n = 1$), side bias as defined by more than 90 % looking to one side (6-month-old infants, $n = 2$; 12-month-old

infants, $n = 1$), and experimental error (6-month-old infants, $n = 1$). No infants were born more than 3 weeks premature or had experienced birth complications. Infants were recruited as in Experiment 1. The infants were all White British and from families of moderate to high socio-economic status.

Stimuli

The familiarisation stimuli were 4 commercially available fabric glove puppets; a monkey, a lion, an elephant, and a toucan (see appendix B). The puppets were all 16cm in height; they were similar in shape but differed in colour. Stimuli were presented in a pseudo-randomised and counterbalanced order over both familiarisation and test periods. Stimuli were presented in two conditions; 'MPG' and 'live'. In the former, digital video clips were used as the habituation stimulus and digital image stills were used at test. In the latter, live puppets were used both for habituation and test. The lion stimulus was always paired with the monkey, and the elephant with the toucan. This was to control for the background colour of each video; although the background material was the same dark blue cloth for each stimulus, the video camera's metering was such that it appeared considerably darker for the elephant and the toucan than it did for the monkey and lion.

MPG Condition: Habituation Stimuli

30 second videos of each puppet was created with a digital video camera and presented as an MPG video file, back-projected onto a 45cm * 32 cm screen positioned approximately 60cm in front of the infant. To standardise the presentation of each puppet, they were videoed being moved in the same way. Each video comprised 5 seconds during

which the puppet was stationary and facing forwards; the puppet then made twenty smooth arcing movements from left to right, each arc lasting one second. Following this movement was another five seconds period in which the puppet remained static.

Test stimuli

The test period comprised two five second randomised and counterbalanced presentations of a digital image of the puppet along with the matched novel stimulus. Digital images were .jpg files of stills taken from each video during a period of inactivity. A camera positioned centrally above the screen recorded the infant's eye movements between the two items.

Live puppet condition: Habituation stimuli

The habituation stimulus was one of the four puppets, presented live to the infant in a plain wooden puppet theatre with dark blue backcloth measuring 45 * 32 cms positioned approximately 60cm in front of the infant. The puppet was moved by a hidden experimenter in the standardised manner used in the MPG condition.

Test stimuli

The test period again comprised two 5-second randomised and counterbalanced presentations of the habituation puppet presented along with the matched puppet. Puppets were presented 30 centimetres apart. A camera positioned centrally above the puppet theatre recorded the infant's eye movements between the two items.

Procedure

All infants were tested in the baby research laboratory at the University of Sheffield at a time of day that was defined by the caregiver as an alert/play period. The experimenter interacted with the caregiver and the infant in a reception room for

approximately 5 minutes prior until the infant appeared comfortable with the experimenter. During this time informed consent was obtained from the caregiver.

Familiarisation session: During the familiarisation period the infant sat on their caregiver's lap on a chair in the experimental room, facing either a projection screen (for the MPG condition) or the puppet theatre (the same apparatus with the screen removed, for the live condition). The infant was then presented with either the MPG video or live habituation stimulus described above. The total familiarisation period was approximately 30 seconds. Infants were required to attend to the stimulus for a minimum of 20 seconds to be included in the study (all infants met this criterion). At the end of the familiarisation session, the stimulus was removed from the infant's sight.

Test session: The test session occurred approximately 5 seconds after the familiarisation in the same room. The test session began once the infant was looking towards the screen. During the test for the MPG condition, a photograph of the familiar puppet was presented alongside a matched photograph of a new puppet. In both the MPG and in the live condition, there were two 5-second test trials separated by a delay of around 2 seconds. In the second test trial the lateral position of the puppets (or puppet photographs) was reversed. During the live condition, infants were presented with the familiar puppet itself and the matched novel puppet.

Results and discussion

Videoed looking data was coded using the same software as all VPC experiments conducted in this thesis. A sample of the data was coded by an additional postgraduate student to ensure reliability.

Preliminary analysis was conducted to determine whether there were effects of gender of the infant on proportional fixation times. A between-measures analysis of variance (ANOVA) revealed no effect of gender or interaction between gender and age, on proportional fixation times. The groups were therefore collapsed across gender.

The effect of interaction on the expression of recognition memory was then examined at each age.

Live Condition

A series of one-tailed paired t-tests were conducted. All three age groups demonstrated a null preference (see table 2, bottom three rows).

Of these age groups, 64.3%, 46.2% and 70% respectively showed a looking time in the direction of a novelty preference.

MPG condition

A series of one-tailed paired t-tests were conducted. 6 month-old infants and 18-month-old infants demonstrated a null preference; 12 month-old infants demonstrated a novelty preference ($t(12) = 3.786$, $P < 0.01$; see table 2.2). Of these age groups, 36.4%, 84.6% and 33.3% respectively showed a looking time in the direction of a novelty preference.

Age group	Stimulus	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	Two-tailed t-test (P)
6 month (N = 11)	MPG	3676.34 (344.96)	3978.18 (372.99)	47.89 (3.23)	0.966
12 month (N = 13)	MPG	4353.85 (243.6)	3476.92 (168.21)	55.37 (1.42)	0.004
18 month (N = 12)	MPG	3996.67 (404.98)	3830.0 (334.56)	50.8 (3.793)	1.592
6 months (N = 14)	Live	4248.57 (277.96)	3977.14 (313.83)	52.14 (2.63)	0.518
12 months (N = 13)	Live	4545.38 (247.57)	4593.84 (208.72)	49.61 (2.44)	0.92
18 months (N = 10)	Live	4296 (263.26)	4202 (201.34)	50.37 (2.34)	0.816

Table 2.2: the mean percentage looking time to the novel stimulus as a function of age

In almost all cases, the research hypothesis has been supported. The novelty preference expected in standard VPC tasks was attenuated. In all live puppet conditions

and in 6- and 18-month MPG conditions a null preference was observed. Only 12-month-old infants in the MPG condition display a novelty preference.

The live condition thus caused more universal disruption to the novelty preference than did the MPG. Despite taking care to keep the live and MPG tasks fully equivalent, habituating and testing when the puppets were directly physically observable to the infant in 3D led to disruption across the ages studied. In contrast, the MPG condition only eradicated the novelty preference at two of the three age-points studied. There might, then, be broad grounds for arguing that live stimuli have increased salience for infants, and are therefore more novel, to the extent that even following an habituation period both puppets presented at test are still worthy of attention. However, such theorising is based on a single age-group – 12-month-olds, and the success of this age group in the MPG condition is not easy to explain. It is true that the MPG condition is more akin to traditional VPC paradigms than most of the experimental designs involving puppets. Nonetheless, the success of 12-month-olds in exhibiting a novelty preference but the failure of 18-month-olds is not readily explainable, and will be considered further in the following section.

General Discussion

These two studies provide further evidence that, when the habituation phase comprises a period of attending to a brightly coloured moving stimulus, a novelty preference may not be observed. In the first study, when infants were habituated to a glove puppet presented by an experimenter in an individualistic and engaging manner and tested with still images, a null preference was observed in 6-, 9- and 12-month-olds, whilst a familiarity preference was observed in 18- and 24-month-olds. This occurred

despite the familiarisation period of 60 seconds being well in excess of the period required to elicit a novelty preference when typical, static VPC stimuli are employed (see Courage & Howe, 2004). In the second study, null preferences were observed in 6-, 12- and 18-month-olds when familiarised to a live puppet when the experimenter was not in view and tested with live puppets. Performance of the youngest age group is consistent with the findings of Gross et al. (2002). When familiarised with standardised videos of puppets and tested with still pictures, 6- and 18-month-olds displayed a null preference, whilst 12 month-olds showed a novelty preference.

Considering the findings of experiment 1 and of the live condition of experiment 2 together, the findings up to 18 month-olds – i.e. null preferences – are the same. Why then at 18 months of age do infants show a different pattern of results across the experiments? In experiment 1, a familiarity preference is observed; in experiment 2, a null preference is obtained. One candidate reason for this discrepancy is the difference in stimulus presentation during the habituation period between experiments. In experiment 1, the habituation stimulus is, in essence, the combined experimenter and puppet that the infant encounters. It is reasonable to suppose that the picture of the puppet on its own presented to the infant during the test period is therefore a novel stimulus of sorts; it is recognisable to the infant, but is only part of what has been encoded. It may be, therefore, that the increased looking time to the familiar caused by this, when combined with the null preference that is observed to occur during a live, interactive VPC, tips the looking preference in favour of the ‘familiar’. By way of contrast, the test stimulus in experiment two is an identical version of what was encountered during familiarisation. It would be interesting in further experimentation, therefore, to continue testing the refined

methodology with 24 month-old infants to observe whether this null preference continues. If it was indeed the case that 24 month-olds demonstrated a null preference, this would be further evidence for failure on the puppet task being a function of the task itself rather than an age-related anomaly such that the task is passed as increasingly adult-like memory systems are in place. The heterogeneity of age groups in terms of the number of infants in each looking longer to the novel stimulus suggests that the effects of employing a non-typical familiarization stimulus might alter with age and that a more detailed consideration of performance at different ages might be beneficial.

A further candidate explanation for the difference between experimental results concerns differences in the degree of positive elicited emotion and genuine interactivity. In experiment 1, infants genuinely interacted with a puppet and experimenter, and the demonstration of positive emotion via laughter or smiling was an inclusion criterion. In experiment 2, however, infants passively observed a controlled sequence of actions intended to *represent* genuine interaction, and a display of positive emotion was not necessary for experimental inclusion. Variables concerning the habituation phase were altered in experiment 2 to allow for tighter control of what participants observed; by the same token, as positive emotion was now less observably elicited it was not a suitable inclusion criterion. Such experimental differences highlight the complexities of balancing sufficient experimental controls with naturalistic interaction in such research, and demonstrates that a more substantial programme of research would be necessary to fully unpack these variables.

The MPG data of experiment two is harder to explain within the current framework. The novelty preference at 12 months is unexpected, and is hard to reconcile

with the literature concerning this sort of habituation procedure. One pertinent observation, however, is that of all the conditions here, the MPG paradigm is most similar to typical VPC tasks, in that both the habituation and test stimuli are 2D images presented on a projector screen. This would therefore be the condition in which a novelty preference would be most likely. At present, it is unclear why a novelty preference was observed with 12 month-olds whilst both 6 and 18 month-olds displayed a null preference. One manner in which such variables could be considered in greater detail would be to systematically explore the relationship between stimulus type and looking preference, including conditions in which the habituation phase was static and the test phase was a moving video, and one in which both habituation and test incorporated moving videos. It is hard to predict how the inclusion of additional moving stimuli would affect looking preference; it might seem reasonable to hypothesise, however, that as attentional demands increase with the inclusion of additional movement, a null preference might again be observed in infant subjects even up to 24 months or beyond.

Given that the present results suggest the importance of considering emotional salience of stimuli, one methodological aspect that needs to be refined concerns measuring the emotional response shown by subjects. Several measurement tools exist for this purpose. The Facial Action Coding System (Ekman & Friesen, 1978; Ekman, Friesen & Hager, 2002) has been adapted specifically to code baby faces (the baby FACS, Oster & Rosenstein, 1988). Similarly, the AFFEX system (Izard, Doherty & Hembree, 1983) can be used to holistically assess displayed emotion in infants (Camras, Sullivan & Michel, 1993). Such methods were not employed here due to the exploratory nature of the research. Although infants appeared to show few large displays of emotion

throughout testing, there may have been subtle positive expressions that were not immediately observable to the experimenter. Measuring and quantifying displayed emotion should therefore be considered a research priority. It may, for instance, be possible to adapt a VPC methodology to maximise elicited emotion, for example by including cartoon characters identified by caregivers as favourites, or by making the habituation section even more interactive, perhaps incorporating a 'peekaboo' game. If such events reliably elicited strong emotion in infants, it would be possible to compare memory performance when such emotion was present at encoding with performance under emotionally neutral conditions.

Three further factors can be forwarded that impact on a consideration of the results of both experiments. Each concerns cognitive development emerging within the first 18 months of life.

The first is the emergence of *social referencing*, the ability to extract emotional information from others to provide information about objects in the world. This ability develops in the second year of life and encompasses both the ability to use such information to allow safe objects to be approached, and also the ability to regulate or inhibit behaviour in the presence of negative emotional reaction. For example, 14-month-olds, but not 11-month-olds, are able to inhibit exploratory responses to novel objects when an unfamiliar adult expresses disgust (Hertenstein & Campos, 2004). By 15- to 20-months of age, infants show greater fear response and more avoidance behaviour to rubber snakes and spiders when they are paired with negative maternal facial expressions (Gerull & Rapee, 2002). In the second year of life, infants not only learn to respond to events on the basis of adults expressed emotions, they also become competent at

regulating their own emotions. For example, Blackford and Walden (1998) found that 11- to 15-month-old girls displayed a relationship between temperamental fear and emotional regulation, whereas 16- to 22-month-old girls did not. The infant's own affective state was thus more able to be controlled, and their behaviour more able to be based on external information, in the older age group.

It is possible that the development of social referencing abilities is accompanied by a comparable development in the infant's ability to suppress his or her own emotional response and subsequently allow encoding and recognition memory to operate without unconstructive interference. By the age of 18 months, infants may be able to suppress preference to novelty and to express a familiarity preference to a positive stimulus, as seen in experiment 1. Prior to this, the competition between attention to novelty and to emotional salience may be confounded by an inability to sufficiently process a stimulus eliciting positive affect. It is likely that preference for positive stimuli becomes more salient than a preference for novelty during the second year life; positive affect begins to form the basis by which the world is most appropriately explored. Thus, infants in experiment 1 may only be capable of suppressing emotional response by 18 months; at this point, a familiarity preference is driven by the attractiveness of a previously enjoyable stimulus, whereas at younger ages this attraction may be in competition with an intrinsic preference for novelty. In experiment 2, a null preference continues to be observed at 18 months. Whilst a positive experience of the habituation stimulus may still be occurring in experiment 2, it is feasible that this does not statistically outweigh the attentional draw of the novelty preference because the habituation period in which the infant experiences an interaction with an isolated puppet is not as emotionally salient as it

is in experiment 1, in which positive interaction with a live experimenter occurred (and indeed was an inclusion criterion).

Secondly, a complimentary neurophysiological explanation concerns the development of the amygdala and the interaction between this and the medial temporal lobe memory system. When the stimuli are more interactive or interesting, and thus likely to elicit positive affect, it is probable that the amygdala may also be activated (for a review of amygdala functioning see Aggleton, 2000). Given that the amygdala is known to modulate hippocampal activity (McGaugh, 1996; 2004), and is crucial for processes translating an emotional reaction into a long-term memory response (Cahill & McGaugh, 1998), it is possible that social interaction during encoding may facilitate learning and alter the duration or expression of memory. Based on the present results, it is suggested that there may be developmental changes in these structures, or the interconnections between them, occurring at around 12- to 18-months of age. An account of developing ability in social domains seems to fit the age at which differences in memory performance are observed in the present study.

The third topic of relevance here is that of preexplicit memory; more specifically, the degree to which preexplicit memory necessarily entails hippocampal-driven automaticity, and the age at which there is a switch to explicit memory proper. The main issue raised by the data here, and in previous studies in the literature employing puppet-based VPC tasks (e.g. Nachman, Stern, and Best, 1986), is: if VPC performance can be altered by manipulating the experimental parameters, does this bring into question claims concerning the 'reflexlike' mechanism with which preexplicit memory is held to operate? Such discussion is only relevant to the youngest age groups tested here; as the switch

from pre-explicit to explicit memory is contended to take place in the second half of the first year of life, any observable transition would be seen here between the 6-, 9- and 12-month-olds (Nelson, 1995). The performance of these groups on experiment 1 and on the live condition of experiment 2, however, is identical. In the MPG condition of experiment 2, the 12-month-olds displayed a novelty preference. This is exactly the age group in which a measurable difference might be expected during the transition between memory systems, although how this result could be explained in terms of transition of memory systems is unclear. If an explanation for altered VPC performance requires, as it would seem to, an explanation in addition to length of habituation times, then the best that can be said of the mechanisms of the preexplicit memory system is that it operates automatically only within quite specific parameters. It is possible to suggest that, in experiment 1, the response of younger infants response is a null preference precisely because the automatic preference for the novelty is pitted against the emotional demands of the habituation stimulus; by 18-months, due to the neurodevelopment that allows the amygdala to control emotional responses and the MTL system to be sufficiently developed to allow attentional preferences to now be under the auspices of conscious control, a familiarity preference is seen.

In conclusion, when the standard habituation period of a VPC task is replaced by an interactive period with a puppet and experimenter, a moving puppet or a video of a moving puppet and recognition is then tested with static puppets or static images of puppets, the typical novelty preference is replaced with a null preference in all infants less than 12 months of age. When the habituation period constitutes genuine interaction, 12-month-olds also demonstrate a null preference; 18 and 24-month-olds demonstrate a

familiarity preference. When the habituation period is a video of a moving puppet, 12-month-olds alone displayed a novelty preference (6- and 18-month-olds displayed a null preference). Such findings have ramifications for future use of the VPC task involving movement or interactivity.

One way to allow further consideration of how such stimuli are processed by the explicit memory system proper is to test an experimental population in which there can be no doubt that the MTL system is fully functioning. To this end, the focus of the next experimental chapter will be a consideration of the performance of human adults on versions of the VPC which incorporate varying degrees of social interaction.

Chapter 3 – The VPC with adults – the novelty preference is disrupted by interactive habituation

Whilst the VPC was developed from observations with human infants and has historically been used to assess the mnemonic abilities of such populations, there is recent evidence that it is also suitable for use with human adults (e.g Fagan & Vasen, 1997; Pascalis et al., 2004; Pascalis & Bachevalier, 1999; Richmond, Sowerby, Colombo & Hayne, 2004; Manns, Stark & Squire, 2000). Under the right conditions (i.e. relatively short habituation and test periods to account for faster encoding), adults show a reliable novelty preference to traditional VPC stimuli in the same manner as do young children. The recognition of the applicability of the VPC to adults is an important development. One of the strengths of the task is its simplicity, which provides the theoretical potential for robust ontogenetic and phylogenetic comparison in a manner not suitable in tests of memory requiring language comprehension. If used carefully, the VPC has the potential to be a memory task suitable for use right across the human life span and between species, and thus can be a rare tool that allows both memory development and mature functioning to be measured and directly compared. An additional advantage of using the VPC with adults is that it can then be directly compared to other, more established explicit memory tests designed for use with adults (such as forced-choice memory tests). Furthermore, due to the superior cognitive and attentional capacities of adults, tests can employ a greater number of trials than VPCs used with infants (which typically employ only two trials); such tests can therefore allow greater within-subject comparison, for example with different categories of stimuli.

It is also the case that testing the performance of adults on non-standard versions of the VPC might allow a more detailed understanding of the factors responsible for the performance of infants on such tasks as those administered in chapter 2. Such variations of the VPC have not previously been administered to adults.

As outlined in the discussion of Chapter 2, the puppet tasks which disrupted the memory performance of infants contain two variables that might impact on the expression of memory. Firstly, there was an 'interaction' component to the tasks; infants were presented with moving puppet stimuli that may have been construed as attending to the infant. Secondly, there is a presumed emotional processing component; interaction may induce affect. These variables will be considered in turn over the next two chapters. Such variables will be considered with stimuli designed to be age-appropriate (although, for purposes of comparison, one of the puppet tasks employed in chapter 2 is additionally employed with adults below).

In this chapter, a series of VPCs incorporating different durations of social interaction in the habituation procedure will be undertaken with undergraduate students. The purpose of these studies is to allow detailed consideration of the hypothesis that social interaction during the familiarisation phase of the VPC will disrupt the novelty preference in adults in the same manner as has been observed in infants.

In the first experiment, the standard VPC habituation trial was replaced with a sixty-second period of talking to an experimenter who then appeared as one of the test stimuli. A sixty-second period was chosen as a starting-point because it was considered necessary to have a period of sufficient length to ensure that genuine interaction could

take place, but also to be sufficiently brief to allow reasonable comparison to a VPC habituation period.

Experiment 1a

Method

Participants

10 Undergraduate students aged 19-21 years were tested. Participants were all White British, and 9 of them were female. Such a female / male ratio reflects the population available to be tested in a psychology department. Participants received participation stickers as part of the course requirements, and were only drawn from years 1 and 2 of the undergraduate psychology course because of their unfamiliarity with the VPC task. All participants were unfamiliar with the experimenter (AB).

Stimuli

For the social interaction condition, test stimuli images were created of experimenter AB and three male volunteers, each of whom wore AB's glasses to be photographed. This was necessary to control for AB's glasses which participants encountered during the interaction period and would have functioned as a distinctive feature for recognition. These stimuli were randomised for presentation with AB's face as the test stimuli. Faces were masked to control for differences in facial outline and hairstyle (i.e. cropped so that external features were not visible – see appendix C). The test stimuli for the control VPCs were drawn from an archive of face stimuli that have been used in previous studies by the research team and were of people unknown to the participants. Four colour male face digital images were selected and masked in the same manner as the interaction stimuli (see appendix C for examples of all stimuli). Stimuli

were presented in the same lab as the infant studies presented in chapter 2 and were back-projected onto a 45cm * 32 cm screen positioned approximately 60cm in front of the participant. A camera positioned centrally above the screen recorded the participant's eye movements between the two items.

Procedure

Participants were met by experimenter AB in the infant laboratory reception room. There then followed a 60-second period during which AB explained that they would be participating in a very brief task involving looking at pictures, but that it was first necessary to quickly ask them some questions. AB then asked the participant a series of filler questions: their date of birth, the course year they were in, the name of their tutor, and whether they had any siblings and if so their gender and age. During this period, AB interacted as naturally as possible with the subject, taking care to make eye contact when asking questions and noting responses.

Participants were then taken by AB to the testing lab and seated in front of the screen. It was explained to them that they were going to see some pictures appear on the screen, and that all they were required to do was to relax and simply watch the pictures. In addition, they were instructed to try not to 'second-guess' the purpose of the experiment.

Participants were then presented with a masked version of experimenter AB's face paired with another male face wearing the same glasses. Presentation was for two counter-balanced periods of five seconds. Participants were then presented with the two standard VPC tests. Each VPC consisted of a five-second habituation trial and two counterbalanced and randomised five-second test periods.

Results and Discussion

Due to the sample being 90% female, it was not possible to conduct an ANOVA with the intention of collapsing groups across gender. Gender differences, however, are not typically reported in VPC studies with either infants or adults.

The effect of interaction on the expression of recognition memory was examined. A series of one-tailed paired t-tests were conducted; the VPC in which the habituation period was 60 seconds of live social interaction demonstrated a null preference. The standard VPCs were analysed together and demonstrated a significant novelty preference ($t(9) = 0.553, p < 0.05$; see table 3.1). For the social interaction condition, 40% of subjects showed a looking time in the direction of a novelty preference. For the control condition, 70% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type	Mean looking time to novel stimulus in milliseconds (standard error)	Mean looking time to familiar stimulus in milliseconds (standard error)	Mean % looking time to novel stimulus (standard error)	one-tailed paired T-test (p value)
60 second social interaction	4540 (235.66)	4808 (149.05)	48.57 (1.76)	0.302
Control vpcs (5 seconds)	5244 (180.8)	4398 (194.61)	54.39 (1.89)	0.024

Table 3.1: the mean percentage looking time to the novel stimulus

The result of this initial investigation with adults suggests that substituting a static habituation session with a period of interaction disrupts the novelty preference in adults in a similar fashion to the disruption seen in infants in chapter 2. However, one immediately notable difference between the social interaction condition and the standard VPC controls used in the present study is the difference in the duration of the habituation period. Given that a 60 second VPC is far longer than that normally used in a standard VPC, it may be important to determine whether the length of time necessitated by the social interaction component was a contributing factor in the observed null preference. Experiment 1b, then, seeks to clarify this by increasing the habituation time for the standard VPCs used for comparison to the social interaction condition to 60 seconds.

Experiment 1b

Method

Participants

10 Undergraduate students aged 19-21 years were tested. Nine participants were White British; one was Asian British. 8 participants were female. Participants were drawn from the same population and in the same manner as in experiment 1a. None of the participants had been participants in experiment 1a.

Stimuli

Stimuli were identical to those employed in experiment 1a.

Procedure

Procedure was identical to that in experiment 1a, except that in the standard VPC trials the habituation period was 60 seconds.

Results and Discussion

Videoed looking data was coded as in Experiment 1a. Due to the sample being 80% female, it was again not possible to conduct an ANOVA with the intention of collapsing groups across gender.

The effect of interaction on the expression of recognition memory was examined. A series of two-tailed paired t-tests were conducted; the VPC in which the habituation period was 60 seconds of live social interaction demonstrated a null preference. The standard VPCs were analysed together and demonstrated a significant novelty preference ($t(19)$, $P < 0.05$; see table 3.2). For the social interaction condition, 40% of subjects showed a looking time in the direction of a novelty preference. For the control condition, 65% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type	Mean looking time to novel stimulus in milliseconds (standard error)	Mean looking time to familiar stimulus in milliseconds (standard error)	Mean % looking time to novel stimulus (standard error)	Two-tailed paired T-test (<i>p</i> value)
60 second social interaction	4811 (322.06)	4456 (294.98)	51.92 (3.27)	0.284
Control vpcs (60 seconds)	5190 (271.18)	4172 (300.22)	55.44 (3.08)	0.044

Table 3.2: the mean percentage looking time to the novel stimulus

A two-sample, two tailed t-test was conducted between control stimuli with 5-second habituation periods (experiment 1a) and those with 60-second habituation periods (experiment 1b). This demonstrated that there were no significant differences in looking times across conditions (see table 3.3).

Stimulus type	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
Control trials with 5-second habituation periods	54.39	0.66
Control trials with 60-second habituation periods	55.44	

Table 3.3: t-test comparison between different control trial looking times

Such a finding excludes the difference in habituation time between the conditions as an explanatory factor for the null preference in the interaction condition. These findings provide further evidence that it is some other aspect of the interaction period itself that accounts for the observed behavioural differences.

A further potential explanation for the null preference could have been that the habituation stimulus is itself atypical, and that the null preference found is in some important manner related to this. Although this explanation may be theoretically uninteresting, it is clearly an important factor to eliminate. To this end, a further experiment was conducted in which AB's face was included as part of a standard VPC methodology. As there is no interaction involved, a standard novelty preference is

hypothesised. If a null preference or even a familiarity preference is obtained, the results of experiments 1a and 1b would be called into question as subjects could not be assumed to be reacting typically to the habituation stimulus in these experiments.

Experiment 1c

Method

Participants

10 Undergraduate students aged 19-21 years were tested. Eight participants were White British, one participant was Black British, and one was Asian British. Nine participants were female. Participants were drawn from the same population and in the same manner as in experiment 1a. One female participant was rejected from statistical analysis because her glasses made coding of eye-movement data impossible.

Stimuli

Stimuli were identical to those used in experiments 1a and 1b. Three VPCs were employed; one employing experimenter AB's face as a five-second JPG habituation stimulus, followed by two test trials as in the previous experiments. Two standard VPC trials were then conducted in exactly the same manner as in the previous experiments using stimuli that were of people who were unfamiliar to participants.

Procedure

The procedure was identical to the procedure used above for static VPCs, with the exception that it was conducted by another experimenter (EJ) – participants never came into contact with experimenter AB.

Results and Discussion

Videoed looking data was coded as in Experiment 1a. Due to the sample being 90% female, it was not possible to conduct an ANOVA with the intention of collapsing groups across gender. The effect of interaction on the expression of recognition memory was examined. A series of one-tailed paired t-tests were conducted; The VPC in which the habituation stimulus was a JPG of experimenter AB demonstrated a novelty preference ($t(8) = 2.049, P < 0.05$). The standard VPCs were analysed together and demonstrated a significant novelty preference ($t(19) = 1.802, P < 0.05$; see table 3.4). For the AB's face condition, 77.7% of subjects showed a looking time in the direction of a novelty preference. For the control condition, 61.1% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	One-tailed paired T-test (<i>p</i> value)
VPC with AB's face	5177.77 (303.76)	3924.44 (315.63)	56.93 (3.35)	0.037
Control vpcs	5422.22 (375.82)	3988.89 (3305.84)	57.39 (3.72)	0.044

Table 3.4: the mean percentage looking time to the novel stimulus

The difference between the interaction condition and the standard VPCs in Experiments 1a and 1b cannot, therefore, be explained by the choice of habituation

stimulus. That is, when participants had no prior interaction with the person presented as the stimulus in the VPC procedure, they exhibited the traditional novelty preference. Based on the results of these three experiments, there seems to be something about the act of engaging in social interaction with an individual, rather than being habituated to a static picture, that causes a null preference to result.

As a means of investigating this further, an additional single visual preference task was conducted with participants who had substantially longer to habituate to a face. Whilst the traditional VPC presents a visual stimulus for a short period of time for habituation, real-world object exposure is obviously a much longer process. In essence, replacing the habituation phase with a more protracted period of naturalistic learning is an important adjunct to experiments 1a, 1b and 1c. It is hypothesised that a null preference will be obtained in the same manner as was observed in these previous experiments, as the attenuation of the novelty preference is held to be attributable to the social interaction component of the habituation period.

Experiment 1d

Method

Participants

12 Undergraduate students aged 19-21 years were tested. Eleven participants were White British and one was Asian British. Ten participants were female. Participants were drawn from the undergraduate psychology population and had all been members of four, 1-hour small group tutorials taken by experimenter AB. No participant had taken part in the previous experiments. One male and one female participant was rejected from statistical analysis; the former failed to spend more than 10% of the looking time

attending to one of the stimuli, and the latter produced uncodable data due to a reflection in her glasses obscuring eye movement recordings.

Stimuli

Participants were tested with a single VPC. The habituation period to experimenter AB consisted the four hours spent in tutorials; test stimuli were a digital image of AB matched with another male face in the manner described in the previous experiments.

Procedure

The procedure was identical to that used in experiment 1a, except that only the interaction condition trial was conducted. The experiment was conducted at the end of the 4th 1-hour tutorial, at the end of a period of 8 weeks during which an additional three 1-hour tutorials had been attended at two-week intervals. As in Experiments 1a and 1b, the present experiment was conducted by AB.

Results and Discussion

Videoed looking data was coded as in Experiment 1a. Due to the sample being 83% female, it was again not possible to conduct an ANOVA with the intention of collapsing groups across gender. The effect of interaction on the expression of recognition memory was examined; a one-tailed paired t-test was conducted. Participants demonstrated a null preference (see table 3.5). 40% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	One-tailed paired T-test (<i>p</i> value)
4 hours social interaction	4536 (210.58)	4368 (181.14)	50.88 (2.02)	0.327

Table 3.5: the mean percentage looking time to the novel stimulus

On the basis of experiments 1a to 1d, then, it can be argued that the expression of adult visual recognition memory is altered in the VPC task when the standard habituation period to a static picture is replaced with a period of real-life interaction. A null preference is observed whether this naturalistic ‘habituation’ is brief (60 seconds) or extended (4 hours). In contrast, standard VPC trials demonstrate robust novelty preferences across groups.

A methodological shortfall of experiments 1a to 1d is that a large majority of the participants tested were female. Whilst there is no reason to suppose that a test as simple as the VPC is affected by gender, it must be borne in mind that the experimental sample was not matched for gender. To address this in further research, both male and female participants should be tested with both male and female faces (only male faces were used in the experiments in this chapter). Nonetheless, the findings with standard VPCs were robust novelty preferences as hypothesised, and results from all experiments are striking in their consistency.

There remains the possibility that the current series of findings are in some manner being compounded by a 'mere exposure' effect of sorts. The 'mere exposure' hypothesis (Zajonc, 1968) contends that simple pre-exposure to a stimulus is sufficient to predispose participants to subsequently state a preference to that stimulus rather than previously unencountered stimuli. Interestingly, the greatest 'mere exposure' effects are observable when stimuli are initially presented subliminally, clearly suggesting the involvement of implicit memory. However, there is also empirical evidence for the 'mere exposure' effect when participants are consciously aware of stimulus presentation (see Bornstein & Dagostino, 1992).

It is possible that the length of exposure provided here to a live face is sufficient to disrupt the expected novelty preference, because the preference that has been engendered to the familiar stimulus is now in competition with the novel stimulus. Experiment 2, then, investigates this possible variable.

Experiment 2 – Famous Faces

A parsimonious way to investigate the possible role of the effect of familiarity preference competing with novelty preference is to conduct a simple visual preference task in which looking time in adults is measured when participants are presented with a pair of face stimuli, one of which is famous and one of which is unknown. Famous faces make the ideal stimuli because they have been encountered in a wide variety of contexts, both moving and static, but crucially not in an interactive manner. If a null preference was found in a VPC which used famous faces as the stimuli, it would suggest that it is not

interaction per se that is influencing the null preference found throughout this chapter but mere exposure.

Method

Participants

20 Undergraduate students aged 19-21 years were tested. Seventeen participants were White British, two were Asian British and one was mixed race. 10 participants were female. Participants were drawn from the undergraduate psychology population and were rewarded for participation with participation stickers as part of the course requirements. Although each subject was presented with two visual preference trials, two male participants and one female participant failed to report recognition of the famous face on one trial each; these trials were excluded from analysis.

Stimuli

Black and white digital images were created of 18 famous faces (for stimuli see appendix D.) Each famous stimulus was paired with a nonfamous face matched as closely as possible for gender, race, age, approximate orientation of face, approximate hairstyle, and any notable features such as glasses. Prior to experimentation, the famous faces were presented to a pool of undergraduate participants to determine that they were easily recognizable. The faces used in this experiment were recognized 100% of the time.

Procedure

The general procedure was identical to that used in the previous experiments which were conducted with static VPC. Each participant was presented with two pairs of faces; one male pair and one female pair drawn from the pool of matched stimuli and

presented in random order. For each pair, participants were presented with two five-second trials in randomised, counterbalanced order. Following the test, participants were asked to identify the famous face in each trial. Participants who were unable to do so were excluded from analysis. Famous face identification was an inclusion criterion because failure to recognise a face suggests insufficient exposure to it for it to be regarded as familiar.

Results and Discussion

Videoed looking data was coded as in the previous experiments.

. A two-sample t-test was firstly conducted between genders to determine whether the gender of the participant affected looking time. There were no significant differences in looking times across conditions (see table 3.6). The groups were therefore collapsed across gender.

Participant gender	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
male	55.147	0.399
female	50.934	

Table 3.6: t-test comparison by gender

The effect of interaction on the expression of recognition memory was then examined; a one-tailed paired t-test was conducted. Participants demonstrated a preference for the non-famous face in contrast to the famous face seen during the

familiarisation ($t(36) = 1.565, P = 0.017$; see table 3.7). 65% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	One-tailed paired T-test (p value)
Famous faces versus unknown faces visual preference task	2434 (88.16)	2153 (93.08)	53.1199 (1.93)	0.017

Table 3.7: the mean percentage looking time to the unknown stimulus

When tested with faces they have seen before in a variety of contexts, t-test analysis indicates that participants spent more of the available looking time looking at the novel face. This suggests that the mere exposure effect is an unlikely cause of the results in Experiment 1. Such a finding provides further evidence that it is the *nature* of the habituation periods employed here that leads to the observed elimination of the novelty preference in experiments 1a, 1b and 1d.

Experiment 3 – The puppet task with adults

The final experiment in this series of studies considers the role of interaction in the task by examining how adults perform on the video condition of the same puppet task developed for use with infants in Chapter 2. As it would be inappropriate for this age group to be watching a live puppet show, it was decided to investigate performance on the MPG condition. If adults also express a null preference in this task it would provide additional evidence that the VPC is disruptable by the inclusion of interaction at habituation across the human lifespan, and would raise theoretical questions concerning how different the mnemonic processes in infants and adults, as measured by the VPC, can be argued to be.

Method

Participants

12 Undergraduate students aged 19-21 years were tested. Participants were all white, and 8 participants were female. Participants were drawn from the same population and in the same manner as in experiment 1a; they were rewarded for participation with participation stickers as part of the course requirements, and were only drawn from years 1 and 2 of the undergraduate psychology course.

Stimuli

Stimuli were identical to the MPG condition of the puppet experiment conducted in chapter 2 experiment 2.

Procedure

Participants were seated in front of the projection screen as described above. It was explained to them that they were going to see a video and some pictures appear on the screen, and that all they were required to do was to relax and simply watch the film. In addition, they were instructed to try not to 'second-guess' the purpose of the experiment.

Results and Discussion

Videoed looking data was coded as in the previous experiments. A two-sample t-test was firstly conducted between genders to determine whether the gender of the participant affected looking time. This demonstrated that there were no significant differences in looking times across conditions (see table 3.8). The groups were therefore collapsed across gender.

Subject type	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
male	50.928	0.501
female	46.678	

Table 3.8: t-test comparison by gender

The effect of interaction on the expression of recognition memory was then examined; a one-tailed paired t-test was conducted. Participants demonstrated a null preference (see table 3.9). 50% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	One-tailed paired T-test (<i>p</i> value)
Puppet video	4304.17 (280.63)	4660 (298.05)	48.09 (3.05)	0.268

Table 3.9: the mean percentage looking time to the unknown stimulus

These results demonstrate that exposure to a dynamic moving stimulus (the puppet task) during habituation leads to a similar disruption of the novelty preference in adults as has been observed in 6- and 18-month-olds in chapter 2. This is further evidence that the parameters within which the VPC can be expected to induce a novelty preference in infants is narrower than has previously been considered; a non-static habituation period is outside these parameters.

General discussion

In summary, Experiment 1 ascertained that when the standard habituation period of a VPC methodology is replaced with a 60 second period of naturalistic social interaction, the novelty preference that is reliably observed with adults tested in the standard task is attenuated to such an extent that a null preference is instead reliably observed. The same finding is obtained if the interaction period is increased to four hours experience in the context of small group tutoring. Static face VPCs, in contrast, demonstrate the novelty preference when the habituation period is either 5 seconds or 60

seconds long, and when it is conducted with the same face employed as habituation stimulus in the social interaction conditions.

In contrast to the null preference observed following interaction, experiment 2 revealed a significant novelty preference when the stimuli were highly familiar (famous faces) but had not been encountered through interactions. Finally, in experiment 3, it was demonstrated that adults demonstrate a null preference when tested with the video version of the puppet task designed for use with infants, of whom 6 and 18-month olds performed similarly.

A number of conclusions can be drawn from this data. Firstly, in the task's standard, static form, all data here support the assertion that the VPC is a suitable test for use with adults. Strong novelty preferences were consistently and reliably elicited when the traditional stimulus presentation was used. The standard VPC task therefore appears to be a task suitable for use right across the human lifespan. The use of the VPC is less common with adults than with infants, and at present only a handful of studies have been reported (e.g Fagan & Haiken-Vasen, 1997; Pascalis et al, 2002; Pascalis & Bachevalier, 1998; Richmond, Sowerby, Colombo & Hayne, 2004; Manns, Stark & Squire, 2000). A possible next step in synthesising such findings would involve systematically investigating the development of visual recognition memory through childhood, and also into old age. There is also a great deal of scope for investigating the relationship between visual recognition memory and other forms of memory in later childhood and adulthood. It has been demonstrated here that a standard habituation can be up to 60 seconds in length and still elicit a novelty preference in adults, providing evidence that the task has

the potential to be used in situations requiring more complex encoding than is possible in studies with infants.

A second conclusion concerns the failure of adults on versions of the test incorporating social interaction. It is highly unlikely to be the case that adults produce null preferences because they are unable to remember which face they have previously seen; indeed, this is empirically confirmed in the next chapter. Rather, what is being disrupted is eye movement and looking behaviour during the first few seconds of stimulus presentation. The data from the famous faces looking task (experiment 2) provides evidence that this is not due to the expression of a 'mere exposure' preference for the previously encountered stimulus.

This finding is directly relevant to any VPC research that seeks to manipulate the task in novel ways. Specifically, the rationale of the standard task is that, providing sufficient habituation has occurred, the novelty stimulus will be the focus of the majority of attention during the test period because the familiar stimulus is no longer as attractive. Such an assumption rests on the two test stimuli being equally attractive, and on the habituation period not having been encoded as salient or attractive in any manner that might then impact upon the intrinsic preference for novelty underpinning attention to the new stimulus. What *may* be happening in VPC task variants in which the habituation period involves some sort of interaction (or, in the case of infants, engenders emotion) is that, rather than attention for the habituation stimulus being satiated by sufficient habituation time, the likelihood of further attention occurring during the test period is actually increased due to the attractiveness, complexity or salience of the stimuli itself.

In future research, such a possibility could be addressed by a systematic manipulation of the variables outlined here. The length of presentation of the habituation stimulus, the complexity of the habituation stimulus, the degree of movement of the habituation stimulus, the degree of interactivity employed if the stimulus was a human face, and the degree to which the test stimuli were matched to resemble the habituation stimulus are all amenable to systematic manipulation. The length of the habituation period could be tested between very brief (a few seconds) to very long (several minutes) exposures.

If the hypotheses expounded here were correct it might be reasonable to suppose that a strong familiarity preference would be observed at very brief habituation exposures due to insufficient encoding. There might then follow an optimal habituation exposure during which stimulus encoding was complete. Following this optimal period, and depending on the attractiveness or salience of the habituation stimulus, a null preference engendered by the competing attractiveness of both stimuli might be observed.

The effect of the complexity of the habituation stimulus itself could be similarly explored. Moving, interactive faces are a particularly salient stimulus. If much less salient but nonetheless moving stimuli were employed – simple geometric shapes, for example – it would be interesting to see whether it would be possible to observe a novelty preference. The employment of an intermediate level of complexity of habituation stimuli – for example, a geometric shape that nonetheless had discernible ‘eyes’ that moved and attended to the subject – might shed further light on the impact of this variable. The effect of the degree of movement of the habituation stimulus could be similarly explored. This is a variable that has begun to be explored with the puppet stimuli used here in

experiment 3; easily-discernible puppet stimuli have been shown to elicit a null preference with adults. This could be explored in further detail with a series of increasingly simple objects that retained discernible 'eyes' and possibly other facial features.

A variable which would be particularly interesting to scrutinize is the degree to which the test stimuli match the habituation stimuli. If, for example, the habituation stimuli was a video of a moving human face, it would be of interest to employ test stimuli which also moved. Such exploration would bring with it a methodological challenge; the movement of the two test stimuli would have to be very carefully controlled in order to ensure that the movement of one of the pair was not more likely to demand attention than the other. If both habituation and test stimuli incorporated a small amount of movement, however, such a problem would not be insurmountable.

On the basis of the results obtained here and in chapter two, however, one of the most interesting directions for future research concerns to what extent the standard VPC task has to be manipulated, both in infants and adults, before the novelty preference is attenuated to a statistically significant degree. Before taking such consideration any further, however, another variable that appeared to impact on infant visual recognition memory performance in chapter 2, emotion, requires examination with an adult population. Chapter 4 will consider the impact of emotional processing on adult performance on the VPC task.

Chapter 4 – The Expression of Memory in Adults is Altered by the Inclusion of Emotional Processing

The effects of the interaction component of the adapted VPC puppet task administered in chapter 2 have been shown to have an equivalent in tasks adapted for use with adults. A further component that can be seen to impact on infant performance is emotion. In the infant experiments in chapter 2, an additional variable that can be presumed to be impacting upon the attenuation of the novelty preference concerns the emotion experienced by participants.

The results of chapter 3 robustly demonstrated the suitability of the VPC for use with an adult population. Adult participants are also a valid population for consideration of emotional processing.

It is possible that emotional processing similarly impacts on the expression of visual recognition memory in adults. In infants, it is theorised that the failure to demonstrate a novelty preference in the adapted task at ages at which a robust novelty preference is elicited by a standard task has its roots in the developing connectivity between the amygdala and the medial temporal lobe memory system. If, however, a similar disruption is observable in adults, this will provide information about the parameters within which the task can be usefully employed, and will also inform discussion about the putative automaticity of the memory system responsible for task success in infants.

In investigating the role of emotional processing in the expression of memory as measured by the VPC in adults, it is necessary to implement age-appropriate

methodologies as reviewed in chapter 3. One potential way to examine the impact of emotion processing on the VPC task in adults is to incorporate emotional faces into standard VPC methodologies. Visual emotion processing, in which images of faces displaying emotion are presented to participants, is a substantial research field (e.g. see Ekman, 2003; Koff, Zaitchik, Montepare and Albert, 1999).

An additional methodological issue that is addressed here concerns the problem that the majority of experimental stimuli employed in the previous chapter lack the 1:1 correspondence between habituation and test stimulus that *is* observed in the typical VPC. In the standard task, the habituation stimulus and the familiar stimulus employed at test are exactly the same; in the majority of experiments conducted here, they have not been identical. To address this, an additional control group will be employed here in which there is not a direct correspondence between habituation and test stimuli. Images of faces in a quarter profile (i.e. facing the camera and then turning 45 ° to the side) are to be employed as habituation stimuli; the test stimuli will be standard images of faces looking directly at the camera.

The first experiment conducted here, then, will employ three categories of stimuli. Neutral control faces will be employed as in the previous chapter. In addition, quarter profile control stimuli will be presented. The emotional test stimuli themselves will be presented in two conditions; in one, faces showing emotion will be presented at the point of habituation whilst neutral faces will be employed at test. In the second condition, a neutral face will be employed at habituation and emotion faces will be presented at test. If the role of emotional processing on disrupting the novelty preference is restricted to the condition in which it is presented at habituation rather than at test, this would be grounds

for concluding that it is the encoding, and not the retrieval, process that is amenable to disruption.

Experiment 1 – emotional processing and the VPC in adults

Method

Participants

32 Undergraduate students aged 19-21 years were tested. 30 participants were White British, one was Black British and one was Asian British. Seventeen participants were female. Participants were either drawn from the undergraduate psychology population or were non-psychology undergraduates of the same age and known to the experimenter. Undergraduate students were rewarded for participation with participation stickers as part of the course requirements and had not participated in previous VPC studies. Two participants were rejected from statistical analysis for failing to spend more than 10% of the looking time attending to one of the stimuli on one or more trials. One subject was excluded from statistical analysis due to equipment error.

Stimuli

Neutral controls

Two female faces and two male faces, all with the hair masked, were selected from the laboratory archives. Each pair was selected to be distinguishable but similar (see appendix E)

Quarter profile controls

Two masked female faces and two masked male faces were selected from the laboratory archives. Each face was captured in three positions – facing the camera, facing 90° to the left and facing 90° to the right. Each pair was selected to be distinguishable but similar.

Emotion faces

Two masked female faces and two masked male faces were selected from the laboratory archives of faces that have been used in many face processing and VPC studies. Each face was depicted looking fearful, happy and neutral. Facial expressions were rated by a pool of separate participants to ensure robust recognition of the emotional states they represented.

All stimuli used were of people unknown to experimental participants. Stimuli were back-projected onto a 45cm * 32 cm screen positioned approximately 60cm in front of the subject. A camera positioned centrally above the screen recorded the subject's eye movements between the two items.

Procedure

Participants were tested individually in the babylab, seated in front of the screen. As in the previous studies reported in Chapter 3, adults were informed that they were going to see some pictures appear on the screen, and that all they were required to do was to relax and simply watch the pictures. They were also instructed to try not to 'second-guess' the purpose of the experiment.

Participants were then presented with 6 VPC trials: two neutral control trials, two three-quarter profile trials, and two emotion trials. The three categories of stimuli were randomised; within each stimulus type, all stimuli were randomised and counterbalanced

such that each subject was presented with one VPC with female faces and one with male faces for each stimulus type.

The emotion stimuli were presented in two separate conditions; emotion at habituation and emotion at test. In the former, participants viewed either a happy or a fear stimulus at habituation and neutral faces at test. In the latter, the subject was habituated to a neutral stimulus and was presented with emotional faces at test (see appendix E for examples of stimuli).

Results and Discussion

A two-sample t-test was firstly conducted across gender to determine whether the gender of the participant affected looking in the VPC. There were no significant differences in looking times across conditions (see table 4.1). The groups were therefore collapsed across gender for subsequent analyses.

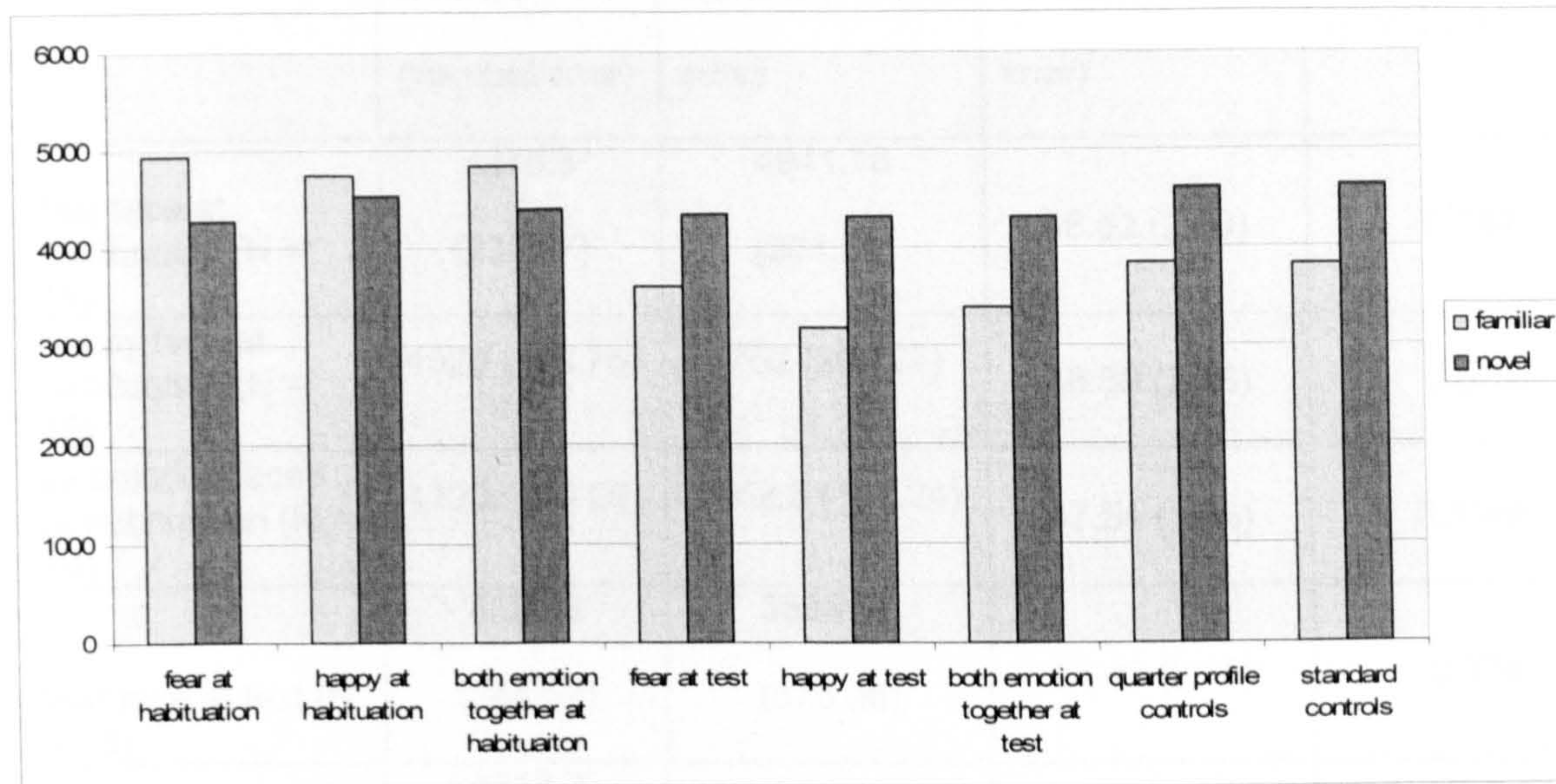
Gender	Stimulus type	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
Male	standard controls	55.403	0.467
Female	standard controls	53.298	
Male	quarter-profile controls	52.823	0.259
Female	quarter-profile controls	55.955	
Male	emotion at habituation	48.686	0.555
Female	emotion at habituation	46.64	
Male	emotion at test	53.218	0.153
Female	emotion at test	58.968	

Table 4.1: t-test comparison between looking times by gender of participant

The effect of interaction on the expression of recognition memory was then examined through a series of one-tailed paired t-tests (see table 2 and graph A). When emotion was present at habituation, a null preference was obtained for all emotional stimuli.. Such a result is in the direction of a familiarity preference, and in the cases of fear stimuli and both stimuli together approaches statistical significance (see graph 4A and table 2). This demonstrates that the inclusion of emotional processing demands at habituation impacts on visual recognition memory performance. When emotion was instead present at test and the habituation stimulus was emotionally neutral, a significant novelty preference was observed for both emotion together ($t(30) = 2.925, P < 0.01$) and for happiness ($t(14) = 2.175, P < 0.05$); fear stimuli fell short of significance ($t(14) = 1.931, P = 0.074$); see graph 4A and table 4.2). This demonstrates that the inclusion of emotion at test rather than at habituation does not alter the novelty preference that would be expected in a typical VPC. When emotion was presented at habituation, 40.6 % of subjects showed a looking time in the direction of a novelty preference. When emotion was presented at test, 76.65 % of subjects showed a looking time in the direction of a novelty preference.

For standard control stimuli, a novelty preference was observed ($t(61) = 3.168, P < 0.01$). 69.4% of subjects showed a looking time in the direction of a novelty preference. For quarter-profile controls, a novelty preference was also observed ($t(61) = 3.222, P < 0.01$). 64.6% of subjects showed a looking time in the direction of a novelty preference. This demonstrates that for non-emotional controls, adult performance is as hypothesised. Furthermore, additional evidence that the lack of 1:1 correspondence in the emotion conditions is not the exclusive reason for the lack of a novelty preference when emotion

is present at habituation is provided by the quarter-profile controls, in which a typical novelty preference is observed.



Graph 4A: group average looking times in milliseconds by condition

Stimulus type	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	Two-tailed paired T-test (<i>p</i> value)
fear face at habituation (N = 16)	4275.3 (236.67)	4941.18 (264.56)	46.52 (2.59)	0.194
happy face at habituation (N = 16)	4520 (215.76)	4752 (200.27)	48.69 (2.13)	0.571
all emotion faces at habituation (N = 16)	4390 (160.29)	4852.5 (167.24)	47.54 (1.68)	0.1566
fear face at test (N = 16)	4325.3 (344.52)	3598.67 (375.06)	55.43 (2.35)	0.074
happy face at test (N = 16)	4313.3 (422.9)	3184 (336.59)	57.14 (3.28)	0.047
all emotion faces at test (N = 16)	4319.3 (267.99)	3391.3 (250.57)	56.285 (1.99)	0.007
quarter-profile controls (N = 32)	4606.45 (177.62)	3835.48 (161.34)	54.25 (1.37)	0.002
standard controls (N = 32)	4622.42 (188.83)	3820.65 (146.83)	54.54 (1.43)	0.002

Table 4.2: the mean percentage looking time to the unknown stimulus by condition

There is strong evidence, therefore, that adult performance on the VPC is affected by the inclusion of emotional expression in face stimuli. Furthermore, this effect is dependent upon whether emotion is included at the point of habituation or of test. When emotion is present at habituation, a novelty preference as obtained with neutral control

stimuli is observable. When emotion expressions are instead included at test, however, there is instead a familiarity preference approaching statistical significance for the fear faces and for both emotion faces analysed together. This finding is perhaps because a face displaying emotion (particularly negative emotion) is particularly salient and as such required immediate attention such that this need is in competition with the preference for novelty in the test period.

It is not the case, of course, that the emotion component of the experiment conducted here is directly equivalent to the role of emotion in the infant experiment in chapter 2 or in previous research with infants (e.g. Nachman, Stern, & Best, 1986), in which emotion is *engendered* in the subject. Nevertheless, taking both sorts of experiment together, it is reasonable to conclude that the novelty preference is disruptable in the VPC in both infants and in adults when an emotional processing element is introduced at the habituation stage.

A further ramification of the findings presented here concerns the complexity of human faces as stimuli in VRM paradigms. The finding that the novelty preference is disrupted when (and only when) an expression associated with an emotion is presented at the point of habituation demonstrates just how attuned to facial nuances humans are. In turn, this leads to a consideration of the stimuli that are used in VPC research, and the robustness of findings with stimuli of varying complexity. Many different stimuli have been employed in the history of the VPC task, often with the assumption that the expected novelty preference is normally obtainable regardless of the categories of stimuli used. In addition to human faces, Line drawings, pictures of cars, pictures of houses, pictures of household objects, pictures of monkey faces, and pictures of static and

moving shapes of varying levels of complexity have also been employed. Such different stimulus categories differ not only in their individual complexity, but also in their within-category similarity; hence, some stimuli are more readily discriminable than others. An investigation of these variables is overdue; the purpose of the next experiment, then, will be to compare VPC performance on stimuli ranging from the readily discriminable to the comparatively homogenous.

Experiment 2a: greebles and other animals

Some of the most complex *and* homogenous stimuli are *greebles* (see appendix F). Greebles are abstract, monochromatic shapes designed to be difficult to discriminate, and are most typically used as an adjunct to face recognition research as a comparably difficult data set with which participants have had no previous experience, but can become 'expert' with intensive training (see Gauthier, Williams, Tarr & Tanaka, 1998; Gauthier & Tarr, 1997). In addition, greebles have been used with neurological patients to investigate the putative specialisation of the face detection system (see Gauthier, Behrmann & Tarr, 2004; Duchaine, Dingle, Butterworth & Nakayama, 2004).

Greebles are an advantageous data set to use with VPC tasks because they are difficult to discriminate, unlikely to have been previously encountered, and sufficiently dissimilar from ordinary objects to remove any possible confounding variables concerning learned preference or even partial familiarity. Thus, the *a priori* assumption of the VPC – that the habituation and the test stimuli are equally attractive – is firmly met. Furthermore, running VPC methodologies with stimuli that are intentionally difficult to discriminate between addresses an important methodological question; in terms of the

VPC, are all stimuli equal ? Whilst, intuitively, the answer must be 'no', there has been no systematic consideration within the field of the effects of stimulus complexity on the VPC, with the result that stimuli ranging from the extremely simple to complex, sometimes moving shapes (often presented along with sound) are in effect regarded synonymously. Greebles themselves have also been used as VPC stimuli (Snyder, K., unpublished).

A further collection of abstract shapes, *fribbles*, (copyright Michael J. Tarr (<http://www.tarrlab.org/>)) have been developed for similar purposes as greebles, but are more complicated shapes consisting of subcomponents that can be altered to provide discrete differences between exemplars. In addition, they are multicoloured (see appendix F)

The role of the comparative complexity and similarity of VPC stimuli is obviously an essential variable to understand when designing tasks. To this end, a comparison of four different categories of stimuli was conducted, in which adults were presented with VPC trials including human faces, chairs, greebles and fribbles. If, at typical presentation rates, stimulus complexity is not a critical feature of task design, it would be reasonable to expect a novelty preference to be observable in response to all categories of stimuli. If, on the other hand, stimulus complexity *does* impact on task performance, it would be hypothesised that whilst a novelty preference would be observable in the least complex stimulus categories (chairs and faces – although faces are of course objectively complex stimuli, human adults are experts at distinguishing between them), this effect will be attenuated for greeble and fribble stimuli such that a novelty preference will be observed. Stimulus similarity is an additional important factor explored here. The rationale of the VPC rests on the two presented stimuli being

distinguishable; if they are hard to distinguish, a null preference might be expected to result.

Method

Participants

14 Undergraduate students aged 19-21 years were tested. Participants were all White British, and 9 were female. Participants were drawn from the undergraduate psychology population; students were rewarded for participation with participation stickers as part of the course requirements. Two participants were rejected from statistical analysis for failing to spend more than 10% of the looking time attending to one of the stimuli on one or more trials. No participants had undertaken previous VPC studies.

Stimuli

Four categories of stimuli were presented. Photographs of masked male faces and of chairs were drawn from lab archives; greeble and fribble digital images were provided by Michael J. Tarr and used with permission. Greeble stimuli were chosen so that, although they were similar, they were still easily distinguishable (as the rationale of the VPC depends on the discriminability of stimuli). Three categories of fribble stimuli were chosen, and were again matched within-families so that they were similar but distinguishable.

Procedure

The general procedure was identical to Experiment 1 with the exception that participants were presented with 6 VPC trials: one with chairs, one with faces, one with greebles, and three with fribbles (one with each of the three different categories). The three categories of stimuli were randomised; within each stimulus type, all stimuli were randomised and

counterbalanced. The order of presentation was additionally randomised. Each VPC consisted of a five-second habituation period and two five-second test periods.

Results and Discussion

Videoed looking data was coded as in the previous studies.

A two-sample t-test was conducted across gender to determine if participant gender affected looking behaviour. This demonstrated that there were no significant differences in looking times across conditions (see table 4.3). The groups were therefore collapsed across gender for subsequent analyses.

Gender	Stimulus type	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
Male	chairs	57.175	0.717
Female	chairs	59.332	
Male	faces	63.567	0.317
Female	faces	55.191	
Male	fribbles	53.857	0.553
Female	fribbles	51.619	
Male	greebles	53.108	0.858
Female	greebles	54.14	

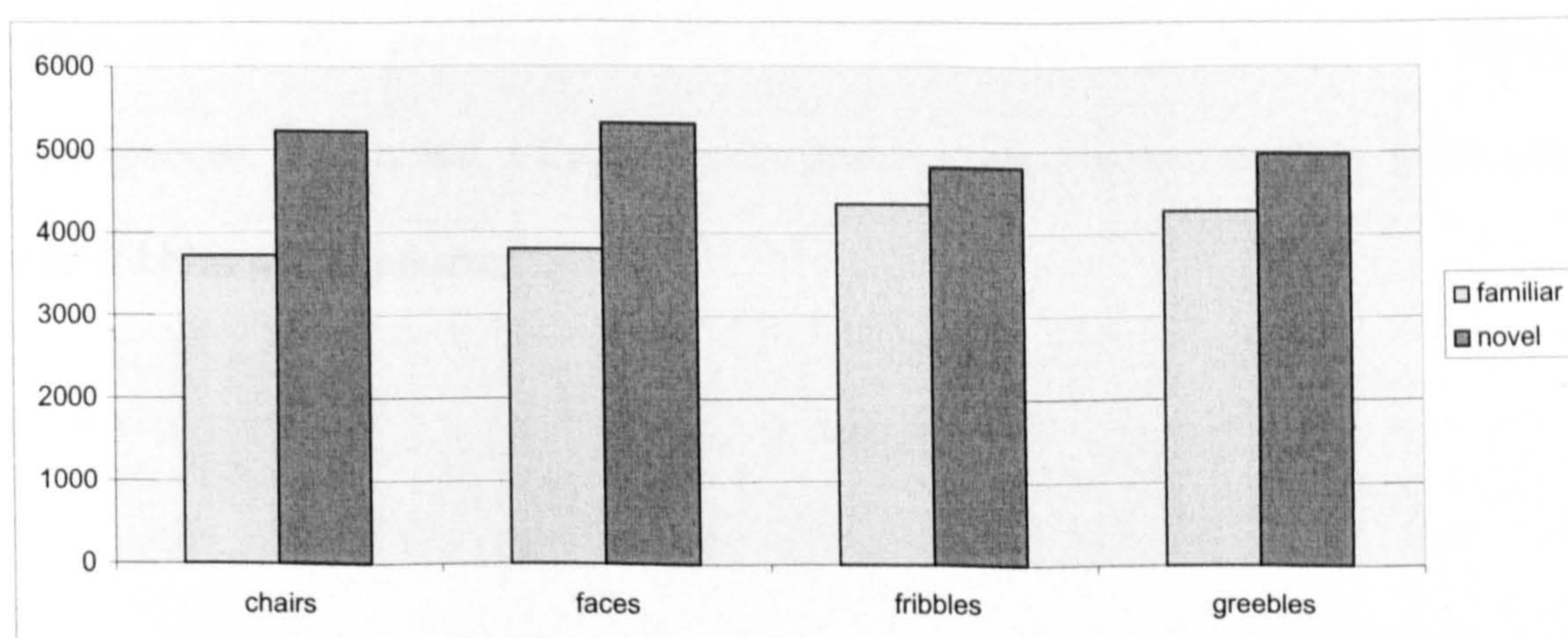
Table 4.3: t-test comparison between looking times by gender

The effect of interaction on the expression of recognition memory was then examined. A series of one-tailed paired t-tests were conducted. The VPC with chair stimuli ($t(13) = 3.402, p < 0.001$) and the face stimuli ($t(13) = 2.112, p < 0.05$) demonstrated a novelty preference. For chair stimuli, 85.7% of subjects showed a looking time in the direction of

a novelty preference. For face stimuli, 71.4% of subjects showed a looking time in the direction of a novelty preference. The VPC with greeble stimuli and with the fribble stimuli both demonstrated a null preference in the direction of a novelty preference (see table 4.4 and graph 4B). For greeble stimuli, 57.1% of subjects showed a looking time in the direction of a novelty preference. For face stimuli, 50% of subjects showed a looking time in the direction of a novelty preference.

Stimulus type (N = 14)	Mean looking time to novel stimulus (standard error)	Mean looking time to familiar stimulus (standard error)	Mean % looking time to novel stimulus (standard error)	One-tailed paired T-test (<i>p</i> value)
Chairs	5214 (210.67)	3734 (265.58)	58.27 (2.51)	0.002
Faces	5317 (366.98)	3811 (354.05)	58.25 (3.86)	0.027
Greebles	4974 (200.42)	4266 (230.30)	52.35 (2.58)	0.076
Fribbles	4791(200.423)	4360 (212.65)	53.83 (2.23)	0.078

Table 4.4: the mean percentage looking time to the unknown stimulus by condition



Graph 4B: group average looking times in milliseconds by condition

Whilst results are in the expected direction for all stimulus categories, then, for the more complex stimuli the novelty preference is not statistically significant. Such a finding has implications for the design of VPC methodologies. Whilst different stimuli are used with infants with widely different habituation times by different researchers, it is of interest that even in an adult experimental population stimuli are non-equivalent. Anecdotally, there can be little doubt that adults recognise the habituation stimuli even for categories in which the novelty preference was not significant; this will be borne out empirically in the next experiment. The contention, then, is that visual recognition memory as measured by the VPC is sensitive to stimulus complexity: the magnitude of the novelty preference is modulated by the degree to which the two presented stimuli are discriminable.

One advantage of testing visual recognition memory in adults is that comparison is afforded between experimental paradigms. It is therefore possible to verify empirically whether the results of the VPC are similar to the results of a forced-choice task with the same stimuli used here. If it is the case that the tests have some equivalence, the argument for the suitability of the VPC being used right across the lifespan is strengthened. To this end, a forced choice memory task employing chairs, faces, greebles and fribbles was conducted.

Experiment 2b: forced-choice memory task

Method

Participants

20 Undergraduate students were tested, 14 of whom were also tested on experiment 2A (for those tested on both, experimental order was counterbalanced). Participants were all White British, and 13 of them were female. Participants were drawn from the undergraduate psychology. Undergraduate students were rewarded for participation with participation stickers as part of the course requirements.

Stimuli

A pool of the four categories of stimuli was created, consisting of 20 chair digital images, 20 masked face digital images (10 male and 10 female), 20 fribble digital images (from three different families – seven of type A, seven of type B, six of type C – see appendix G), and 20 greeble digital images. Stimuli were paired together within-category; in addition, faces were always presented with a face of same gender, and fribbles always presented with a fribble from the same family. All 80 trial were presented in random order using purpose-built software Devlab (version 2004, developed in conjunction with UCL) such that one of each pair was presented for a brief period (either 200ms or 400ms depending on condition), and was then re-presented simultaneously with the novel paired image.

Procedure

Participants were tested on a laptop computer in a quiet office in the department of psychology at the University of Sheffield using a forced-choice task. Participants were instructed that they were going to see an individual picture briefly presented centrally on the computer screen, then two pictures, one to the left of the screen and one to the right.

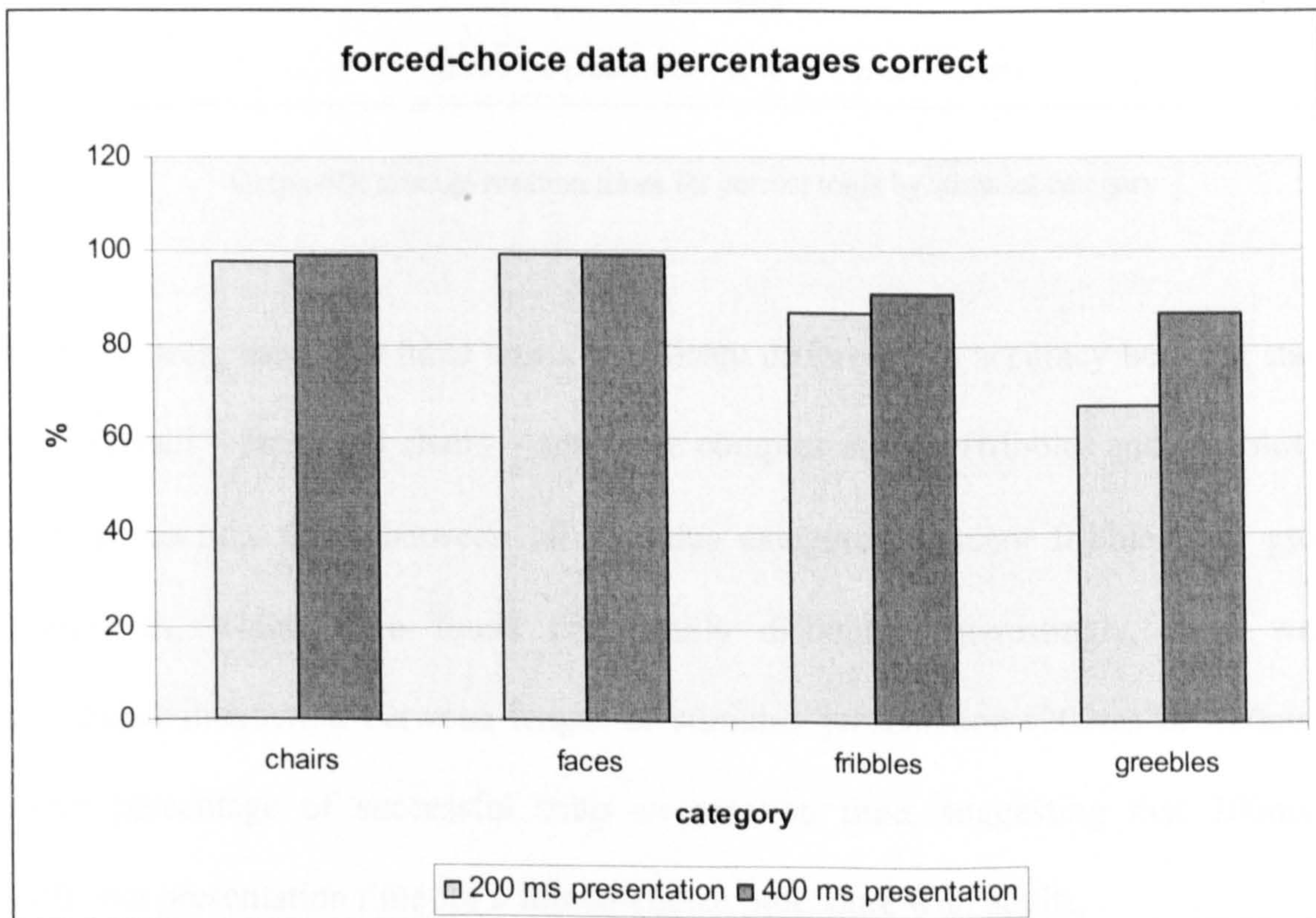
They were informed that one of these two pictures would be identical to the picture presented individually; if they believed the identical image to be the one presented to the left of the screen, they were to press the 'Z' key. If they believed it to be the image on the right, they were to press the 'M' key. They were instructed to do this as quickly but also as accurately as they could. Following six practice trials, the complete experiment was conducted. There were two experimental groups; those for whom the initial image presentation was 200ms, and those for whom it was 400ms. Two presentation conditions were included to ascertain whether even comparatively brief presentation was sufficient for recognition, and yet to allow presentation to be sufficiently long to allow a degree of comparison with the VPC.

Results and Discussion

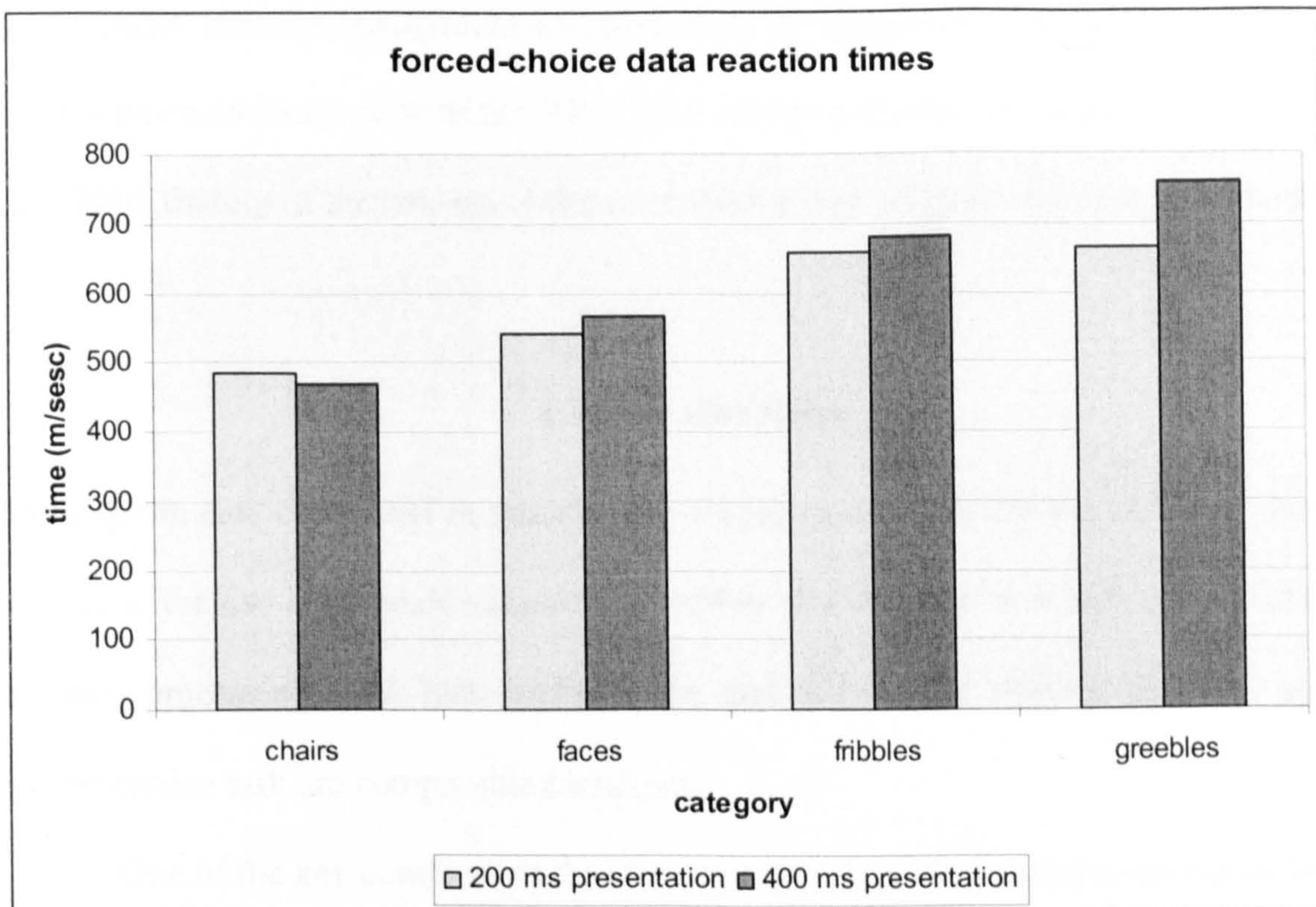
Two multi-factor ANOVAs were conducted. The first was a 1-within, 2-between factor ANOVA comparing the percentage of correct trials in each category, with stimulus type as the within-factor variable and gender and presentation length as between-factor variables (see graph 4C). A significant main effect of stimulus type was observed ($F(3,48) = 13.790, P < 0.001$). There were no other significant main effects or any interactions. Post-hoc analysis (with a Bonferroni adjustment) revealed no significant difference between the chair and face stimuli or between the greeble and fribble stimuli. However, greebles differed significantly from chairs ($P = 0.001$) and from faces ($P = 0.000$). Fribbles also differed significantly both from chairs ($P = 0.031$) and faces ($P = 0.007$). Fribbles and greebles did not differ significantly from each other ($P = 0.115$).

The second ANOVA was again a 1-within, 2-between factor design comparing the reaction time to stimuli, with stimulus type as the within-factor variable and gender

and presentation length as between-factor variables (see graph 4D). A significant main effect of stimulus type was observed ($F(3,48) = 19.257, P < 0.001$). There was no significant interaction between stimulus type and length of presentation or gender. Post-hoc analysis (with a Bonferroni adjustment) revealed that chair stimuli differed significantly from face, greeble and fribble stimuli ($P < 0.001, < 0.001$ and < 0.001 respectively). Face stimuli also differed significantly from greeble and fribble stimuli ($P < 0.001$ and 0.01 respectively). Greeble and fribble stimuli did not, however, differ significantly from each other.



Graph 4C: average percentage correct by stimulus category



Graph 4D: average reaction times for correct trials by stimulus category

It can be seen, then, that there was a significant difference in accuracy between standard VPC stimuli – faces and chairs – and more complex stimuli (fribbles and greebles), and also in reaction times between all stimulus categories (except fribbles and greebles themselves, which were found comparably difficult). Interestingly, there was no significant interaction between length of stimulus presentation (200ms or 400ms) and either percentage of successful trials *or* reaction time, suggesting that 200ms is a sufficient presentation time for a forced-choice procedure with adults.

There do, though, seem to be similarities between the forced-choice data and the VPC data. Fribbles and Greebles *are* found by participants to be more difficult in both sorts of test. Such a finding demonstrates the non-equivalence of different categories of stimuli when used in tests of visual recognition memory. In the forced-choice

experiment, stimulus recognition was high even for categories of stimuli in which a null preference was observed with the VPC. This evidence in adult subjects supports Gross et al's 2001 finding of the non-equivalence of memory paradigms when testing infants.

General discussion

The experiments conducted in this chapter sought to establish the suitability of the VPC as a task for use with adult subjects, to explore the manner in which the inclusion of emotion processing alters task performance, and to consider whether the VPC and the forced-choice task are comparable paradigms.

One of the key conclusions that can be drawn from these studies concerns the role of emotion in the VPC. The results from Experiment 1 reveal that when an element of emotional processing is included in the VPC task, the expected novelty preference is attenuated (to such a degree here, that a significant *familiarity* preference is almost evident). However, such disruption occurs *only* when the element of emotional processing is included at habituation. When emotional information is instead included at test, a standard novelty preference is observed. When considered along with the puppet data with infants reported in chapter 2 and with previous infant studies incorporating emotion (Gross et al., 2002; Nachman et al., 1986; Rose et al., 1999) the clear conclusion is that if a task element requiring emotional processing and/or eliciting emotion is included at habituation, a novelty preference cannot be expected to be reliably obtained in either infants or adults.

There are two obvious potential explanations for the emotion effects on the VPC. Firstly, it may occur because the emotion element in some way leads to poorer encoding

of the habituation stimulus. If this were the case, the 'familiar' stimulus would then be in competition with the new stimulus at test because it is *not* fully familiar; it has been insufficiently encoded, and thus further attention is demanded to achieve this. This is, however, an unlikely explanation. Intuitively, a stimulus displaying or eliciting emotion is likely to be of *greater* salience to the subject and hence encoded more rapidly. A subject who experiences positive emotion upon exposure to a stimulus is, intuitively, likely to wish spend a greater amount of time attending to it. Conversely, a stimulus demonstrating or eliciting a negative emotion such as fear then it is biologically imperative to attend to it for a greater amount of time. In any case, an insufficient level of encoding is demonstrably not the explanation of the failure of adults to demonstrate a novelty preference, as when the emotion component is instead included at test a strong novelty preference is observed.

An alternative explanation for emotion effects on the VPC is that encoding a stimulus with an emotional component (or which engenders an emotional response in the subject in the case of infant research) affords it greater salience. In essence, the processing of such stimuli involves the amygdala in addition to the medial temporal lobe memory system proper. This leads to a stronger encoding of the stimulus and an imperative to attend to it further, which is then in competition with the intrinsic preference for novelty engendered by the appearance of a new stimulus at test (which, in the adult experiment here, did not involve emotion). Indeed, this effect is arguably complicated by the design of the study used here, in which habituation and test stimuli are not identical. Whilst the face seen at habituation was demonstrating an emotion, the same face encountered at test was instead neutral. This might either cause greater

attention to the familiar face because, whilst it is identifiably the same face, the emotional element has changed and it is thus important to attend to it more; alternatively, it might cause *less* attention to the familiar face than would occur if the emotional element was still present – and, indeed, if it was identical to that observed at habituation.

Such alternative theories of the role of emotion on the expression of preferences in the VPC are amenable to testing systematically with a series of VPC tasks in which the role of emotion is examined at both habituation and at test. Whilst the experiment undertaken here place emotion at either habituation only or at test only and in which case in both presented stimuli, a further series of experiments could test the effect of including emotion at *both* points. In addition, it would be interesting to explore the effect of having an emotion face at habituation and then the same emotion face paired with a neutral face at test; an emotion face at habituation and then the same face with a neutral expression paired with a novel emotion face at test; and finally a neutral face at habituation and an emotional variant of the same face presented at test along with a novel neutral face and vice versa. Such a series of experiments would be able to more robustly establish the role of inserting emotion into visual recognition memory tasks. It might be reasonable to expect, for example, that a particularly strong novelty preference would be obtainable in the permutation in which the habituation face was neutral, and then the same face was presented at test along with a novel face displaying emotion. Conversely, a trial in which an emotion face was the habituation stimulus and the test stimuli were the same emotional face paired with a neutral novel face might result in a robust familiarity preference.

A second key conclusion drawn from this series of studies pertains to the types of stimuli which can sensibly be employed within VPC methodologies. Choice of stimulus type is intuitively an essentially important variable in any experimental methodology, and was the focus of several studies by Fagan at the beginnings of VPC research (see chapter 1). Despite advances in the complexity of stimuli used in recent VPC studies, systematic investigations of stimulus effects have not progressed at the same pace.

The present research demonstrates that a greater novelty preference is observed for simple shapes (chairs) and for faces (with which human adults have arguably more experience than with any other stimuli) than for novel, complex shapes that have not been previously encountered (greebles and fribbles). Indeed, for the latter the novelty preference fell short of statistical significance. Such a finding demonstrates that the effect size of the VPC cannot be expected to be equivalent for different categories of stimuli. Such a conclusion is important for the VPC literature because complex stimuli such as complex moving objects (Bahrick & Pickens, 1995; Bahrick et al., 1997) have been used in VPC methodologies with little explicit consideration being given to the ramifications of such a procedure.

Such a finding is again amenable to further, more detailed experimentation with a series of systematic experiments in which stimulus complexity, habituation time, and the interaction between the two are mapped in human infants, children and adults. Such research, with the goal of identifying an optimal combination of habituation time and stimulus complexity at different ages in order to elicit a novelty preference, would provide an index for researchers seeking to elucidate a reliable novelty preference as the starting point for further variable manipulation.

The final key conclusion concerns the manner in which the forced-choice task can be usefully compared to the VPC. Given the similarity of findings between the forced-choice and VPC task observed here, there are grounds for an additional programme of further research in which this relationship is investigated. It is possible that there is a broad relationship between the two types of tasks that can be discerned. For example, the two stimulus categories that fell short of a significant novelty preference (greebles and fribbles) both also fell short of approximately 90% accuracy in the forced choice task; similarly, both categories of stimuli engendered mean reaction times above 600ms. Formalising a relationship between the VPC and the forced-choice task would require extensive further research but would be of considerable importance in allowing the consideration of visual recognition memory abilities right across the life-span; particularly because, as has been demonstrated here, the forced-choice task can provide empirical evidence that stimuli *can* be remembered, even with very brief presentations, when a null preference is obtained with the VPC.

In broader terms, further wide-reaching conclusions can be drawn concerning the utility of using the VPC with adult subjects. The VPC paradigm has been robustly demonstrated to work with adults; furthermore, the typical novelty preference can be disrupted in adults in the same manner as it can in children. Such findings justify the comparison between infant and adult performance on the task, and are of theoretical concern for accounts of memory development that contend that infant mnemonic processes are qualitatively different to those found in adults. The implications of this for future research and for the account of the developing medial temporal lobe memory system in the infant and the automaticity with which the system is thought to initially

operate will be considered at length in chapter six. Prior to this, attention will be focussed on additional variables that can perhaps account for task performance in human infant populations.

Chapter 5 - Exploring the Role of Cortisol on VPC Performance

Levels of Explanation

Visual recognition research has historically been a cognitive neuroscience research field with the emphasis firmly on the cognitive. Brain regions implicated in memory tasks are often imputed on the basis of comparable animal research in which brain lesioning is possible, and from imaging studies.

Beneath the observable behaviours and considerations of implicated gross neuroanatomical sites, however, it is possible to investigate how memory functions at a cellular level. One such application of finer-grained neurobiology has direct relevance to the investigation of functioning of the MTL memory system that underpins this thesis, and in particular to the role of the amygdala in such a system. The previous chapter demonstrated the impact of the inclusion of emotion processing demands on the VPC; the role of the amygdala in explicit memory processing is therefore an appropriate topic for more detailed consideration. Specifically, the role of the hormone cortisol in learning and memory needs to be elucidated.

What is Cortisol ?

Cortisol is the glucocorticoid hormone secreted by the adrenal gland in humans (the analogous glucocorticoid hormone in rats is corticosterone) which acts on numerous areas of the body and plays a role in a wide range of physiological, behavioural and cognitive functions. Receptors to which cortisol binds are prevalent in a variety of areas in the brain, including the prefrontal cortex, hippocampus, amygdala, basal ganglia,

cerebellum and brain stem (see Erickson, Drevets & Schulkin, 2003; Heffelfinger & Newcomer, 2001; Mizoguchi, Ishige, Takeda, Aburada & Tariba, 2004).

Under normal conditions, levels of glucocorticoids (GCs) in adult humans and animals varies across a 24-hour cycle, or circadian profile (see below). The production of GCs are, however, also stress-responsive. The experience of stress leads to increase in the release of corticotrophin releasing factor (CRF). CRF increases the pituitary release of adrenocorticotrophic hormone (ACTCH), which leads to the adrenal secretion of GCs (Heffelfinger & Newcomer, 2001). Although cortisol is therefore sometimes popularly categorised as a 'stress hormone', the diversity of functions served by cortisol mean that this is not a fully accurate term. Some research has identified high levels of cortisol in normal subgroups. Zorilla, DeRubeis, and Redei (1995) observed that healthy young adult males who self-reported high levels of self-esteem had higher cortisol levels than those who did not. Furthermore, children aged 7-17 years who were described by carers as being 'bold and energetic' displayed similarly elevated cortisol levels compared to other children (Granger, Weisz & Kauneckis, 1994) In addition, abnormal glucocorticoid secretion plays a role in psychiatric disorders including depression, schizophrenia and Parkinson's disease (see Heffelfinger & Newcomer, 2001; Erickson et al., 2003; Mizoguchi et al., 2004). Thus GC levels affect a wide range of cognitive function, and individual differences observed are notable in their diversity.

In several brain areas – for example, the hypothalamic-pituitary-adrenal axis, and in the hippocampus - glucocorticoid secretion is observed to have inhibitory effects (Erickson et al., 2003). Perhaps the most pertinent observable effects regarding emotional processing and memory, however, occur in the amygdala (see Roozendaal, et al.1999;

Roozendaal, 2002). To understand the relevance of such effects, it is first necessary to outline the neurophysiology of cortisol action in greater detail.

The Neurophysiology of Cortisol Mechanisms of Action

Glucocorticoids bind to two receptor types widely distributed throughout the brain. Mineralcorticoid (MR, or Type I) receptors regulate the metabolism of sodium, whilst glucocorticoid (GR or Type II) receptors regulate the metabolism of glucose. In the human brain, endogenous cortisol acts on both receptor subtypes (see Lupien, Wilkinson, Briere, Menard, Ying Kin & Nair, 2002). Due to a differential affinity for glucocorticoids, however, MR and GR receptors are not equally occupied and the ratio between their occupation alters according to the amount of circulating GC. Due to the higher affinity displayed by MRs – approximately 6-10 times higher than that of GRs - when there are low circulating levels of endogenous GCs, they bind to more than 90% of MRs and only approximately 10% of GRs. When circulating GC levels are high, however, MR receptors are saturated and GR receptors are occupied at approximately 67-74% (Reul & De Kloet, 1985; for a review see Lupien et al, 2002). Thus, the mechanism of GC action differs depending on the available level of GCs. Less is known regarding GC functioning and the role of cortisol in human infant cognition than in human adult and animal cognition. Research concentrating on adults and animals will therefore be considered with the aim of elucidating the role of cortisol in the infant; a small number of infant studies will also be examined. To this end, two variables can be observed to directly effect GC levels – the point of the circadian profile at which measurement occurs, and the stress state of the organism.

The Circadian Profile of Cortisol

The levels of GC circulating in adult humans and animals are not constant, but fluctuate over a 24-hour period. In human adults, cortisol concentration is at a maximum (the circadian peak) in the morning; this level slowly decreases over the day, and by late afternoon the circadian trough is reached. This low level is maintained over the nocturnal period until after the first few hours of sleep, when it begins to rise again. In rats, the fluctuation is reversed, such that the circadian trough occurs in the morning, and the peak occurs by late afternoon (see Lupien et al., 2002).

Infants, however, are born without a circadian rhythm in cortisol. Whilst it is generally agreed that human infants acquire the glucocorticoid circadian profile within the first year of life, there is marked variation concerning the age at which this is thought to occur, with any onset from 2 weeks to over 9 months being claimed (see de Weerth, Zijl & Buitelaar, 2003, for a review). Following an analysis of a cohort of infants tested from 2 to 5 months, de Weerth et al. concluded that researchers should be careful when assuming the presence of circadian cortisol rhythms in the first half-year of life, and that even in the second half (when rhythms presumably consolidate), there is still a very marked degree of intrasubject variability with many infants failing to show the expected substantial decrease in cortisol levels over the course of the day.

A further source of contention regarding the onset of adult-like hormonal control in human infants concerns the degree to which the onset of the cortisol circadian rhythm coincides with the onset of the sleep-wake circadian rhythm. Although there is some debate as to this relationship (e.g., Santiago, Jorge & Moreira, 1996), several authors have found a substantial link between the appearance of uninterrupted night sleep and the

cortisol circadian rhythm (e.g., de Weerth et al., 2003; Antinoni, Jorge & Moreira, 2000). Larson, Gunnar and Hertsgaard (1991), for example, found cortisol decreased in 9-month-old infants following naps, and that prenap levels took approximately 45 minutes to be reached. Similarly, de Weerth and van Geert (2002) observed that, in 5- to 8-month-olds, cortisol levels were lower in infants who had just slept in comparison to those who had been awake for at least 30 minutes. This research suggests that developing circadian rhythms in the human infant lead to GC levels that vary across a 24 hour cycle. Sufficient evidence therefore exists to warrant the control of when an infant has last slept to be introduced into infant cortisol research.

The Effect of Stress on GC Levels

In addition to time of day, stress is the other key variable affecting the circulating levels of cortisol in adult humans. This affects the ratio of GC binding to GR/MR; this, in turn, has ramifications for cognitive processes including learning and memory. Mere anticipation of emotionally evocative stimuli in humans has been demonstrated to lead to elevated cortisol levels. Brand (1999) demonstrated that anticipation of a visit to the dentist led to an increase in cortisol levels – when tested immediately prior to a dental visit, adults demonstrated raised urinary cortisol levels, although interestingly no increase in salivary levels was observed, suggesting the effect was one of a longer-term response to stress. Schedlowski et al. (1993) demonstrated similarly raised stress hormone levels in anticipation of a first parachute jump in adults.

In addition, when adults are tested for memory of short films after a three week delay, they are better able to recall films with strong negative emotional content (e.g.

violent crime or animal mutilation) than emotionally neutral films; furthermore, recall of emotional films is significantly correlated with increased glucose metabolism in the amygdala (Cahill, Haier, Fallon, Alkire, Tang & Keator, 1996). Research with rats similarly demonstrates the link between stress such as that induced by electric shocks and increased GC secretion (e.g. Roozendaal, 1999, McGaugh, 2000).

The Inverted-U Function of GCs – a Negative or Positive Effect on Cognition ?

The relationship between memory and GC levels is shown to follow ‘inverted-U’ shaped function. Thus, in the case of memory, optimal effects are observed when glucocorticoid levels are moderate. At extremely low or extremely high levels, mnemonic deficits are observed. Such an effect is well documented in both rat and human studies. In rats, posttraining activation of glucocorticoid-sensitive pathways enhances memory at moderate doses but is either ineffective or actually leads to impairment at high or low levels (for reviews see Roozendaal, 1999, 2000, Lupien et al., 2002). In adult human subjects also, there is evidence that decreasing cortisol below basal levels (via the administration of metyrapnone, an inhibitor of cortisol synthesis) leads to impaired memory performance, whilst increasing cortisol levels via the administration of hydrocortisone led to improved performance (Lupien et al., 2002).

Similar inverted-U modulatory effects involving cortisol are observed for signalling hunger satiation – moderately elevated glucocorticoid levels can elevate the subjective sense of hunger, whilst very high or low doses reduce the state of hunger (Dallman et al., 1993.)

De Kloet, Oitzl and Joëls (1999) have proposed that the effects of the inverted-U pattern of glucocorticoid levels on cognitive and behavioural performance is intimately linked to the ratio of MR/GR activated as a result of the level of circulating cortisol (or corticosterone). They argue that the effect of increasing glucocorticoid levels can be cognitively enhancing when there is a high MR/GR ratio, i.e. when most MR and only a small proportion of the GR are activated. When there is a low MR/GR ratio, however (i.e. when MR are saturated and a large proportion of GR are activated), increasing *or decreasing* glucocorticoid levels result in cognitive impairment. The corollary of this is that during the circadian peak and/or at times of stress, cognitive impairment is the likely result of methodologies increasing GC. During the circadian trough, however, when basal rates are observed, increased GC levels is likely to have a positive effect on cognition.

A meta-analysis of studies with adult humans supports this view. Het, Ramlow and Wolf (2005) reviewed 16 studies that administered doses of cortisol (ranging from 5 to 100 mg) to healthy, 18 – 40 year-old human adults and observed the effects on declarative memory. Studies measured either verbal or visual memory, and tested either immediately or after a delay, via free or cued recall. Het et al. observed that studies in which cortisol was administered in the morning (during the circadian peak) found, on average, a significant memory impairment. Those which administered cortisol in the afternoon, however (when endogenous cortisol levels are lowered) found a significant positive effect on memory.

The relationship between GC levels and cognition can therefore be seen to be a complex one. As the effects of GCs on memory are, of course, the focus here, the

literature considering GCs and human memory will therefore now be considered in more detail.

The Effects of Glucocorticoids on Human Memory

Studies with human adults unequivocally demonstrate that cortisol and memory are related. However, the direction of the relationship is the focus of some debate. A number of studies demonstrate that when cortisol levels are chemically increased, memory impairment results. When GC levels are subchronically increased by the administration of dexamethasone, adult performance is impaired in tests of verbal memory. Wolkowitz et al. (1990) demonstrated that infusions of dexamethasone led to impaired ability to select target words from distractors. Similarly, Newcomer, Craft, Hershey, Askins and Bardgett (1994) observed that a four-day, once-per-24 hours treatment of dexamethasone (0.5mg on the first day, 1mg thereafter) impaired both immediate and delayed recall, without affecting other cognitive abilities. Following a one-week period of no treatment, the experimental groups performance reverted to that of controls. A further experiment with orally administered cortisol (Newcomer, Selke, Melson, Hershey, Craft, Richards & Alderson, 1999) selectively impaired word recall in a similar fashion. Participants were either given a 40 mg or a 160 mg each day for 4 days; when tested on the 4th day, the higher treatment group showed impairments in verbal declarative memory but no impairments in nonverbal memory, executive function or attention. Such effects had disappeared after a 6-day 'washout' period during which cortisol was not administered.

Other studies, however, have found an improvement in mnemonic performance following GC administration. Abercrombie, Kalin, Thurow, Rosenkranz & Davidson (2003), in a study in which either 20 or 40 mg of cortisol was orally administered to

young men, found that the number of errors made on memory tests administered one hour after stimulus presentation, was reduced. In a 48-hour follow-up, performance in the experimental group was better than controls in the 20mg, but not the 40mg group.

There is evidence, therefore, that memory performance can either be enhanced or impaired by manipulation of GCs. One variable seen to impact on the direction in which increasing GC levels alters memory performance is the emotional salience of the stimuli employed. For example, De Quervain et al. (2000, 2003) found mnemonic impairment in studies in which subjects were tested for recall of emotionally neutral words following the administration of 25mg of cortisol. Buchanan and Lovallo (2001), however, found that a 20mg dose of cortisol improved the recall of pictorial stimuli eliciting negative emotion when tested one week later.

Some researchers have opted to explore this role of the emotional salience of stimuli employing methodologies in which endogenous GC levels are measured following exposure to stressful or emotive situations or stimuli. Such 'real world' stress paradigms are obviously more ecologically valid, and are apt to produce greater effects than paradigms involving the observation of emotional pictures. Empirical precedent for the applicability of this type of methodology was demonstrated by Kirschbaum, Wolf, May, Wippich and Hellhammer (1996), who found that comparable impairment in delayed recall tasks were observed both in a condition in which hydrocortisone was administered and in a condition in which subjects were instead exposed to a stressful situation (being required to give a public speech which they believed was being assessed).

Similarly, Payne, Jackson, Ryan, Hoscheidt, Jacobs and Nadel (2006) administered a psychological stressor (subjects were required to give a speech) prior to presenting an emotional slideshow (containing stimuli such as car accident footage). Memory for the emotional elements of the slideshow was better preserved than neutral stimuli when tested at 1 week.

Van Honk, Kessels, Putman, Jager, Koppeschaar and Postma (2003) investigated the relationship in healthy males aged 19-26 of basal cortisol levels and encoding of negative and positive facial expressions. Participants were required to remember the spatial location of happy and fearful faces on a computerised grid. Following an immediate recall test period, it was found that cortisol levels were inversely related to memory performance for happy face stimuli; a similar relationship was observed for fearful stimuli that almost reached statistical significance. Such a finding demonstrates that the mere encoding of static images is sufficient to alter brain function at a cellular level if there is an emotional processing component.

In a further experiment from the same laboratory, Putman, van Honk, Kessles, Mulder and Koppeschaar (2004) in an experiment involving 39 young women, tested memory for photographs of emotional faces using a similar spatial memory task. Participants were either tested immediately after presentation or following a 20 minute delay. Participants remembered happy faces better than neutral faces when tested immediately, and recalled both fearful and happy faces better than neutral ones following a 20 minute delay. Salivary cortisol correlated with better memory for emotion in the long term condition.

It can be seen, then, that the relationship, between GC levels and adult memory performance at least, is a complex one. Broadly speaking, verbal or visual memory is often impaired by pharmacologically increased GC levels. When there is an emotional component, however, memory is often enhanced. Furthermore, this enhancement is specific to items involving emotional processing. Such a conclusion is, however, rather simplistic. Within emotional processing research, evidence of a dissociation between memory *consolidation* and memory *retrieval* has emerged. Such a dissociation will now be considered.

Glucocorticoid Effects on Memory Reconsidered: Consolidation vs. Retrieval

One of the most well-established roles of GCs are their effect on memory. Much research has suggested that increasing GC levels in both animals and humans leads to mnemonic impairment (Landfield, Waymire and Lynch, 1978; Sapolsky, 1986; Lupien et al., 1994; for reviews see Lupien, 2002; Roozendaal, 1999, 2002). The research outlined above, however, suggests that the circadian profile of GCs is a critical factor in determining whether the results of GC infusion will be positive or negative on cognition.

In their 2005 meta-analysis, Het et al. identified a further important variable affecting the cognitive outcome; the timing of GC infusion within the experimental procedure. Studies in which cortisol was administered before learning found on average no effect on memory performance, although substantial heterogeneity was observed (see e.g. Abercrombie, Kalin, Thurow, Rosenkranz & Davidson, 2003; deQuervain, Roozendaal, Nitschi, McGaugh & Hock, 2000; Newcomer, Selke, Melson, Hershey, Craft, Richards & Alderson, 1999). Those in which cortisol was administered before

retrieval, however, displayed a significant impairment in memory (e.g. deQuervain, Roozendaal, Nitsch, McGaugh & Hock, 2000; Lupien, Wilkinson, Briere, Menard, Ng Ying Kin & Nair, 2002; Wolf, Convit, Thorn & de Leon, 2002). A similar effect of timing of GC infusions on memory is observable in rat populations. In avoidance training studies, moderate doses of GCs lead to positive effects on memory in rats, but only if administered shortly after training, as opposed to several hours after training (Pugh, Tremblay, Fleshner & Rudy, 1997; Cordero & Sandi, 1998; see Roozendaal, 2002). If stress is administered prior to memory retrieval, however, memory is impaired; following a learning task, rats exposed to a stressful foot shock 30 minutes before retrieval were impaired compared to controls (de Quervain, Roozendaal & McGaugh, 1999).

Roozendaal (2002) proposes that the differential effects on consolidation and retrieval are linked and dependent on the same neurophysiological substrates. Specifically, he contends that the most important neurobiological structure for this modulatory effect is the amygdala. He postulates that the modulatory effect on memory involves the amygdala serving as a 'switch' between two processing styles. During basal levels of GCs, information recall is unimpeded, but strong consolidation of information is less likely. During stress, however, the basolateral amygdala switches the brain into a 'memory consolidation state', in which strong consolidation is achievable but recall of prior information is compromised. Such an effect, however, is not entirely due to amygdala activity. Direct GC infusions into the BLA in rats is insufficient to impair memory retrieval, so it is hypothesised that retrieval impairment instead is the result of interconnectivity between the amygdala and other brain regions including the

hippocampus and prefrontal cortex. Such a hypothesis is directly relevant to cognitive research involving emotional processing.

The Amygdala, Cortisol and Emotional Processing

The role of the amygdala in emotional memory modulation has considerable empirical support. GC administration has direct physical effects on both the hippocampus and the amygdala. Acute GC administration – which is analogous to what happens endogenously at times of stress – leads to increased cell firing in the amygdala (Feldman, 1983) and lowered glucose utilization in the hippocampus (de Leon, 1997). The exposure to emotionally evocative stimuli in human adults leads to increased endogenous cortisol levels (Brand, 1999; Schedlowski et al., 1993).

The amygdala contains GRs, the receptor subtype activated by stress and emotionally arousing experiences, and activation of the basolateral amygdala has a modulatory effect on brain areas including the hippocampus (McGaugh, 1996, 2000; Erikson et al., 2003). Selective lesioning of the basolateral amygdala in rats blocks the memory-modulating effects of GC infusions, as does the infusion of a GR antagonist into the BLA; infusion of a GR agonist, on the other hand, enhances memory consolidation (Rooszendaal, 2000).

Abercrombie, Kalin, Thurow, Rosenkranz & Davidson (2003) review the literature and identify two additional sources of evidence for the role of the amygdala in emotional memory processing. Firstly, the amygdala is implicated in aversive classical conditioning studies in both rats and humans (e.g. LaBar, LeDoux, Spencer & Phelps, 1995; LeDoux, Cicchetti, Xagoraris & Spencer, 1990). Secondly, imaging studies

demonstrate that the amygdala responds selectively to recall of emotional information in humans (e.g. Cahill, Haier, Fallon, Alkire, Tang and Keator, 1996; Canli, Zhao, Brewer, Gabrieli and Cahill, 2000).

A review of the rat lesioning literature by McGaugh, Cahill and Roozendaal (1996) concludes that the role of the amygdala in memory is as a regulatory system, determining the successful consolidation of information in other brain regions when that information has an emotional component. As such, the amygdala is not involved in the everyday processes of memory but instead plays a selective role. Such a conclusion neurophysiologically corroborates the experimental findings of this thesis, which broadly indicate a dissociability between neutral, traditional visual recognition memory tasks and those in which there is an emotional component.

Cortisol Research with Children

Given the findings of such research and the applicability of such information to a study of human neurodevelopment, it is clear that there are many potential applications of glucocorticoid research to the study of developing humans. Indeed, many studies have implicated cortisol levels as impacting on a variety of cognitive functions in children. In one study, Quas, Bauer and Boyce (2004) tested 4-6 year-old children, in a methodology in which they experienced a fire alarm incident – found to be a substantial stressor to children categorized as ‘physiologically reactive’ on two physiological tests measuring heart-rate and the related cardiac cycle, and a mild stressor to those categorized as less reactive. Children were given an immediate memory test, then a follow-up test at two weeks. At two weeks, children displaying higher cortisol levels were associated with

poorer recall of the event. The style of questioning adopted – warm and friendly or cold and impersonal – did not affect recall in high or low cortisol children.

A number of studies have indicated a relationship between increased cortisol levels and temperamental variations, such as fear of novelty, increased distress in response to frustration, low threshold for emotional reactivity, and marked anxiousness (Granger, Stansbury & Henker, 1994; Macmias, Gunnar, Mangelsdorf, Parritz, and Buss, 1996; see Heffelfinger & Newcomer, 2001).

Given the variation in GC related to temperamental variations, it is perhaps not surprising that developmental researchers interested in cortisol have focused their attention on children who are at risk or otherwise deprived. Reviewing the literature, Heffelfinger and Newcomer (2001) identify several ways in which cortisol methodologies have been used to measure performance in such subjects. Children brought up in orphanages, young maltreated children and those with disorganised or insecure attachment have demonstrated increased cortisol levels alongside increased stress responses. Similarly, early and severe negative childhood experiences can result in increased cortisol levels and decreased memory function (Carlson & Earls, 1997; Hart, Gunnar & Cicchetti, 1995; Hertzgaard, Gunnar, Erickson & Nachmias, 1995).

In contrast to increased stress responses and increased cortisol levels, studies with depressed children have demonstrated reduced cortisol levels are associated with depression (Birmaher, Dahl, Perel, Williamson, Nelson, Stull, Kaufman, Waterman, Rao, Nguyen, Puig-Antich & Ryan, 1996; Dahl, Ryan, Puig-Antich, Nguyen, al-Shabbout, Meyer & Perel, 1991; see Heffelfinger & Newcomer, 2001).

Whilst the majority of studies have focussed on children experiencing problems, then, there is clear evidence of a relationship between GCs and cognition in children.

Cortisol Research with Infants

Cortisol research with infants is a relatively small field. Nonetheless, a small number of experiments with infants suggests a similar correlational relationship between glucocorticoid levels and cognition and/or potential problems such as premature birth.

Grunau, Weinberg and Whitfield (2004) demonstrated that infants born at an extremely low gestational age (less than 29 weeks) showed higher basal levels of cortisol than those born over 29 weeks and at full term.

Lewis and Ramsey (2005), in an experiment with 4- and 6-month-olds, presented two methodologies in which an infant was frustrated when a learned stimulus stops working (either an audiovisual stimulus in response to an arm-pull (in 4 month-olds) or the still-face paradigm (in 6-month-olds)). Facial affect was measured using the AFFEX system (Izzard, Dougherty & Hembree, 1983); sadness and cortisol levels were found to be correlated – the greater the sadness displayed at goal blockage, the higher the cortisol levels. Anger, however, was found to be uncorrelated with cortisol. Such a finding awaits further elucidation; in a similar methodology, Lewis, Hitchcock and Sullivan (2004) found cortisol levels to be unrelated to any emotion, including sadness, elicited by goal blockage. It can be seen, then, that GC levels in infants are connected to emotion.

Given the role of cortisol in amygdala processing, and the demonstrable impact of altering the VPC to include emotion processing (and thus involving the amygdala), it seems reasonable to hypothesise a link between the development of the explicit memory

system and the development of cortisol regulation. Little direct research has addressed such questions, however. The field is a difficult one, both theoretically and practically. Some potential problems with infant cortisol research will now be summarised.

Difficulties Associated with Cortisol Research in Young Infants

Human infants are an intuitively tricky population within which to consider the effects of cortisol on cognition. As has been observed, circadian rhythms have yet to be established in infants; no assumptions can be made concerning basal cortisol levels at different time-points throughout the day. Additional individual differences that may reasonably be expected to impact on cortisol levels are also difficult to control in an infant laboratory setting – the time of day of testing is typically chosen to be convenient to the caregiver, and when the infant last fed or slept is outside of experimenter control.

A further, higher-level problem impacts on any attempt to consider the role of stress or emotion in infants. In addition to the obvious ethical problems in inducing stress in infants, given the developing nature of infant memory and of the connectivity between the MTL system and the amygdala, is also possible that in an infant population the distinction between ‘emotional’ and ‘non-emotional’ stimuli is considerably less clear cut than in adults. In short, it is hard to predict what stimuli will elicit an emotional response in human infants. Such methodological problems become more acute when an attempt is made to factor in the stressors an infant may be experiencing but is unable to report – tiredness, alarm at unfamiliar surroundings, soiled nappy, the darkness of the typical laboratory setting, interacting with unfamiliar adults, strange smells, sounds, and so on. Given that, as has been mentioned, ‘readiness to behave’ is perhaps a more accurate term

for one of the functions of cortisol rather than 'stress', it seems feasible that there are so many variables potentially impacting on an infant's readiness to behave in a novel laboratory setting that the logical starting point is exploratory research in which cortisol levels are measured during and after a simple memory task.

To this end, a simple VPC was conducted with 9-month-old infants whilst measuring cortisol levels and noting demographic and physiological information. The purpose of such exploratory research was to attempt to establish the degree to which individual differences in cortisol levels could be discerned, and whether relatively high or low cortisol levels were related to individual performance on a simple, typical version of the VPC task.

Experiment 1a: Cortisol Levels during the VPC with a Short Habituation Period in 9-Month-Old Infants

Method

Participants

Thirteen 9-month-old infants were tested. Participants were White British, and 6 of them were female. All infants were tested within 5 days of being nine months old. None were born more than 3 weeks premature or had experienced birth complications. The infants were recruited through visits to a maternity hospital and were all from families of moderate to high socio-economic status. An additional three subjects (1 male, 2 female) were not included in analysis due to excessive fussing, crying or side bias.

50% of the sample had siblings; of these, all subjects lived in the same house as their siblings. The average age of mothers of the sample was 35.6 years; the average age

of fathers was 37.8 years. All subjects were being raised by two parents; the majority of parental occupations would be termed middle-class.

The 10-month ASQ questionnaire demonstrated that 1 infant fell below cut-off scores on the Communication index; 3 infants fell below cut-off scores on the Gross Motor index; 1 infant fell below cut-offs on the Fine Motor index; 2 infants fell below cut-offs on the Problem Solving index; and 1 infant fell below cut-offs on the Personal-Social index. No individual subject fell below cut-offs on more than two indices.

Stimuli and Equipment

Four pictures of female faces were selected from the laboratory archives. Each pair was selected to be distinguishable but similar (see appendix H). Test stimuli were back-projected onto a 45cm * 32 cm screen positioned approximately 60cm in front of the infant. A camera positioned centrally above the screen recorded the infant's eye movements between the two stimuli.

Saliva was collected from the infant by means of a sterile microbiological swab (Bibby Sterilin Ltd). Samples were stored at -2 to -8°C until extraction. Saliva was extracted from the swab by centrifugation at 12000 rpm for 6 minutes. Each sample was pipetted into a pre-labelled ependorf tube and stored at -2 to -8°C until analysis. Salivary cortisol was determined by means of a Cortisol Salivary Immunoassay kit (Salimetrics LLC) and read in a luminometer. Each sample was determined in duplicate to identify potential pipetting errors.

The 10-month version of the 'Ages and Stages' questionnaire (Bricker, Squires & Mounts, 1995), were administered to the caregiver (there are no 9-month norms for the

ages and stages questionnaire.) The ASQ measure five indices of behaviour, assessed via caregiver report; the indices are communication, gross motor, fine motor, problem solving, and personal-social behaviours.

Procedure

All infants were tested individually in the baby research laboratory at the University of Sheffield at a time convenient for the caregiver. The experimenter interacted with the caregiver and the infant in a reception room for approximately 5 minutes prior until the infant appeared comfortable with the experimenter. During this time informed consent was obtained from the caregiver, and the first of two saliva samples was taken from the subject. There followed a period before testing. During this time, the two questionnaires were completed by the caregiver.

Familiarisation session: During the familiarisation period the infant sat on their caregiver's lap on a chair positioned in front of the projection screen in the laboratory. The infant was then presented with a single familiarisation image of a female face for ten seconds.

Test session: The test session occurred immediately after the familiarisation in the same room. During the test, the familiarisation image was presented alongside an additional, randomised image of one of the three other female faces. There were two 5-second test trials separated by a delay of around 2 seconds. In the second test trial the lateral position of the images was reversed.

Following the test session, the infant and caregiver returned to the waiting room where the second cortisol sample was taken, 10 minutes after the initial sample.

Results and Discussion

Looking time data

A two-sample t-test was firstly conducted across gender to determine whether the gender of the infant affected looking in the VPC. This demonstrated that there were no significant differences in looking times across conditions (see table 5.1). The groups were therefore collapsed across gender for subsequent analysis.

Gender	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
Male	46.99	P = 0.841
Female	45.59	

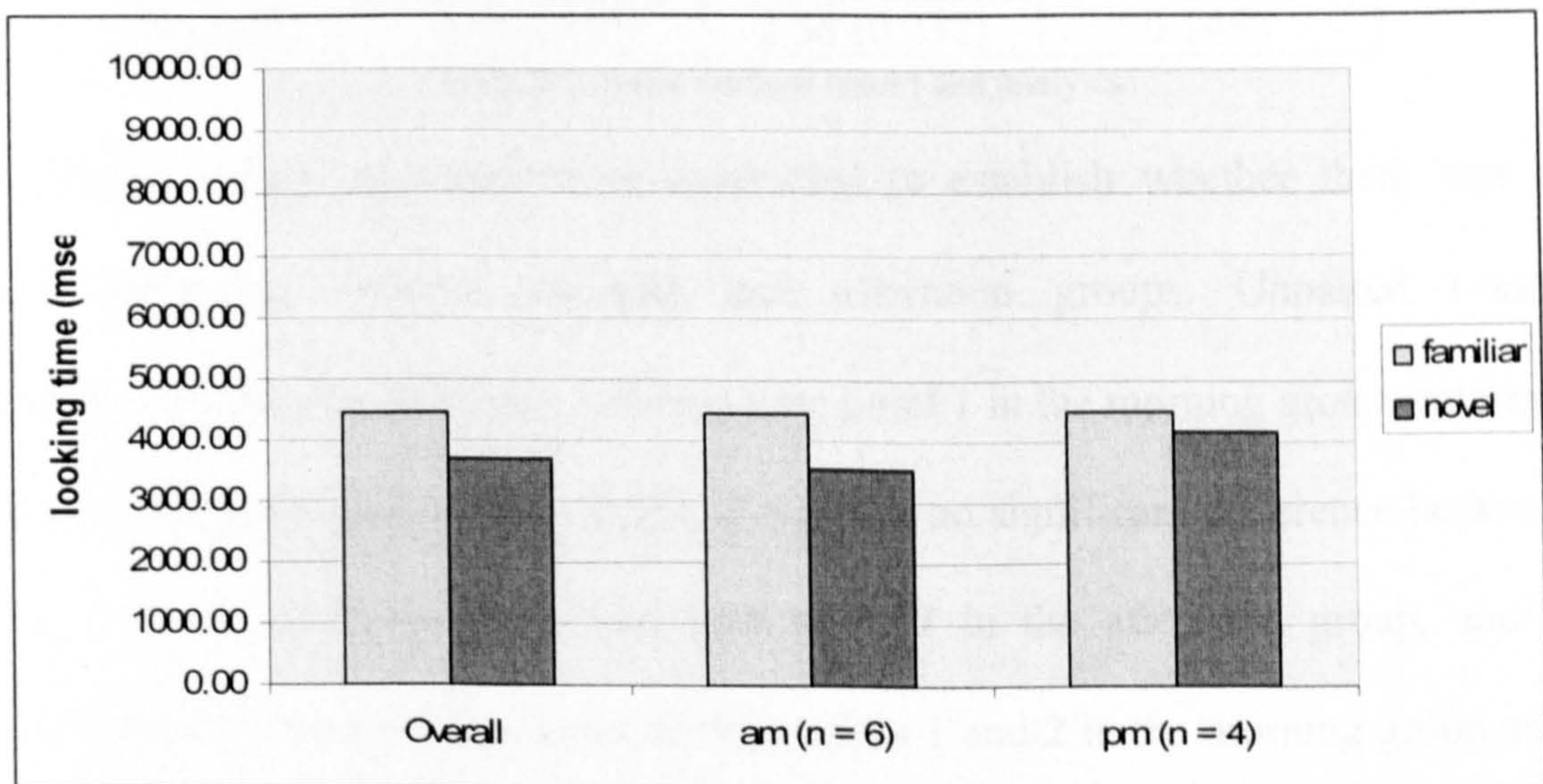
Table 5.1: t-test comparison between looking times by gender

The expression of recognition memory was then examined. A one-tailed paired t-test showed that infants demonstrated a null preference. When data was separated into two groups – one in which the test was administered in the morning, and one in which it was administered in the afternoon – null preferences were also observed for each group (see table 5.2 and graph 5A). The expected novelty preference was thus not observable. 33% of subjects in the morning group showed a looking time in the direction of a novelty preference. 25% of subjects in the afternoon group showed a looking time in the direction of a novelty preference. Overall, 30% of subjects showed a looking time in the

direction of a novelty preference. Such a result should be interpreted with caution, however, because of the comparatively small number of participants.

Condition	Mean looking time to novel stimulus in milliseconds (standard error)	Mean looking time to familiar stimulus in milliseconds (standard error)	Mean % looking time to novel stimulus (standard error)	Two-tailed paired T-test (<i>p</i> value)
Infants tested in the morning	3553 (230.11)	4440 (564.46)	45.40 (3.9)	0.132
Infants tested in the afternoon	4170 (631.01)	4510 (608.03)	46.3 (5.77)	0.122
Overall	3729 (284.41)	4471 (394.5)	46.43 (3.11)	0.387

Table 5.2: the mean percentage looking time to the novel stimulus



Graph 5A: the mean percentage looking times to the novel and familiar stimuli

Cortisol data

A series of t-tests was conducted comparing the cortisol levels at time point one and at time point two. When all participants were considered as a group, a paired t-test demonstrated a non significant difference between time points (see table 3 and graph b). Nor were significant differences observed between time points for the subgroup of infants tested in the morning (see graph c and table 3) or for the subgroup tested in the afternoon (see graph 5B and table 5.3).

Condition	Mean cortisol level ($\mu\text{g/dL}$)		One-tailed paired T-test (p value)
	Time-point 1 (standard error)	Time-point 2 (standard error)	
Infants tested in the morning	5.48 (1.476)	2.996 (0.4)	0.1168
Infants tested in the afternoon	1.926 (0.73)	2.165 (0.6)	0.3733
Overall	3.7 (0.917)	2.58 (0.332)	0.1463

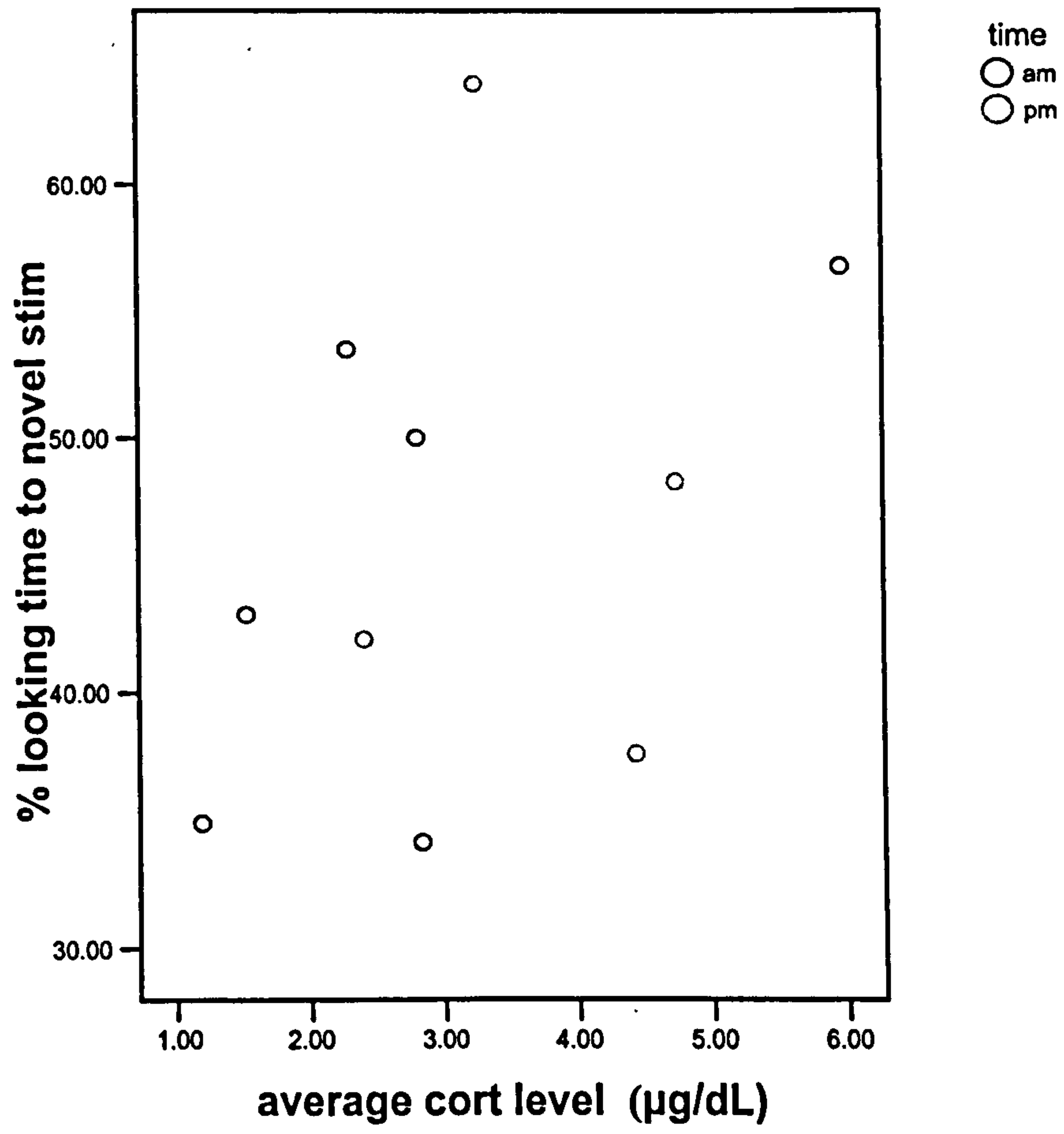
Table 5.3: mean cortisol level t test analysis

A further series of t-tests were conducted to establish whether there was a significant difference between morning and afternoon groups. Unpaired t-tests demonstrated a significant difference between time point 1 in the morning group and time point 1 in the afternoon group ($t(8) = 2.391$, $P < 0.05$), no significant difference between time-point 2 in the morning group and time point 2 in the afternoon group, and a significant difference between the mean of time points 1 and 2 in the morning group and the mean of time points 1 and 2 in the afternoon group ($t(8) = 3.439$, $P < 0.05$; see table 5.4). It can therefore be seen that infants tested in the morning and the afternoon do differ on some measures of cortisol levels.

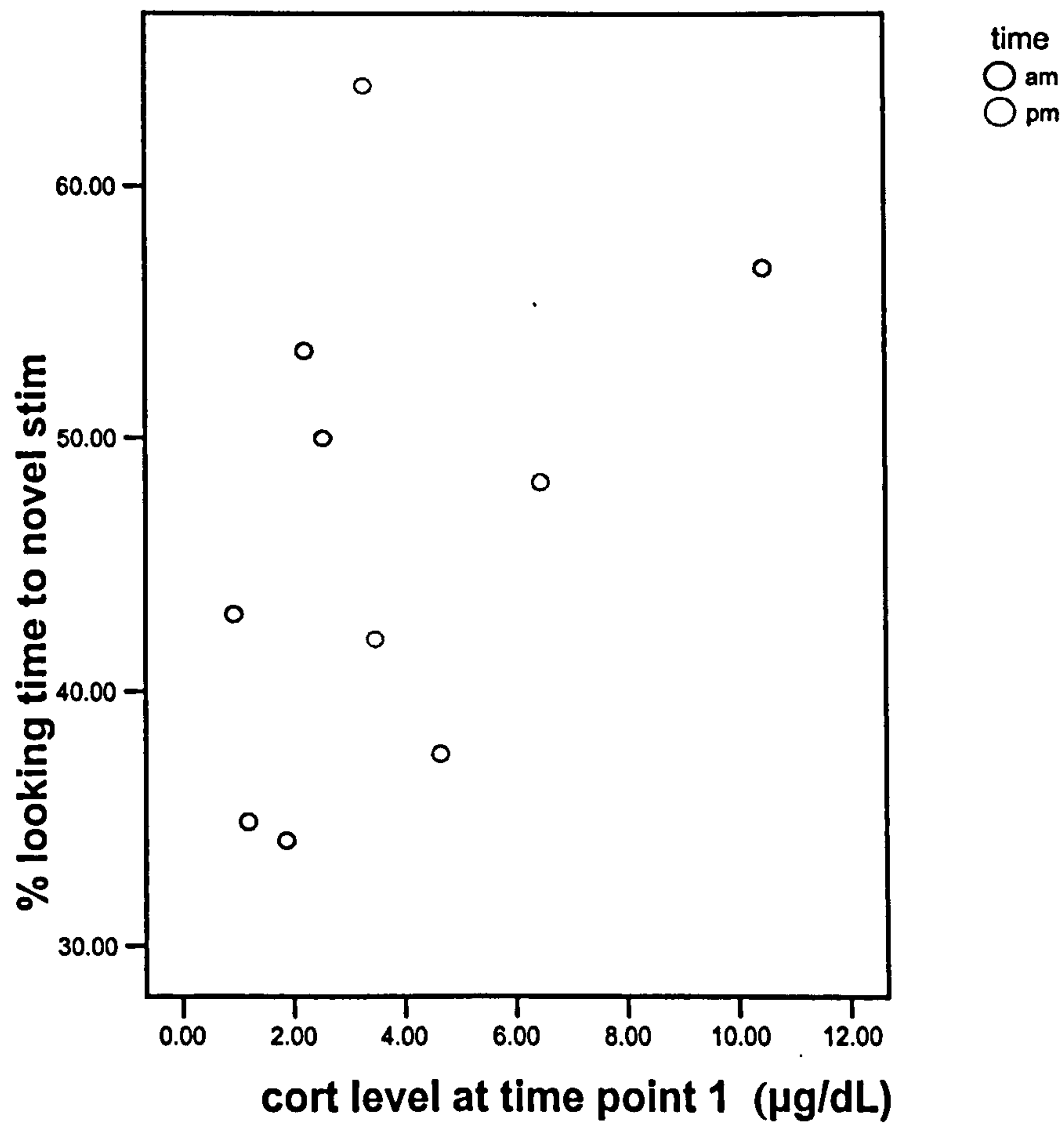
	Mean cortisol level ($\mu\text{g/dL}$)		One-tailed paired T-test (<i>p</i> value)
	AM group (standard error)	PM group (standard error)	
Time point 1	5.478 (1.476)	1.926 (0.73)	0.044
Time point 2	2.996 (0.4)	2.165 (0.6)	0.231
Mean of both time points	4.237 (0.74)	2.045 (0.481)	0.009

Table 5.4: mean cortisol level between-group t test analysis

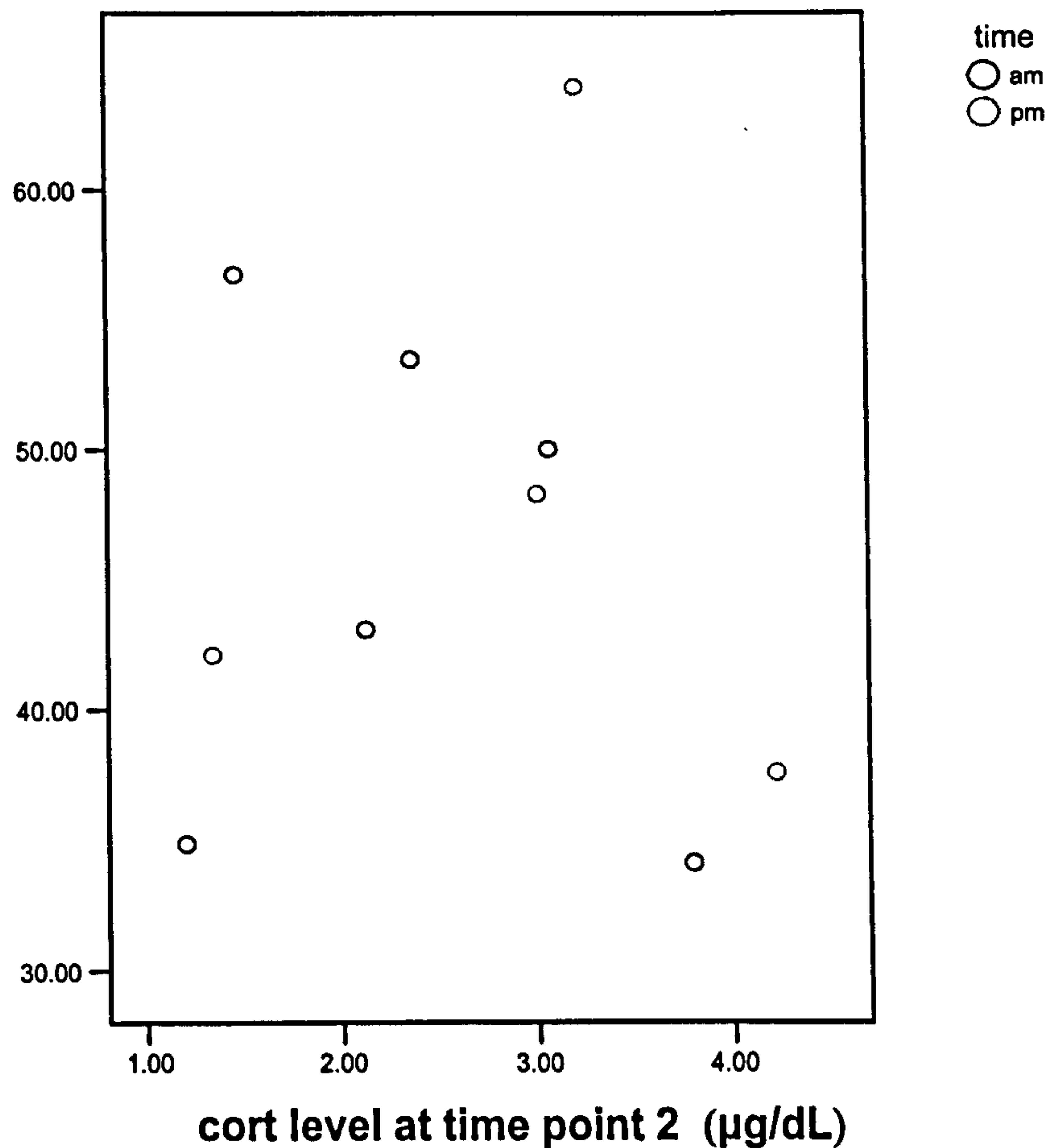
The cortisol and VPC data were also analysed together. The Pearson's correlation coefficient between the cortisol measure averaged over time points 1 and 2 and percentage of time attending to the novel stimulus was .382 and was not statistically significant (see graph 5B). The Pearson's correlation coefficient between the cortisol measure at time point 1 and percentage of time attending to the novel stimulus was .416 and was not statistically significant (see graph 5C). The Pearson's correlation coefficient between the cortisol measure at time point 2 and percentage of time attending to the novel stimulus was -.063 and was not statistically significant (see graph 5D).



graph 5B: scatter plot of percentage of time attending to novel stimulus and averaged cortisol level



graph 5C: scatter plot of percentage of time attending to novel stimulus and cortisol level at time point 1



graph 5D: scatter plot of percentage of time attending to novel stimulus and cortisol level at time point 1

The main finding, therefore, is that a null preference was observed on the VPC. No significant results were associated with cortisol levels. There was an observable difference, however, between overall cortisol levels in infants tested in the morning and those tested in the afternoon, suggesting an emergence of a circadian cortisol profile.

It is difficult to account for the failure of the VPC task to elicit the expected novelty preference. Whilst the habituation should have been sufficient (equivalent habituation times have previously been used within the laboratory), it is possible that for whatever reason this was not the case and that subjects were insufficiently habituated to

the experimental stimulus. To this end, it makes sense to repeat the experiment with a longer habituation period. In a standard, static VPC task such as this one, a typical reason for a null preference is lack of sufficient coding. Whilst the habituation period here should have been sufficient, there is scope for running a version of the same experiment with an extended habituation period.

Experiment 1b: cortisol levels during the VPC with a longer habituation period in 9-month-old infants

Method

Participants

Twelve 9-month-old infants were tested, 7 of whom were female. All infants were tested within 5 days of being nine months old. No infant was born more than 3 weeks prematurely or had experienced birth complications. The infants were recruited through visits to a maternity hospital. All infants were White British and from families of moderate to high socio-economic status. Three additional infants (2 male, 1 female) were not included in analysis due to excessive fussing, crying or side bias.

Seven of the 12 subjects had siblings; of these, all but one subject lived in the same house as their siblings. The average age of mothers of the sample was 33.1 years; the average age of fathers was 34.7 years. All subjects were being raised by two parents; the majority of parental occupations would be termed middle-class.

The 10-month ASQ questionnaire demonstrated that 1 infant fell below cut-off scores on the Communication index; 2 infants fell below cut-off scores on the Gross Motor index; 2 infants fell below cut-offs on the Fine Motor index; 6 infants fell below cut-offs on the Problem Solving index; and no infants fell below cut-offs on the Personal-

Social index. One subject fell below cut-offs on three indices; no other individual subject fell below cut-offs on more than two indices.

Stimuli & Equipment

All stimuli and equipment were identical to those used in experiment 1A.

Procedure

Procedure was identical to experiment 1A, except that a 20-second familiarisation period was employed instead of the 10-second period employed previously.

Results and Discussion

A two-sample t-test was first conducted across gender to determine whether infant gender affected looking in the VPC. This demonstrated that there were no significant differences in looking times across conditions (see table 5.5). The groups were therefore collapsed across gender for subsequent analyses.

Gender	% fixation to the novel stimulus	Two-tailed T-test (<i>p</i> value)
Male	50.186	P = 0.884
Female	50.824	

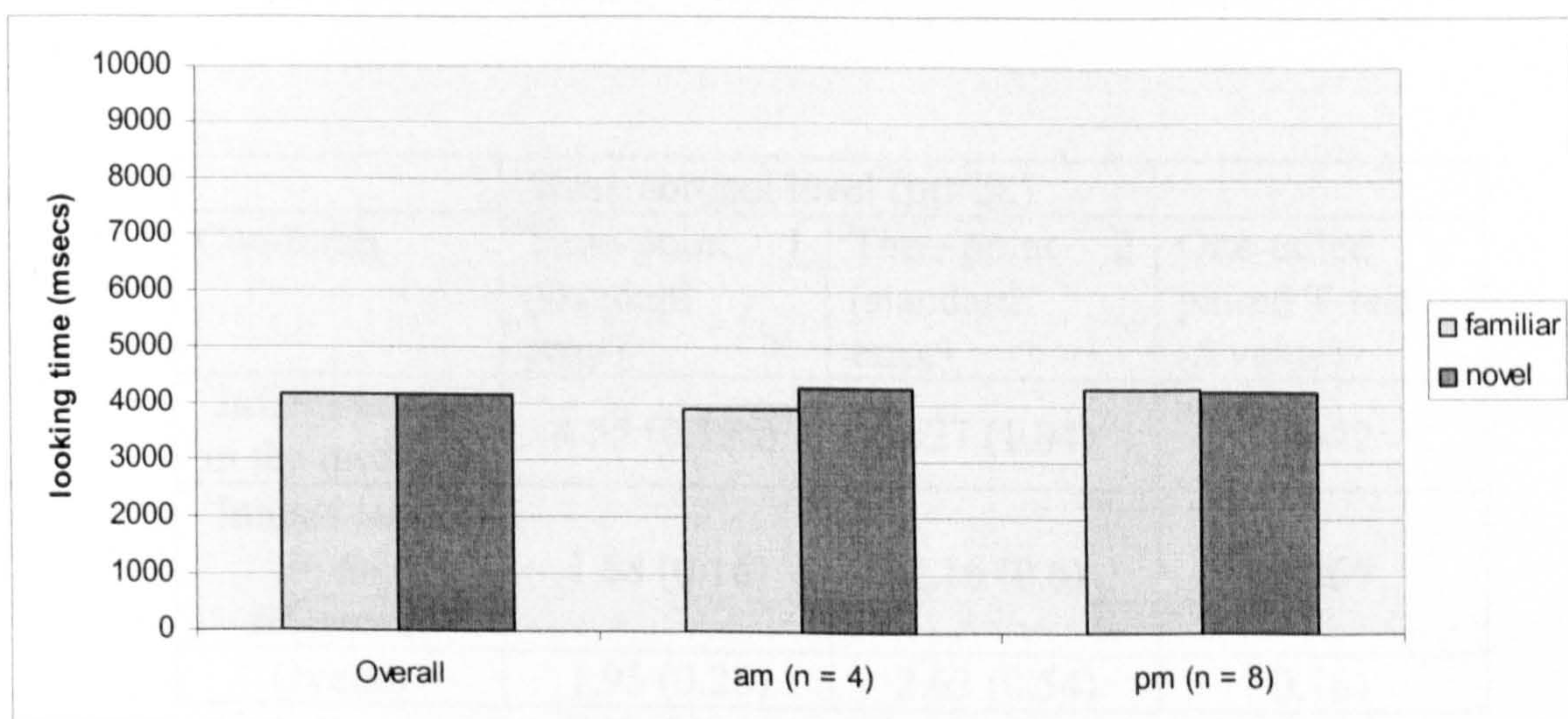
Table 5.5: t-test comparison between looking times by gender

The expression of recognition memory was then examined. A one-tailed paired t-test showed that infants demonstrated a null preference. When data was separated into two groups – one in which the test was administered in the morning, and one in which it was administered in the afternoon – null preferences were also observed for each group (see table 5.6 and graph 5E). The expected novelty preference was thus not observable. 75%

of subjects in the morning group showed a looking time in the direction of a novelty preference. 37.5% of subjects in the afternoon group showed a looking time in the direction of a novelty preference. Overall, 50% of subjects showed a looking time in the direction of a novelty preference. Such a result should be interpreted with caution, however, because of the comparatively small number of participants.

Condition	Mean looking time to novel stimulus in milliseconds (standard error)	Mean looking time to familiar stimulus in milliseconds (standard error)	Mean % looking time to novel stimulus (standard error)	One-tailed paired T-test (<i>p</i> value)
Infants tested in the morning	4290 (752.13)	3910 (742.5)	52.44 (4.84)	0.177
Infants tested in the afternoon	4263 (313.9)	4278 (210.66)	49.62 (2.027)	0.242
Overall	4183 (305.36)	4188 (267.72)	50.56 (2)	0.379

Table 5.6: the mean percentage looking time to the novel stimulus



Graph 5E: the mean percentage looking times to the novel and familiar stimuli

Cortisol data

A series of t-tests was conducted comparing the cortisol levels at time point one and at time point two. Two participants had results substantially higher than the remaining 10 subjects, and were thus categorised as outliers and omitted from statistical analysis. For all remaining participants, a paired t-test demonstrated no significant difference between time points ($P = 0.161$; see table 5.7 and graph 5I)

As there were only 2 participants in the morning condition, comparisons between morning and afternoon data for experiment 1b were not possible. However, as there is no reason to suppose that cortisol levels would be effected by habituation time, the cortisol data of experiments 1a and 1b was combined and compared by t-test for performance across the two time points. Paired t-tests demonstrated that there was no significant difference overall between time points 1 and 2 (see table 5.7 and graph 5J), that there was no significant difference between time points 1 and 2 for participants tested in the morning (see table 5.7 and graph 5K); and that there was no significant difference between time points 1 and 2 for participants tested in the afternoon (see table 5.7 and graph 5L). Thus, no intra-participant differences in cortisol levels were observable.

Condition	Mean cortisol level ($\mu\text{g/dL}$)		One-tailed paired T-test (p value)
	Time-point 1 (standard error)	Time-point 2 (standard error)	
Infants tested in the morning	4.55 (0.195)	3.27 (1.04)	0.342
Infants tested in the afternoon	1.68 (0.16)	2.16 (0.6)	0.269
Overall	1.95 (0.28)	2.63 (0.54)	0.161

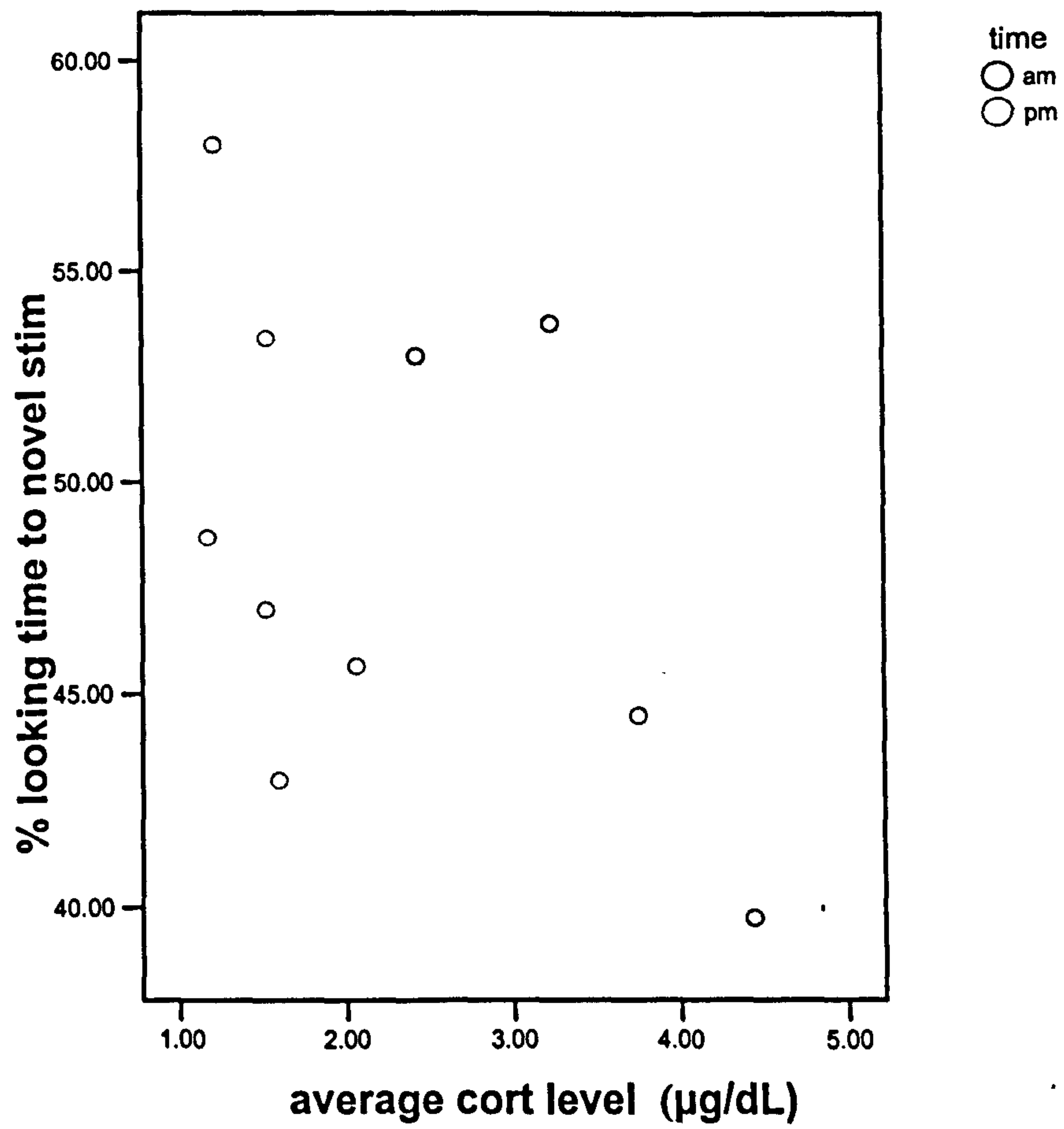
Table 5.7: mean cortisol level t test analysis

A further series of t-tests were conducted on data from experiments 1a and 1b to establish whether there was a significant difference between morning and afternoon groups. Unpaired t-tests demonstrated a significant difference between time point 1 in the morning group and time point 1 in the afternoon group ($t(18) = 3.514$, $P < 0.05$), no significant difference between time-point 2 in the morning group and time point 2 in the afternoon group, and a significant difference between the mean of time points 1 and 2 in the morning group and the mean of time points 1 and 2 in the afternoon group ($t(18) = 4.544$, $P < 0.001$; see table 5.8).

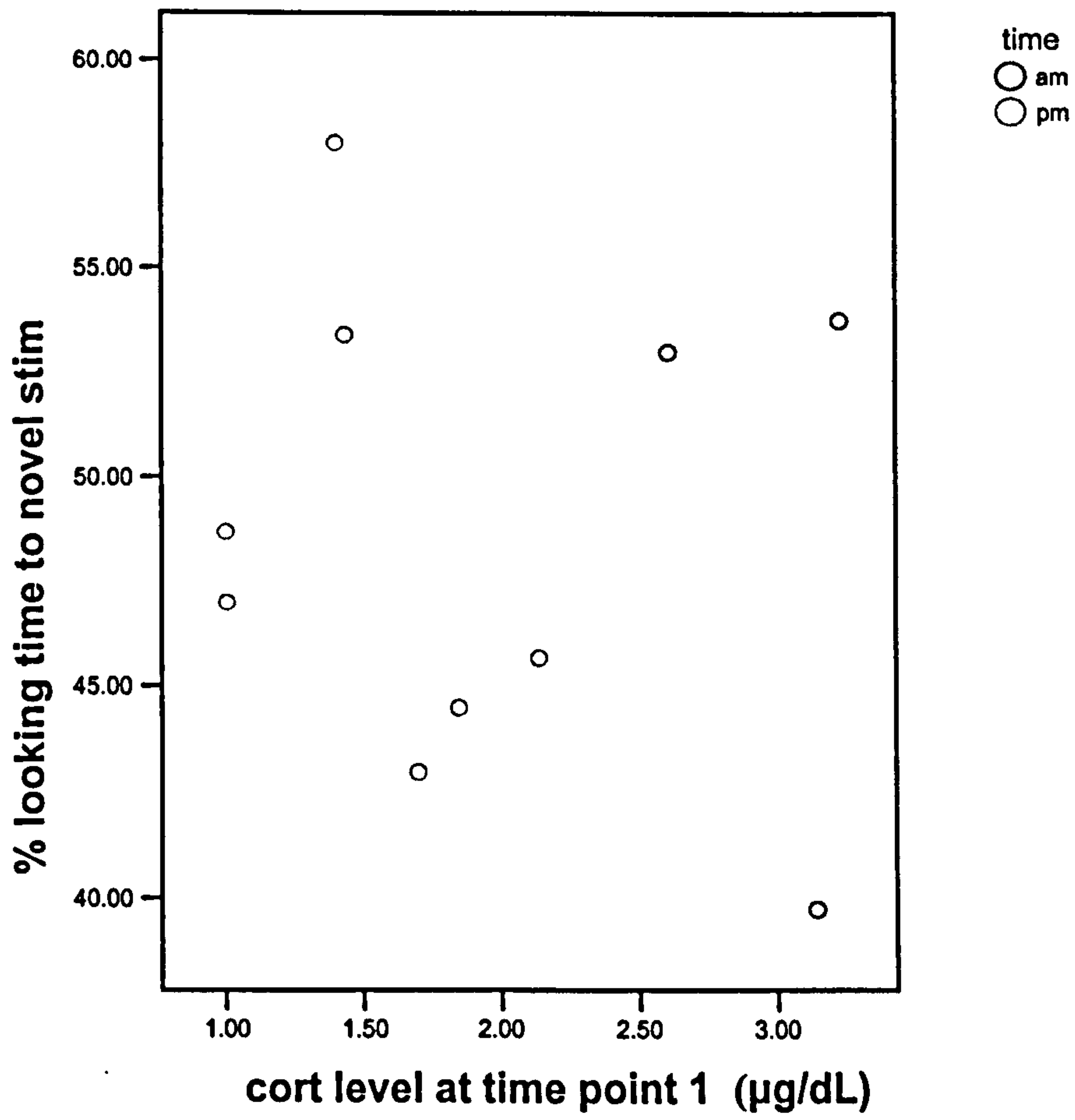
	Mean cortisol level ($\mu\text{g/dL}$)		One-tailed paired T-test (p value)
	AM group (standard error)	PM group (standard error)	
Time point 1	4.55 (0.195)	1.68 (0.16)	0.002
Time point 2	3.27 (1.04)	2.16 (0.6)	0.08
Mean of both time points	3.91 (0.5)	1.92 (0.31)	0.0003

Table 5.8: mean cortisol level between-group t test analysis

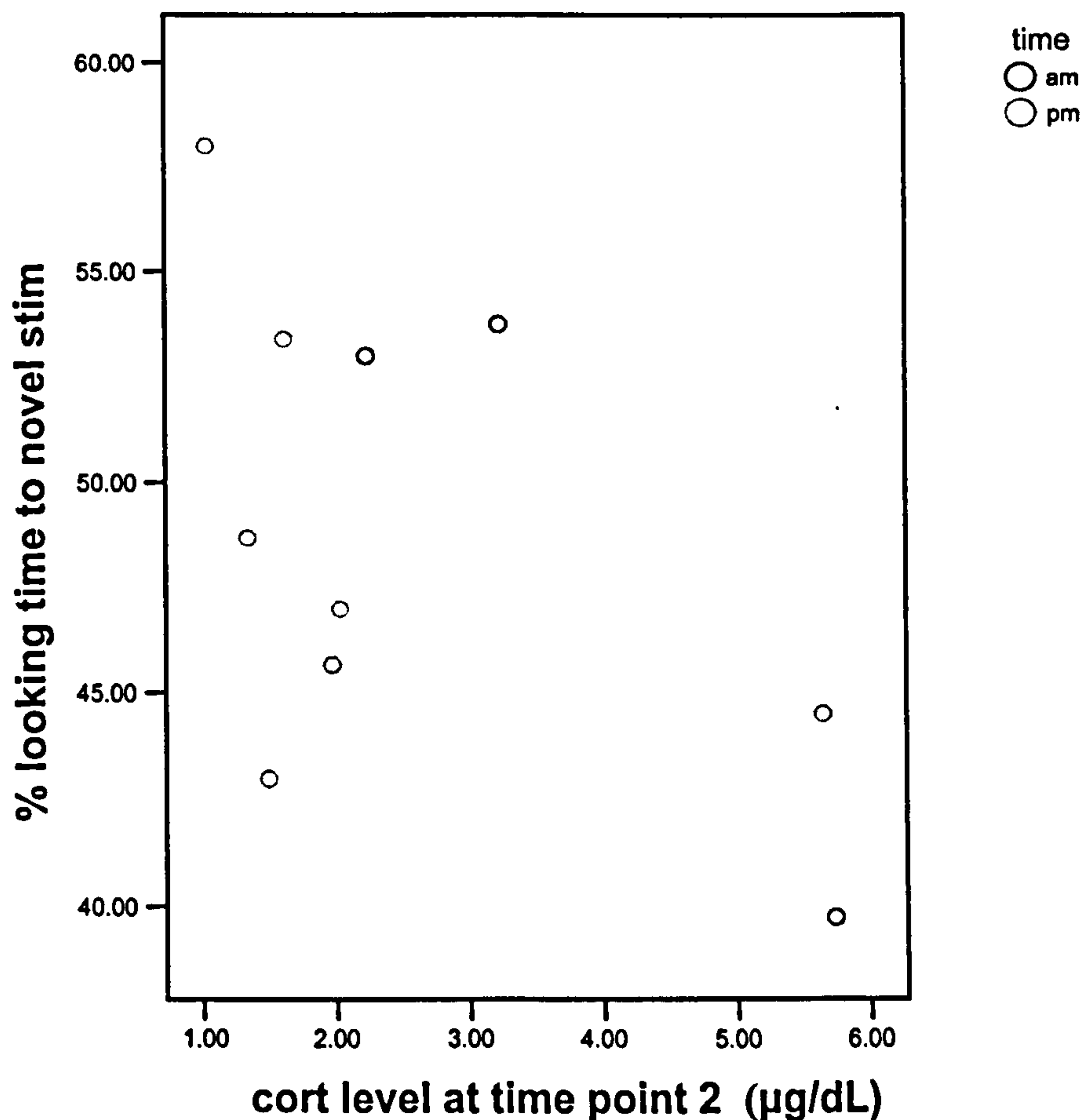
The cortisol and VPC data were also analysed together. The Pearson's correlation coefficient between the cortisol measure averaged over time points 1 and 2 and percentage of time attending to the novel stimulus was $-.467$ and was not statistically significant (see graph 5F). The Pearson's correlation coefficient between the cortisol measure at time point 1 and percentage of time attending to the novel stimulus was $-.141$ and was not statistically significant (see graph 5G). The Pearson's correlation coefficient between the cortisol measure at time point 2 and percentage of time attending to the novel stimulus was $-.555$ and was not statistically significant (see graph 5H).



graph 5F: scatter plot of percentage of time attending to novel stimulus and averaged cortisol level



graph 5G: scatter plot of percentage of time attending to novel stimulus and cortisol level at time point 1



graph 5H: scatter plot of percentage of time attending to novel stimulus and cortisol level at time point 1

General Discussion

It can be seen, then, that a null preference was again observed on the VPC task. It is difficult to theoretically account for this. The same methodology has been used before in the laboratory with faces drawn from the same bank; a twenty second habituation period has also been shown to be sufficient to elicit a novelty preference in lots of studies.

It is possible that the ostensibly small methodological differences between a typical VPC and the procedure conducted here contributed to the observed null preference. Typically, a VPC task occurs within a couple of minutes of the infant and caregiver arriving at the laboratory. In this instance, however, after the first saliva sample was

collected from the infant there followed a pause of several minutes during which the caregiver completed the appropriate questionnaires, and was therefore unable to interact normally with the infant. It is possible that the act of collecting a saliva sample itself, whilst relatively non-invasive, constituted a sufficiently close interaction with a stranger to cause the infant to be less relaxed than s/he would be in a typical VPC task.

It is also possible, of course, that the null result obtained here simply reflects the somewhat temperamental nature of infant recognition memory research; sometimes, significant results are hard to achieve.

Similarly, no significant differences were observed between cortisol levels within conditions. Between conditions, however, there was a significant difference in cortisol levels between infants tested in the morning and those tested in the afternoon. Such a result provides support for the notion that a circadian cortisol profile is already becoming evident in 9 month-old infants, and justifies further research into the role of cortisol levels on the expression of memory.

There are clearly grounds for looking at how glucocorticoid levels impact on visual recognition memory performance in human infants. Unfortunately, neither VPC conducted here yielded a significant preference. It is difficult to provide an explanation for this. Further research would need to start with a VPC task that under normal circumstances elicits a significant novelty preference. In addition to experimenting with varied visual stimuli to achieve this (only one stimuli set of faces was employed here), it might be necessary to consider altering the cortisol collection component of the experiment – perhaps by getting the caregiver to collect the sample, and possibly even

doing it in their car if applicable so it is kept as separate from the experience of being in the laboratory as possible.

A methodological addition that would be of benefit if employed in subsequent research is the gathering of demographic data and information pertaining to when infants last fed and slept and the frequency with which they typically do both. Variables such as feeding and sleeping are wide-ranging and have implications both for cortisol methodologies and also wider implications for attentional abilities.

The ages and stages questionnaire as employed here is arguably of less use; in retrospect, it would be of considerably more worth to test infants with a truly age-appropriate questionnaire. The 10 month version of the ASQ employed here was too advanced for the infants to be particularly informative; scores tended to be low.

Despite the lack of a significant finding here, the measurement of cortisol levels in human infants has at least two potentially important roles in future research. Firstly, elucidating the effect of fluctuating glucocorticoid levels on infant recognition memory in general is an important research aim. Secondly, exploring the role of glucocorticoids in modulating memory for emotionally salient stimuli would help to discern the precise role of the developing amygdala on the medial temporal lobe memory system. Future research, then, should seek to elucidate the relationship between glucocorticoid levels in infants, their response to emotional stimuli, and the development of recognition memory. One programme of research that would be feasible would be a series of VPC task using the fearful and happy faces employed in adult research in previous chapters, with infants varying in age from very young (perhaps 3 months) through to 24 months (when adult-like glucocorticoid circadian rhythms should be present). By testing a large body of

infants on such tests, proper distinctions could be drawn between those tested in the morning and those tested in the afternoon; furthermore, administration of the caregiver questionnaire developed here would allow comparison between babies who had slept recently and those who had not, and also between babies who had recently fed and those who had not. Such a research programme would also have potential application with adult subjects.

Chapter 6 - Conclusions

This thesis set out to investigate a number of variables seen to alter the expression of visual recognition memory in human infants as assessed by the visual paired comparison task. A further aim was to investigate the utility of the VPC with adult subjects, and to explore the manner in which the expression of memory could be altered in an adult population by manipulating the variables seen to modulate recognition memory in infants. To determine the extent to which these aims were met, the principle experimental findings from each chapter will be summarised. It is worth remembering at this point that due to the small numbers of participants typically tested and to the t-test analysis subsequently employed, the power this affords in detecting effects of theoretical interest brings with it the increased possibility of type I errors; future research should strive for data more amenable to analysis with ANOVA tests.

While a novelty preference is the traditional indicator of recognition memory, chapter 2 demonstrated that the novelty preference response is not robust, and is instead influenced by experiences during learning. When the habituation period of the VPC incorporates live interaction with the stimulus, or pseudo-interaction (a moving stimulus presented on video), a null preference is observed with infants. This attenuating of the novelty preference was recorded in every age group from 6- to 24-months of age who participated in the live interaction, and with almost all ages who participated in the pseudo-interaction (12 month olds demonstrated a novelty preference).

Based on these studies it was argued that the child's developing social referencing and emotion regulation abilities, and the maturation of the amygdala are likely all to be

contributing factors in how recognition memory is expressed when learning involves an interactive component.

Chapter 3 examined the effectiveness of the VPC for studying recognition memory in adults before considering whether interaction with the stimulus would also cause disruption to the novelty preference in adult populations. Standard control trials confirmed the presence of novelty preferences when traditional static pictures were used as habituation stimuli, demonstrating that the VPC is a suitable tool for use with adults. As with the infants in chapter 2, a habituation period comprising of social interaction disrupted the novelty preference. A null preference was observed after 60-seconds or 4-hours of interaction with the experimenter whose photo was used as the test stimuli. Further experiments eliminated the experimenter's face as a confounding variable. The use of famous faces as stimuli then demonstrated that "a mere exposure effect" was not an adequate explanation for this disruption; despite having considerable experience in observing famous faces, participants still demonstrated a preference for a novel, unfamiliar face. Finally, it was established that adults tested on the video puppet task employed in chapter 2, demonstrated the same null preference as was observed with the majority of infant age groups. The findings from chapter 3 have important implications for the preexplicit memory account of infant memory forwarded to explain the ability of infants to pass very simple memory tasks despite having an obviously immature MTL system. The fact that adults can be seen to fail the task in almost exactly the same manner as infants calls into question the degree to which a separate, more 'primitive' mnemonic system is required to explain infant performance.

Chapter 4 continued to explore the extent to which variables experienced at the point of habituation disrupt recognition memory in the VPC task with adults. These studies focused on emotion processing because the findings from chapter 2 led to the prediction that amygdala involvement during learning may have a disruptive effect in the memory retrieval. When the habituation stimulus was a face showing either fear or happiness and the test stimuli were the same face with a neutral expression and a novel neutral face, a null preference was observed (in the direction of a *familiarity* preference). In contrast, when the habituation stimuli was a neutral face and the test stimuli were the same face with either a happy or fearful expression and a novel face showing the same emotion, a novelty preference was observed. Such a finding provides evidence that the attenuation of the novelty preference when emotional processing systems are involved is occurring during the encoding phase and not the retrieval phase. The lack of 1:1 correspondence between the habituation and test stimuli in such methodologies is an inadequate explanation for the effect; when the habituation stimuli was a full-face picture and the test stimuli were three-quarter profiles of the same face and a novel face, a novelty preference resulted.

Additionally, it was empirically established in this chapter that using different stimuli in the VPC results in different effect sizes. When photographs of chairs or of faces were used, a strong novelty preference was observed. When 'greebles' or 'fribbles' were used, the novelty preference fell short of statistical significance. A forced-choice memory test on the same categories of stimuli also demonstrated that adults took longer to react to greeble and fribble stimuli than face or chair stimuli. A greater number of errors was made with the greeble and fribble stimuli compared to the chair and face

stimuli. Such observations demonstrate that more complicated stimuli are responded to differently in the VPC task, and also that forced-choice memory tasks can be used in tandem with VPC tasks in adult populations to strengthen this contention. These findings suggest that visual stimuli are non-equivalent, and that care should be taken when selecting stimuli for use with VPC tasks.

Chapter 5 sought to explore the role of emotion on VPC task performance in infants at a lower level of explanation. Previous chapters suggested that it is the activation of the amygdala at the encoding stage of the VPC that disrupts the novelty preference; as the hormone cortisol is robustly demonstrated to be involved in emotional processing and acts extensively on the amygdala, an investigation into the role of cortisol on VPC performance was undertaken. This investigation was unsuccessful inasmuch that no novelty preferences for the VPC could be established using a traditional face stimulus with 9 month-old participants, despite manipulation of the length of the habituation period. It was established, however, that cortisol levels differed significantly between infants tested in the morning and those tested in the afternoon. This provides evidence for an emerging circadian cortisol profile in infants as young as 9 months; and, when combined with the literature review in chapter 5, suggest that further research concerning cortisol levels and their impact on visual recognition memory in infants is warranted.

The experimental findings presented in this thesis together impact directly on the manner in which findings from the typical VPC are usually used to infer the functioning of developing memory systems. In the main, research demonstrating novelty preference has, along with animal and imaging research, underpinned the elucidation of VRM circuitry. Whilst a number of models compete to explain the findings of a familiarity

preference under certain conditions (e.g. Hunter & Ames, 1988; McCall & McGhee, 1977), all models would predict a novelty preference as the standard attentional response when task difficulty and familiarization time are appropriate for the age of the subject. The neuroanatomical substrates required for the VPC task, as have been outlined in this thesis, centre round the medial temporal lobe. More specifically, structures including the hippocampus, parahippocampus, and entorhinal and perirhinal cortices are involved in mnemonic encoding (e.g. Herbert & Pascalis, 2007). In the early stages of consolidation, information is transmitted to the hippocampus from unimodal and polymodal cortical association areas via two routes. Firstly, information is transmitted from the perirhinal and parahippocampal areas to the entorhinal cortex; this structure then projects both immediately to the hippocampus and also to the dentate gyrus, which in turn projects to the hippocampus (for review, see Bauer, 2004, DeHaan, 2006). Long-term memory storage is subsequently depending on cortical areas including the visual association areas, and consequently the maturation of efficient projections between the MTL and these areas (Carver & Bauer, 2001). In essence, the principal neural structures held to be necessary for VRM can be summarized diagrammatically as follows (Herbert & Pascalis, 2007):

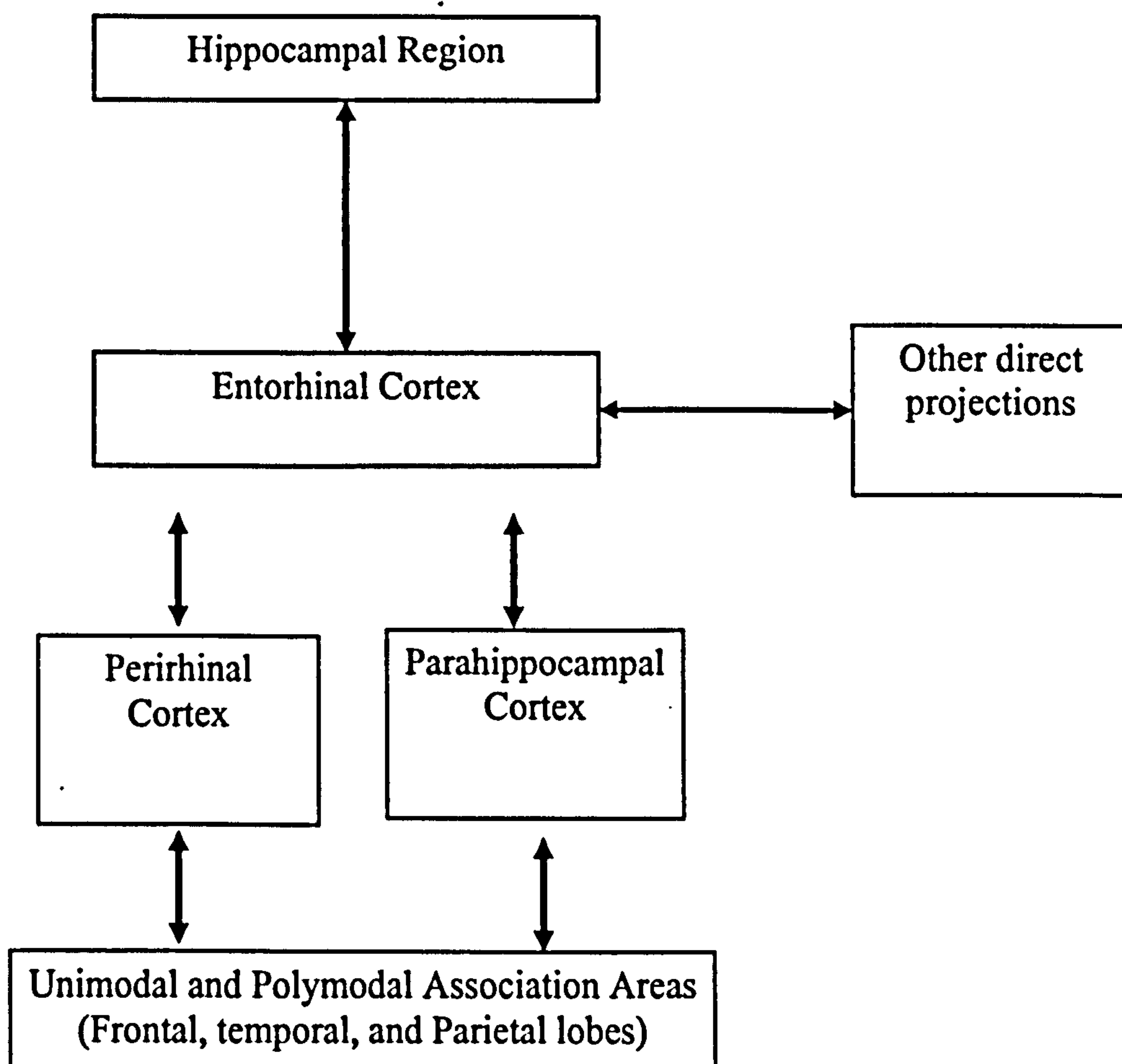


Figure 6.1: schematic diagram of the principal neural structures and pathways necessary for visual recognition memory in humans and nonhuman primates (Herbert & Pascalis, 2007)

The experiments conducted within this thesis, however, add to a body of literature demonstrating that the novelty preference is *not* the only elicitable response of the VPC.

Several theorists have demonstrated that the familiarity preference is also indicative of memory, and make the point that this is as demonstrative of mnemonic-based discrimination as is a novelty preference (for example, see Bahrick, Hernandez-Reif & Pickens, 1997; Houston-Price & Nakai, 2004; Hunter & Ames, 1988; Wagner & Sakovits, 1986). Indeed, the familiarity preference is to be expected in instances where familiarization time is insufficient or where stimuli are too complex for participants of a particular age (Hunter & Ames, 1988). The experimental findings here add to this

literature by demonstrating that when additional demands are added such that processing demands are *qualitatively* increased at habituation, the novelty preference can be reliably and consistently attenuated by introducing additional cognitive demands. Importantly, the same demands seem to disrupt the task in both infants and in adults. This demonstrates the utility of the task with an adult population. It also brings in to question the need to postulate a separate mechanism for the task in young infancy. Nelson's preexplicit model (1995) argues that the memory system employed by infants in the first year of life is qualitatively different to the explicit memory system proper, and that this earlier system is automatic in its operation. Given the similarity between adult and infant populations on the experiments conducted here, either the task is sufficiently simple that it is completed by adults using a similarly basic mnemonic system (and there is some merit in arguing this – the task certainly requires little conscious thought: indeed this is discouraged in the instructions given to adults) or what is being measured in infants *is* explicit memory. The preexplicit account seems to hinge on the putative automaticity of the task. If it *is* an automatic system, not only does one have to account for comparable adult performance but also for the manner in which the automaticity can be seemingly 'overridden' – and automaticity that can be overridden is an obviously limited form of automaticity.

Whether the system in both infants and adults is a simple form of memory, or whether the same explicit memory system is used by both, one neuroanatomical structure seems certain to be involved in the attenuation of the novelty preference – the amygdala.

There is considerable empirical evidence for the role of the amygdala in modulating the effects of memory (see e.g. McGaugh, 2004, Hamann, 2001). As outlined in chapter 5, mnemonic strength is affected by manipulation of Glucocorticoid levels,

either pharmacologically or by increasing the level of stress or emotion experienced by the subject. A particularly pertinent facet of the modulatory capacity of the amygdala concerns the ability of emotional states to influence memory independently of the affective status of the mnemonic stimuli themselves. In an fMRI study with healthy young adults, Erk et al (2003) presented them with either emotionally positive, emotionally negative or neutral pictures, and then a word remembering task with neutral words. Recall when prior exposure was to positive visual stimuli was associated with activity in parahippocampal and extrastriate areas; when exposure was instead to negative stimuli, recall was associated with activity in the amygdala. Similarly, Nielson, Yee and Erickson (2005) demonstrated in young adults that recall in a neutral word memory task was impaired both at 30 minutes and at 24 hours when they were presented with emotionally arousing videos (semantically unrelated to the word list) during consolidation. Neutral videos presented at the same point did not impair word memory.

In a review of the literature, Hamann (2001) argues that these modulatory effects are caused by specific, specialized mechanisms that are not engaged by memory processes in the absence of an emotional processing component. Hamann proposes four key concepts concerning the modulatory role of the amygdala. Firstly, the amygdala is the 'primary orchestrator' of processes of emotional memory, without which emotional effects on memory cannot occur. Secondly, the amygdala can effect explicit memory by modulating the activities of other brain regions. Thirdly, emotional arousal can effect explicit memory through the release of stress hormones that interact with the amygdala. Finally, the modulatory influence of emotional arousal via the amygdala acts specifically on consolidation processes in memory regions such as the hippocampus. This final

observation by Hamann is borne out by the results of chapter 4 of this thesis, in which the inclusion of emotional stimuli at the point of encoding / consolidation impaired the novelty preference, whereas emotional stimuli at point of recall did not.

It can be seen, then, that in adults the amygdala has a clear modulatory role in memory when there is an emotional processing component. The picture for infants, however, is likely to be more complex. As has been described, the MTL is still developing and does not fully reach maturity for years (reference). Even then, however, it would appear that the precise role of the amygdala is harder to determine than in adults. Thomas, Drevets, Whalen, Eccard, Dahl, Ryan & Casey (2001) conducted a BOLD imaging study in which adults and children (mean age 11 years) merely had to observe masked fearful and neutral faces. Adult perception of the fearful faces was associated with increased activation in the left amygdala. Children, however, demonstrated greater amygdala activation to the neutral stimuli.

Given the complexity of the role of the amygdala and its connectivity to other brain regions, it is perhaps unsurprising that its role in the developing memory system in the first years of life appears complicated. Nevertheless, it would seem reasonable to postulate that the developing modulatory capacity of this structure is a likely candidate for explaining the disruption to the VPC demonstrated throughout the thesis. It is inherently possible that this mechanism may also be at the root of the obviation of the novelty preference in cases of social interaction. Interacting with an adult, or observing a puppet seemingly interacting with you, may well be an emotionally arousing experience for the infant. A substantial conclusion of this thesis, then, is that the VPC is an unreliable tool for measuring memory *when the amygdala is involved in processing at the*

point of consolidation. Such a relationship between the amygdala and the VRM system is represented below (figure 6.2).

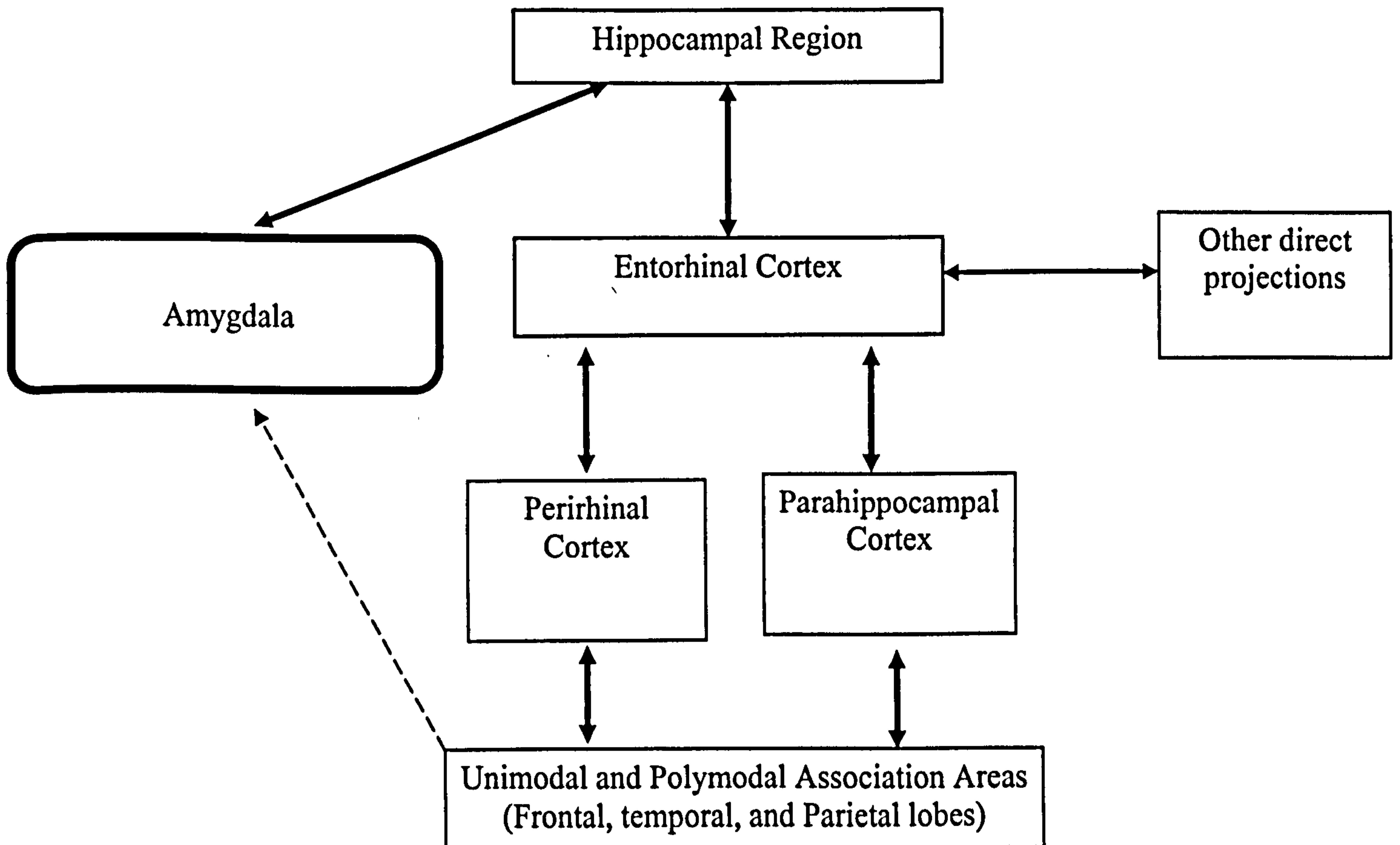


Figure 6.2: schematic diagram of the principal neural structures and pathways necessary for visual recognition memory in humans and nonhuman primates illustrating the putative additional role of the amygdala (adapted from Herbert & Pascalis, 2007)

It is contended, then, that the traditional model of visual recognition memory needs to be adapted to take into account the results of the VPC when the amygdala is involved at the habituation stage. When the amygdala is *not* implicated, the system is

predisposed to direct attention towards novelty. When emotion or interaction is included at habituation and the amygdala is involved in processing, however, subsequent attentional styles are altered by the increased salience of the habituation stimulus; the intrinsic preference for novelty is consequently in competition with the attentional pertinence of the familiar stimulus.

It is possible to draw several conclusions from the research conducted here. Firstly, the novelty preference is not the only useful result of the VPC – a null preference resulting from the attenuation of the novelty preference can be informative concerning the neuroanatomical demands of variants of the VPC task. Secondly, the role of the amygdala in VRM processing in infants is an important area for study. If, as is contended here, the null preferences can be the result of amygdala activation during the encoding / habituation phase of the VPC, the interaction between the amygdala and other MTL components is a likely cause. Thirdly, the VPC has been demonstrated to be an effective tool for use with adults, and as such can be used to examine the developmental trajectory of explicit memory right across the lifespan. Such conclusions could form the basis of a research programme incorporating research with infants, children and adults. Such research would systematically investigate the effect of both interaction and emotion on VPC performance, and would emphasise the expected difference between the inclusion of such variables at the point of habituation / consolidation and at test / recall. It would be hypothesized that any engaging stimulus presented at habituation would attenuate the novelty preference, whilst the inclusion of such variables at test would not. It would be sensible to include actual human interaction, human faux-interaction, and puppet

interaction and faux-interaction with infants of all ages and with adults, and also to include strongly emotional stimuli such as images of violence in adult studies.

In parallel to systematically extending the nature of stimuli used, it would be sensible to thoroughly explore the role of glucocorticoids in mediating the expected results. Glucocorticoid levels could be easily and comparatively cheaply measured routinely in all subjects, with the expectation that higher GC levels would strongly correlate with attenuated novelty preferences (i.e. null preferences). In addition, affective coding measurement should be undertaken with infant subjects.

If it could be robustly demonstrated that amygdala activation accounted for novelty preference attenuation in both infant and adult subjects, this would elucidate the MTL explicit memory and lay the foundations for the routine inclusion of the amygdala in discussion of the system's functioning. It would also shed interesting light on the current debate concerning preexplicit memory.

In summary, then, a number of claims can be made on the basis of the empirical work conducted here. Most generally, it has been shown to be the case that the VPC is a more complex tool than has often been regarded. It is possible, through the inclusion of interaction or emotion, to alter the expression of memory in the task, i.e. to attenuate the typical novelty preference, and in some cases to elicit a familiarity preference. Furthermore, studies with adults can demonstrate the similarity of the developing infant explicit memory system to the fully-fledged system, and can also shed light on the equivalence between memory methodologies.

Lastly, the demonstration of the involvement of the amygdala in the MTL memory system is an important topic for further research, both in terms of elucidating the

development of the system in infancy and in exploring the parameters within which the VPC can be used, both in infants and in adults.

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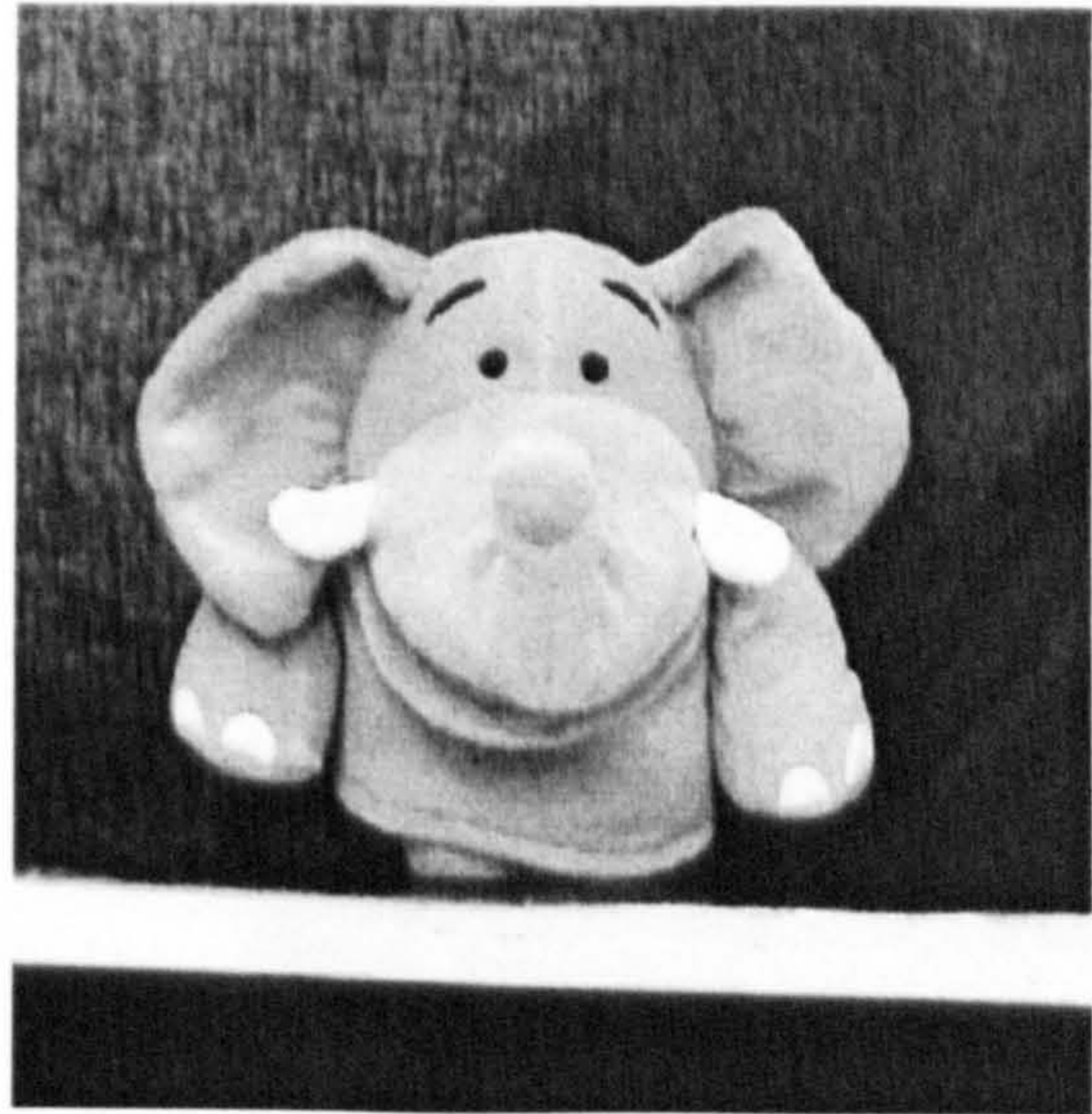
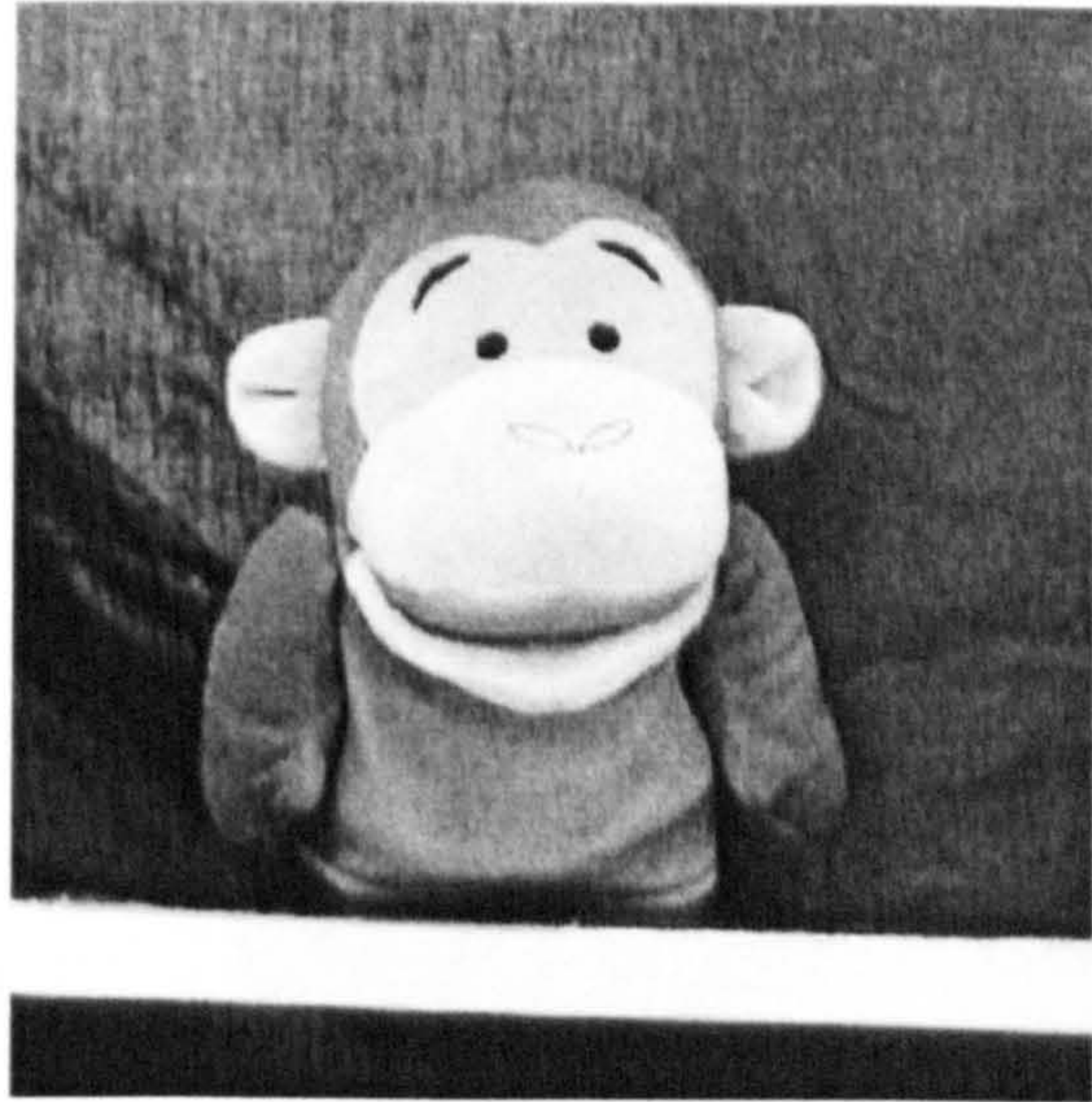
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Appendices

Appendix A – example puppet stimuli

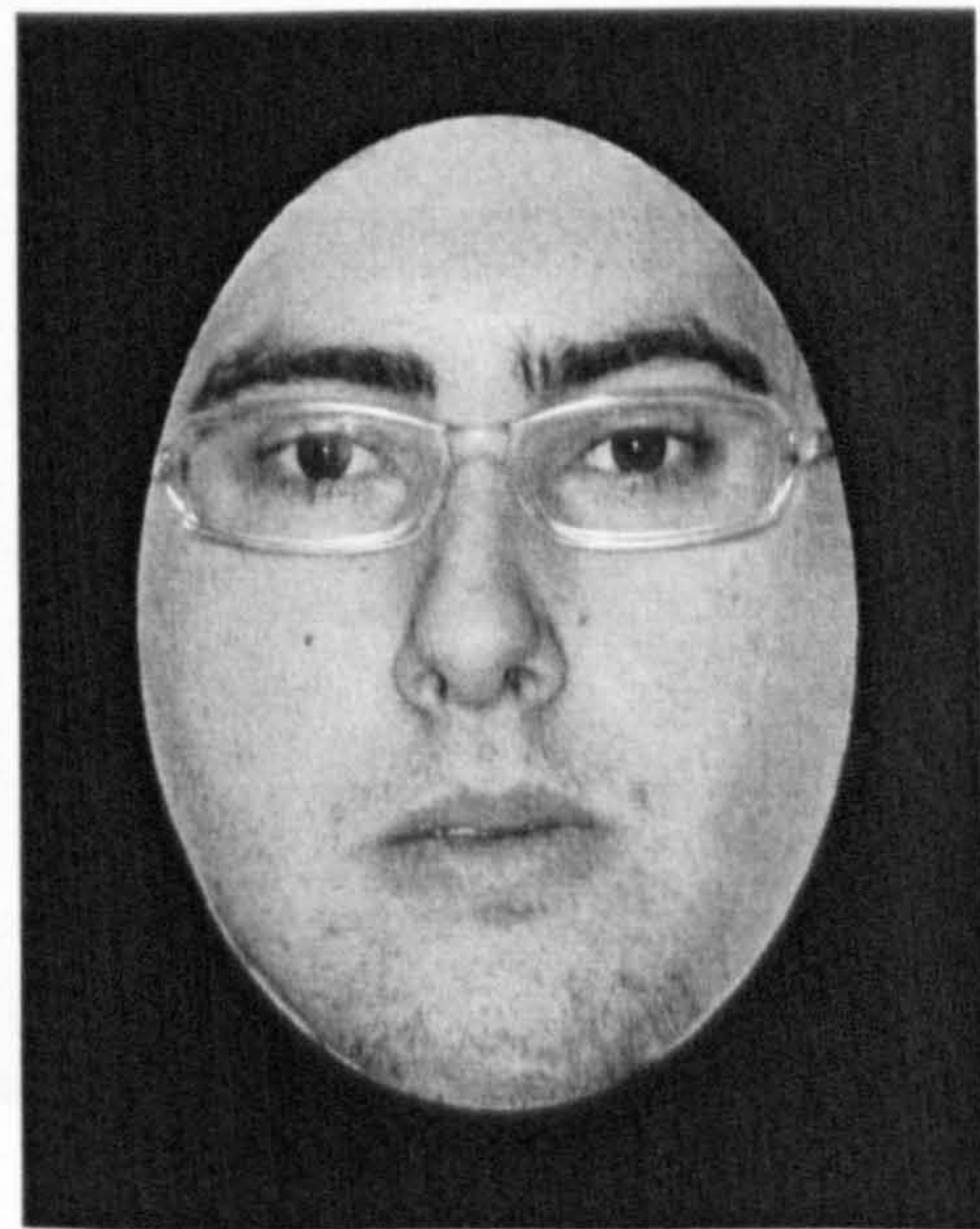
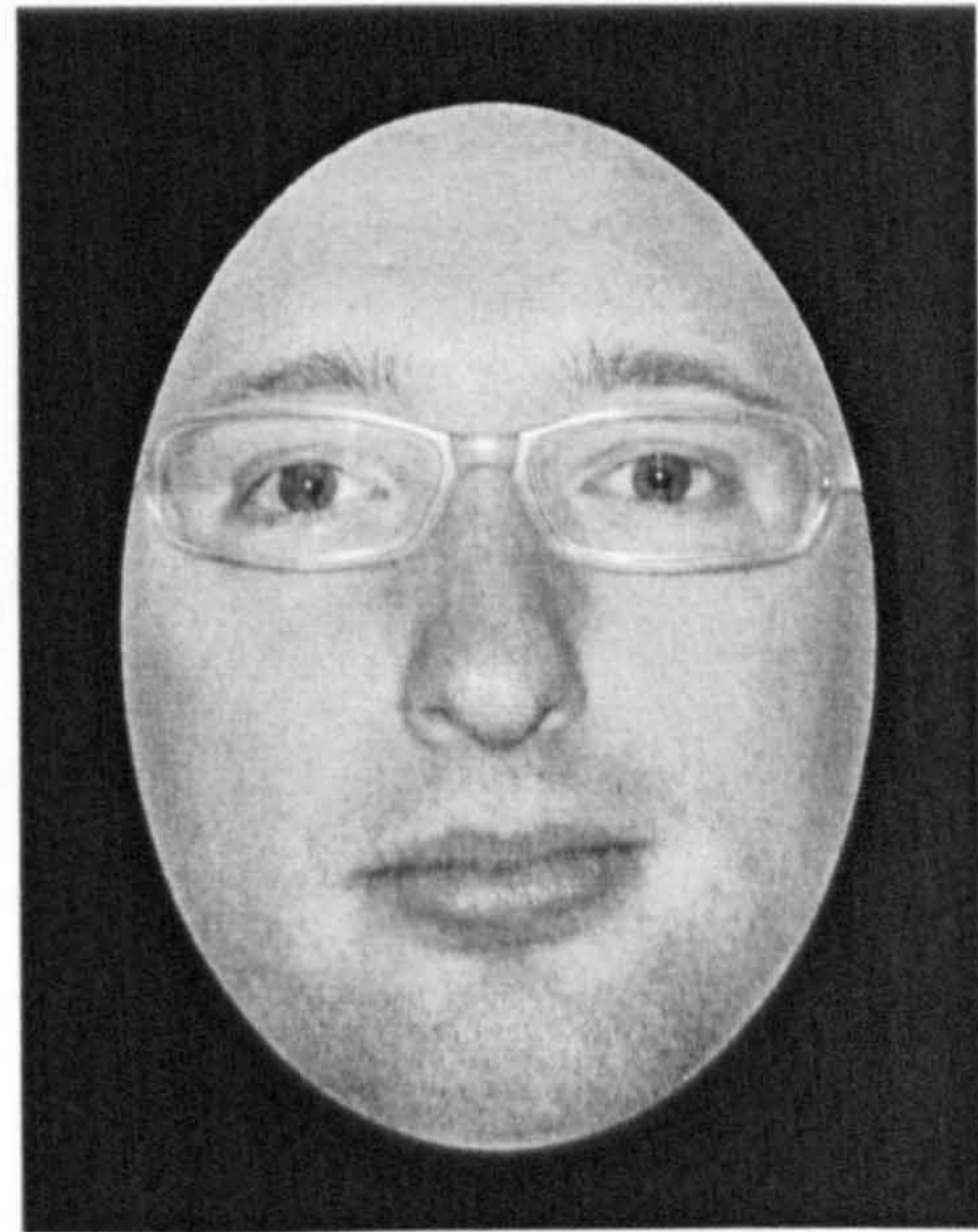
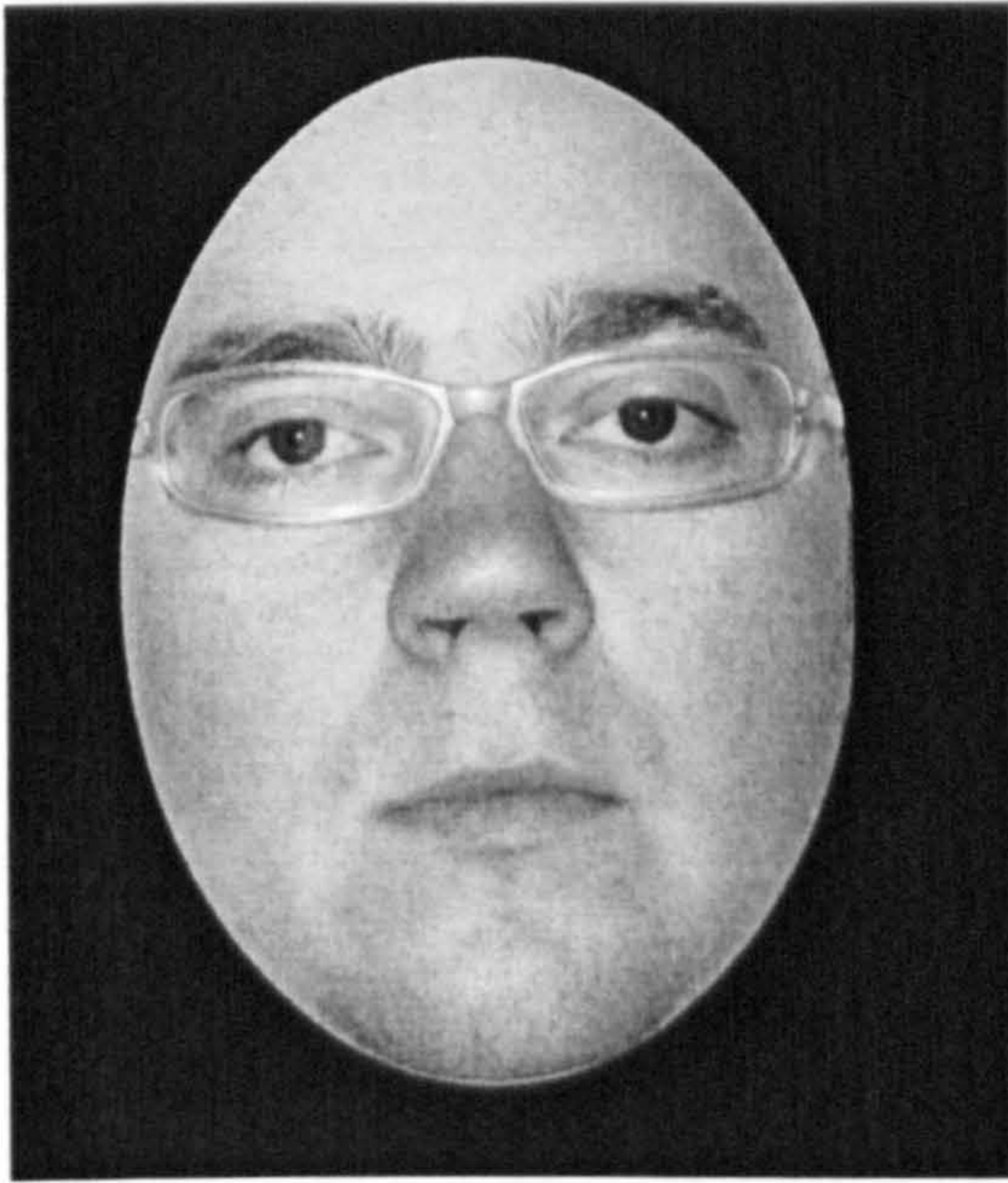


Appendix B – images of puppet stimuli

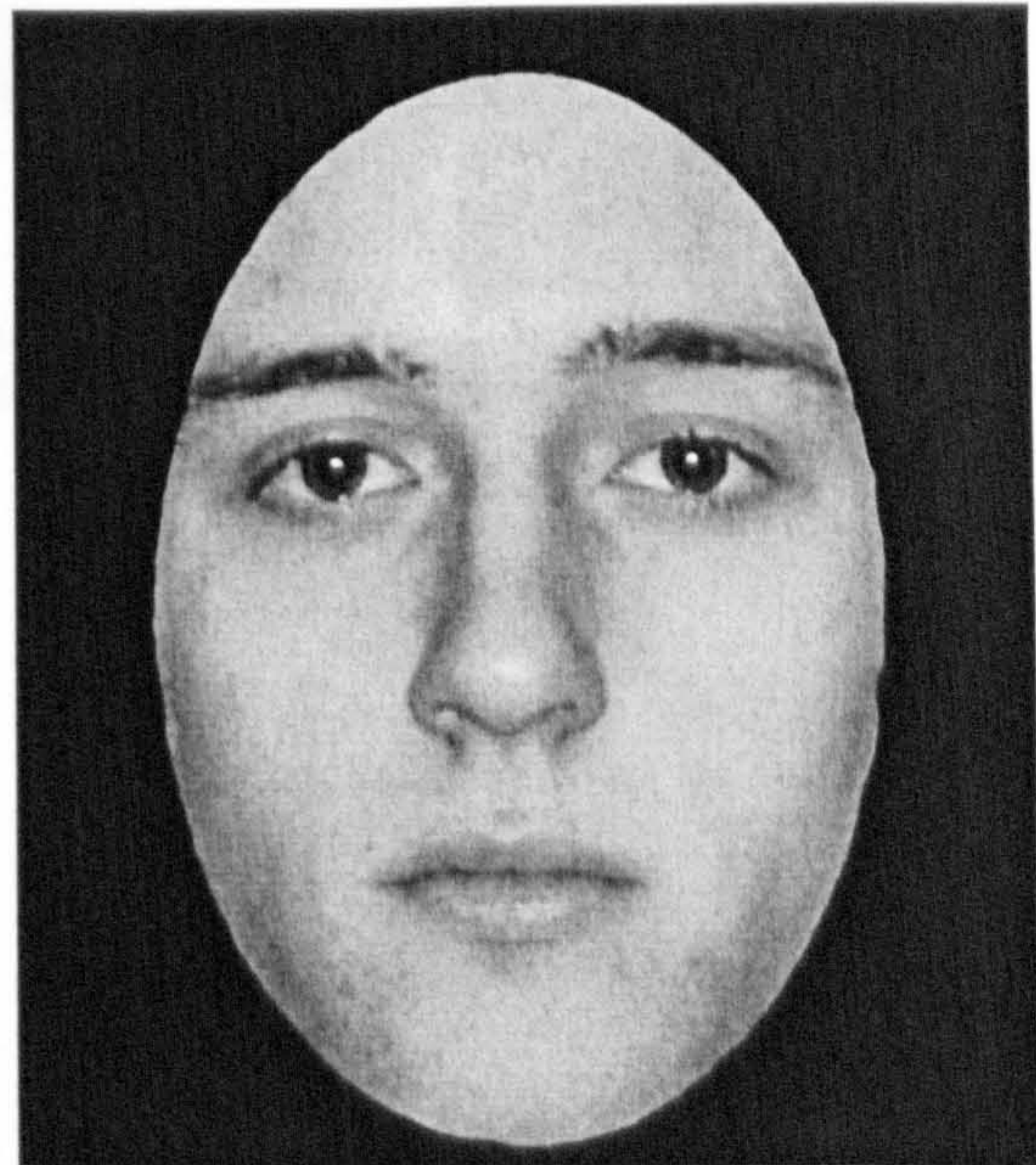
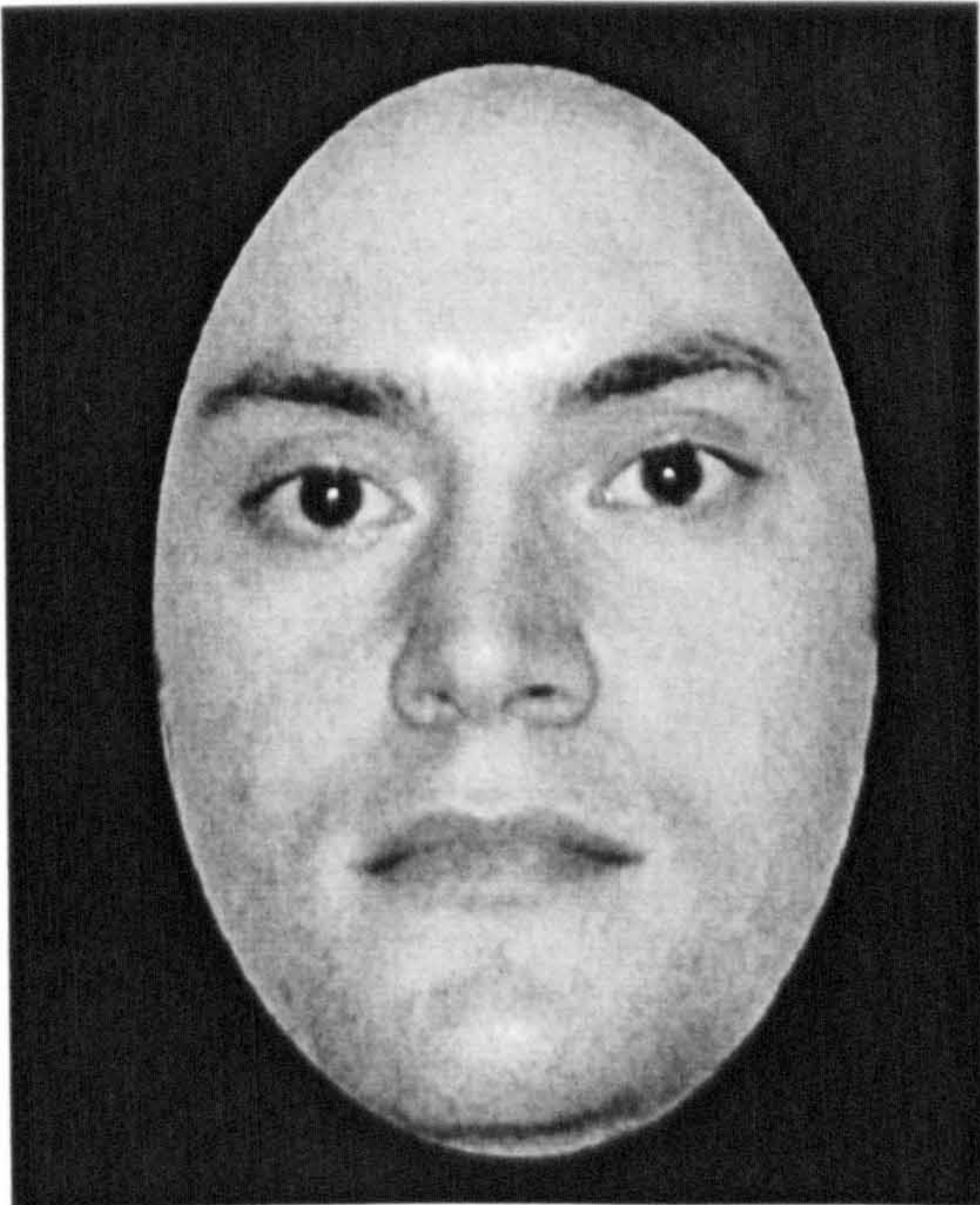
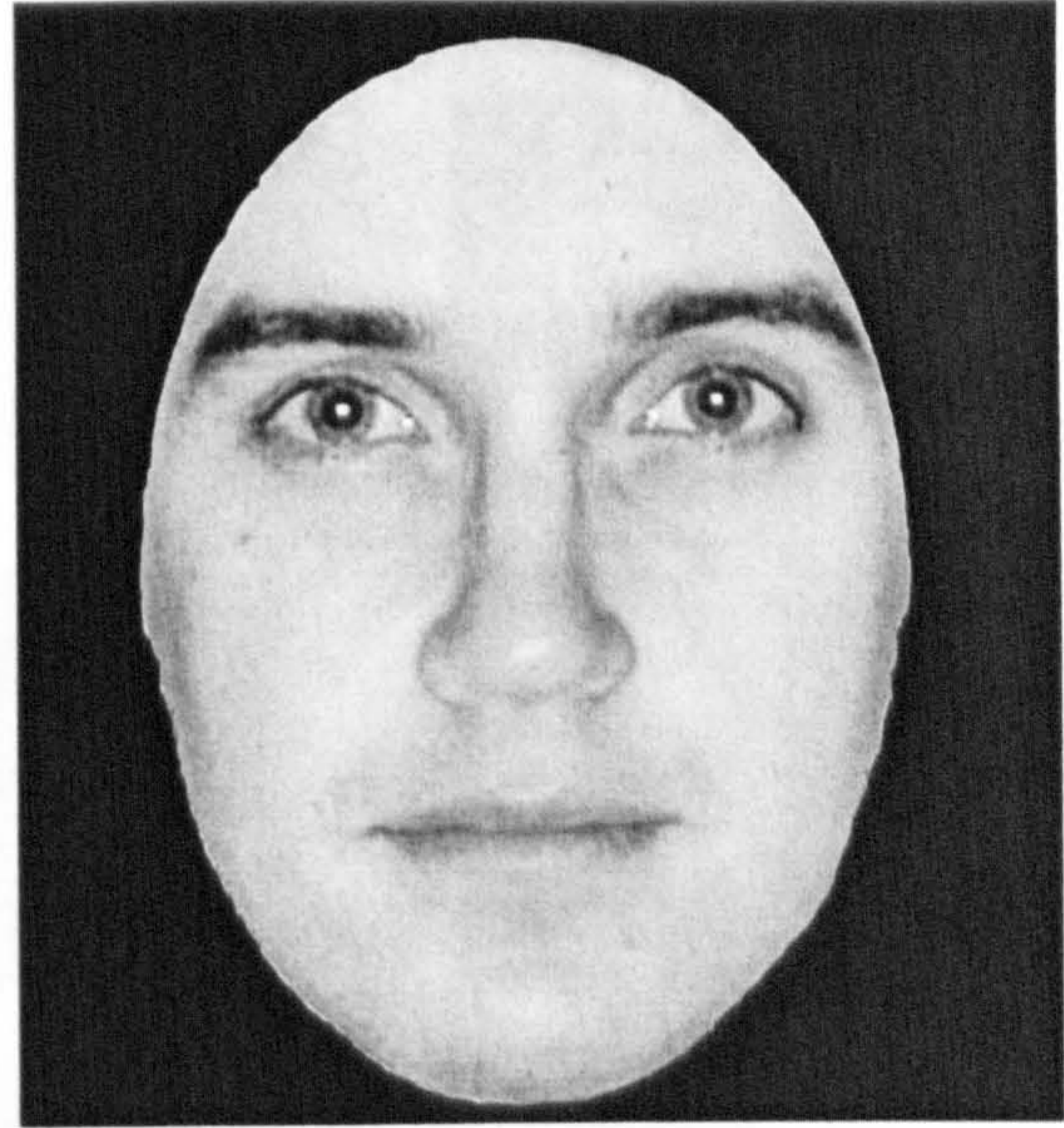
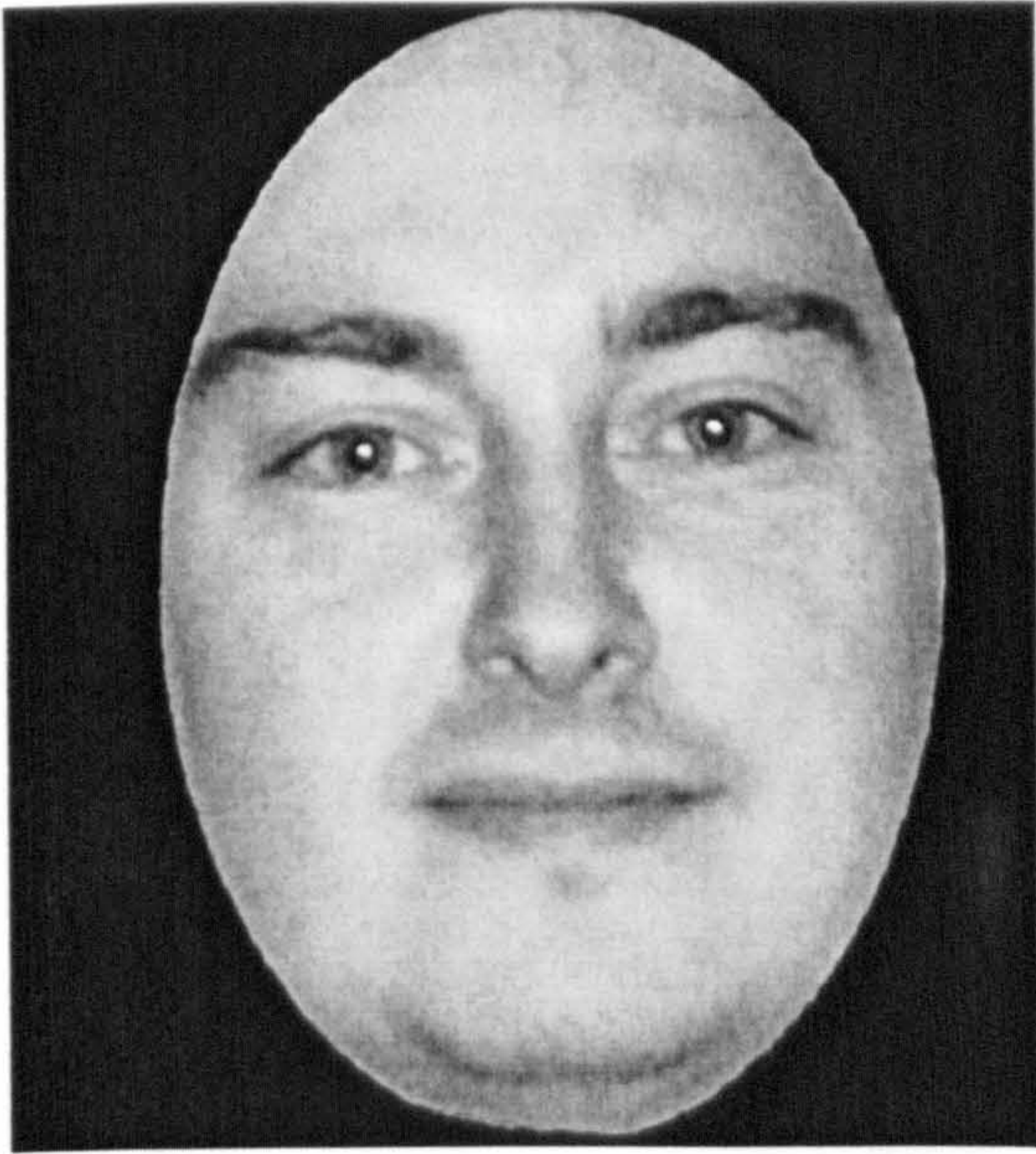


Appendix C – images of experimenter and typical control stimuli

Experimenter and matched stimuli



Typical controls



Appendix D – Famous Faces



F1.jpg



F10.JPG



F11.JPG



F12.JPG



F13.JPG



F14.JPG



F15.JPG



F16.JPG



F17.JPG



F18.JPG



F2.jpg



F3.jpg



F4.JPG



F5.jpg



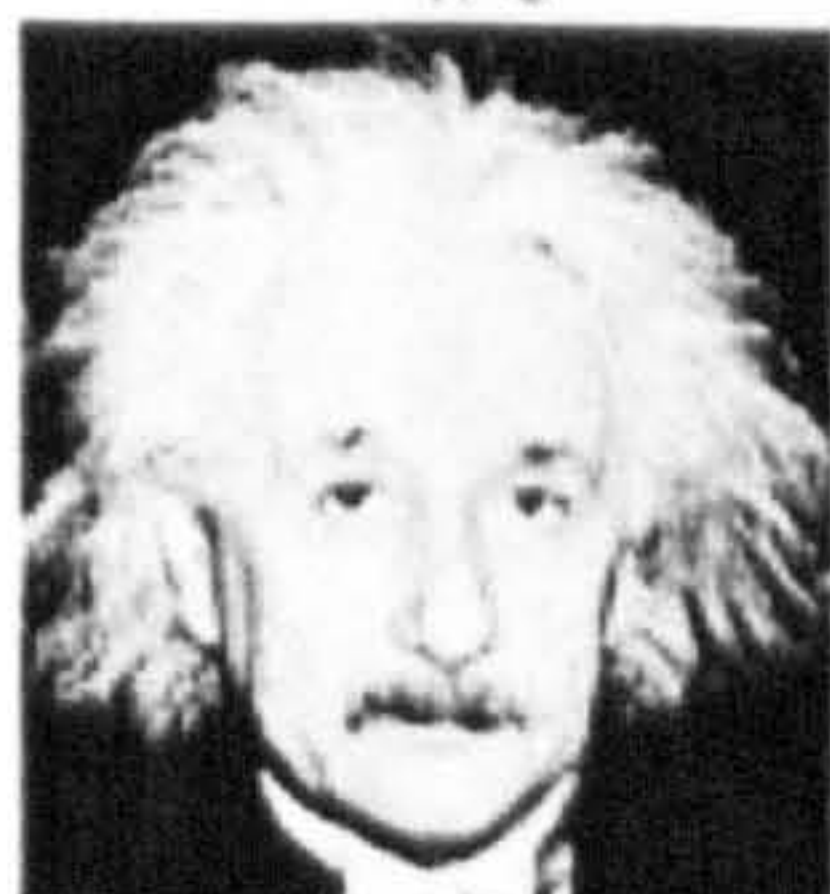
F6.JPG



F7.jpg



F8.JPG



F9.JPG

Appendix D – Famous Faces – Nonfamous control stimuli



U1.jpg



U10.JPG



U11.JPG



U12.JPG



U13.JPG



U14.JPG



U15.JPG



U16.JPG



U17.JPG



U18.JPG



U2.jpg



U3.JPG



U4.JPG



U5.JPG



U6.JPG



U7.JPG



U8.JPG

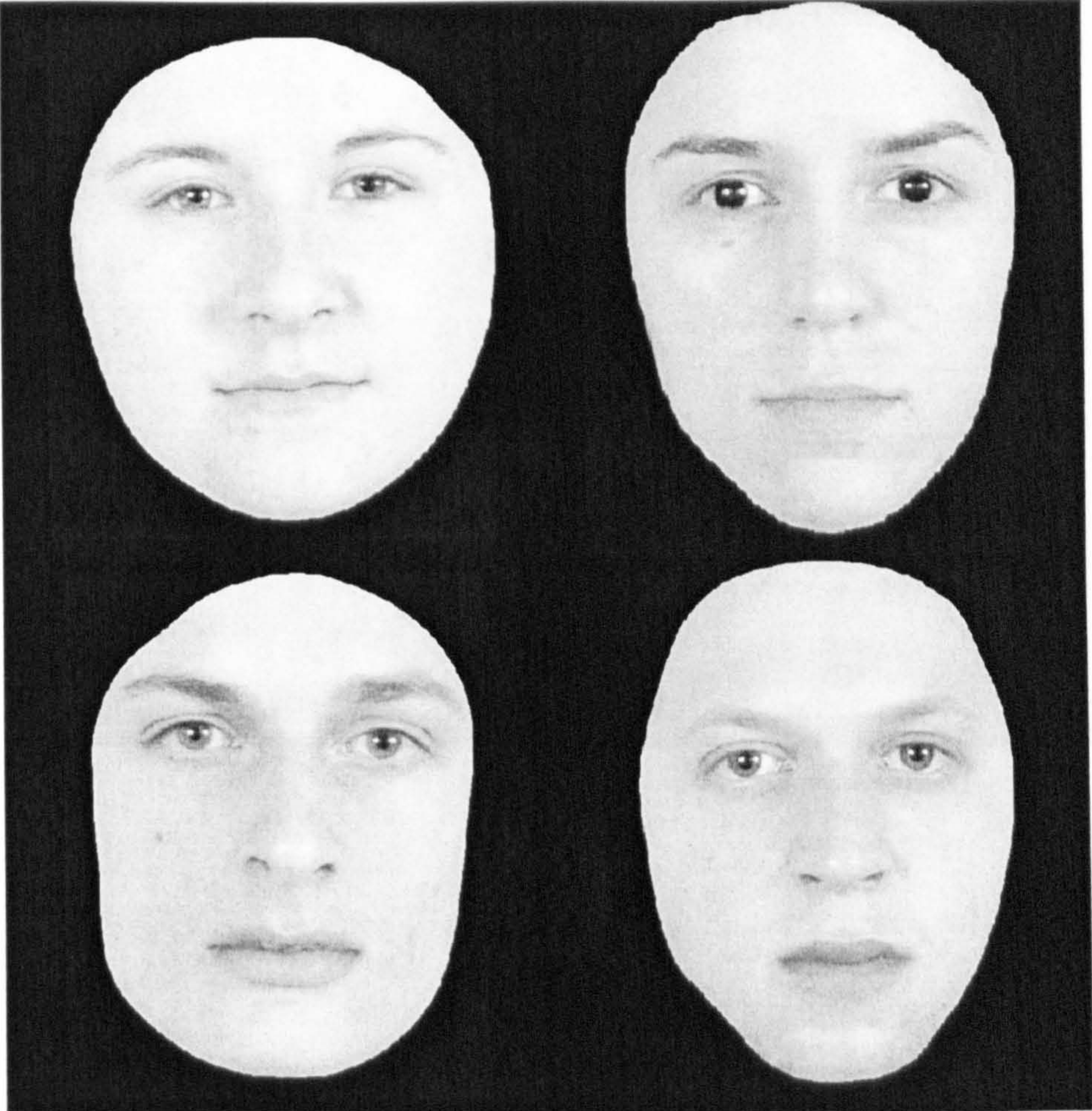


U9.JPG

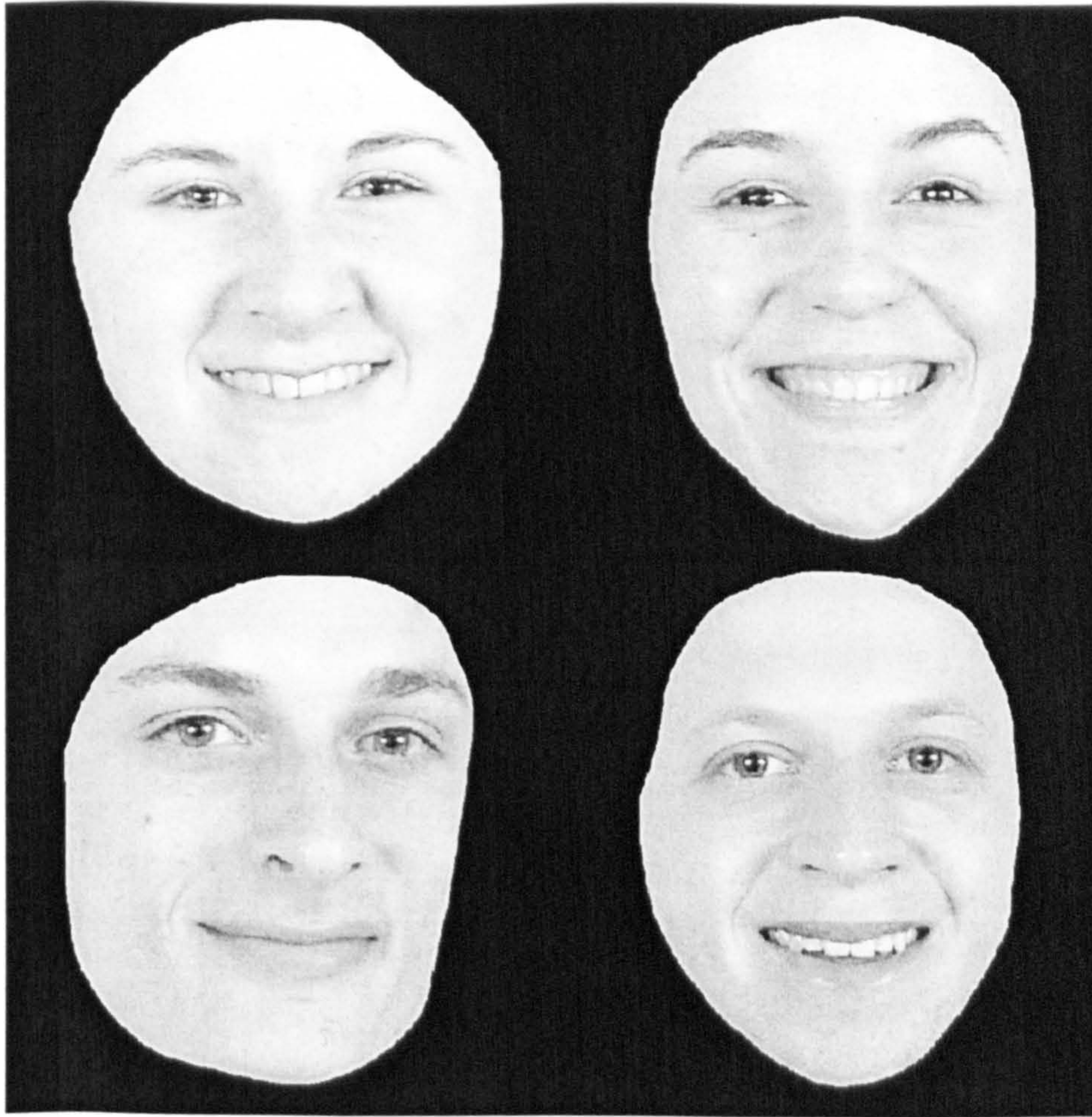
Appendix E – images of emotion, typical control and three-quarter profile stimuli

Emotion stimuli

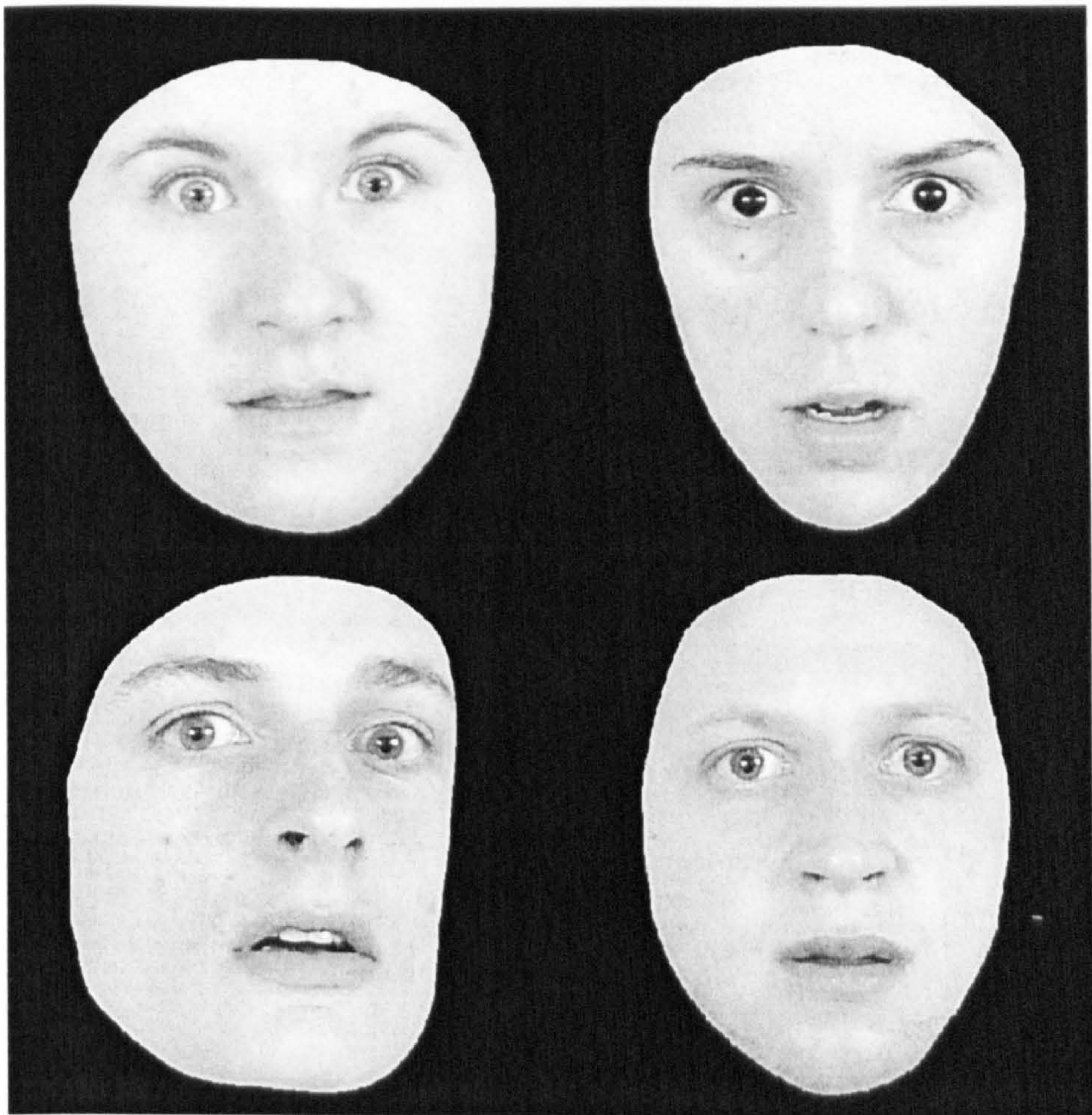
Neutral



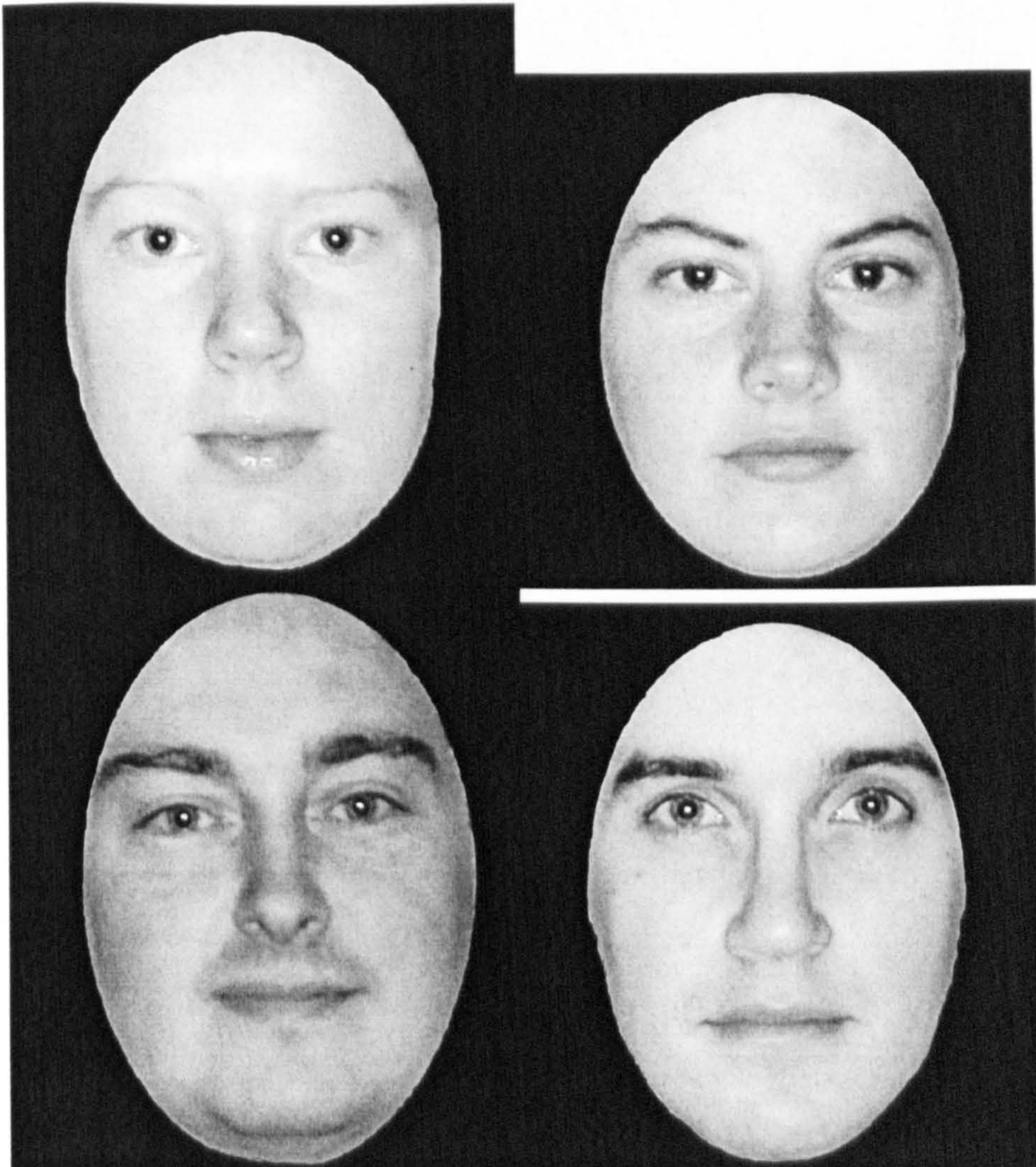
Happy



Fearful

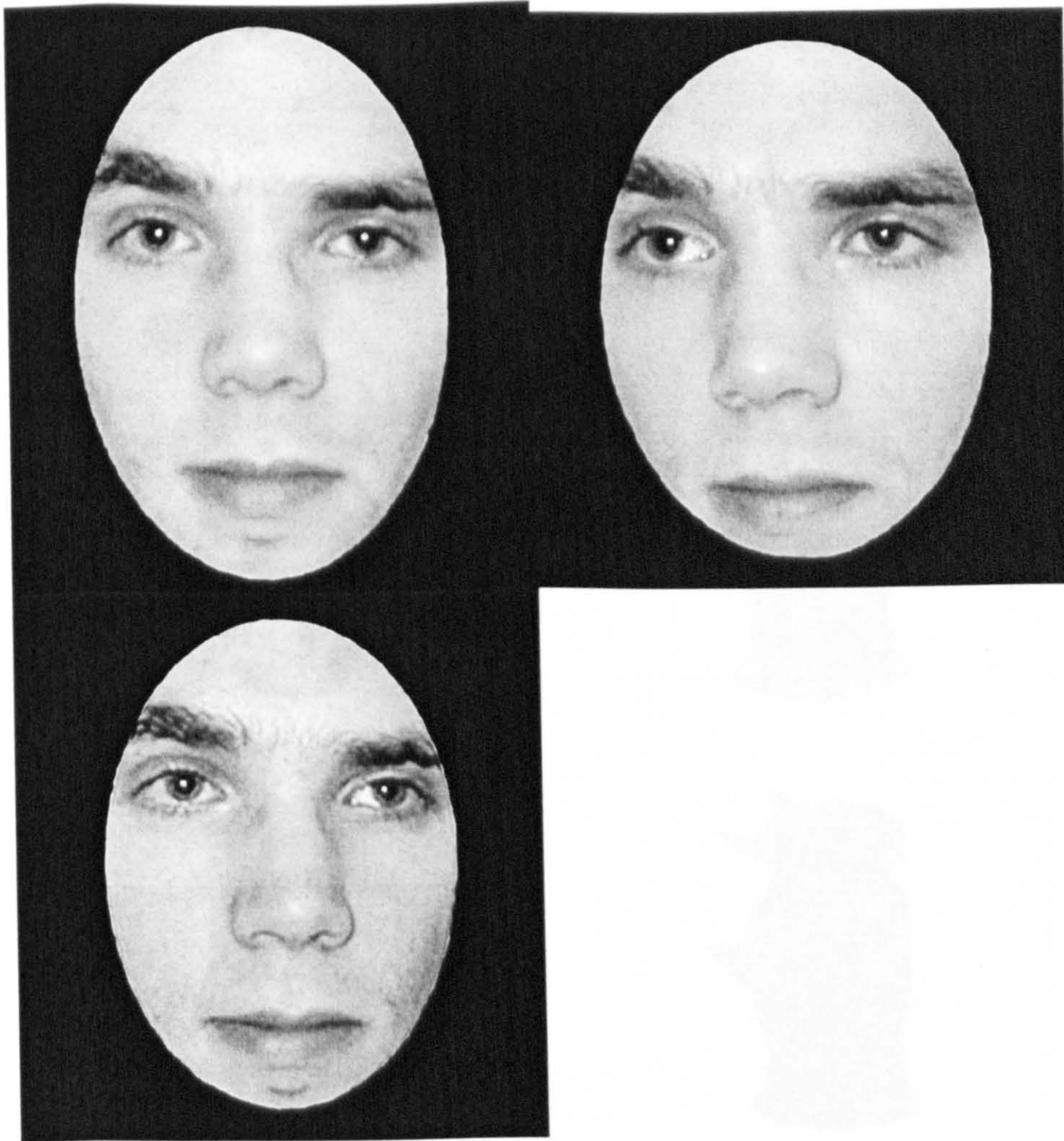


Typical controls



Three quarter profile examples

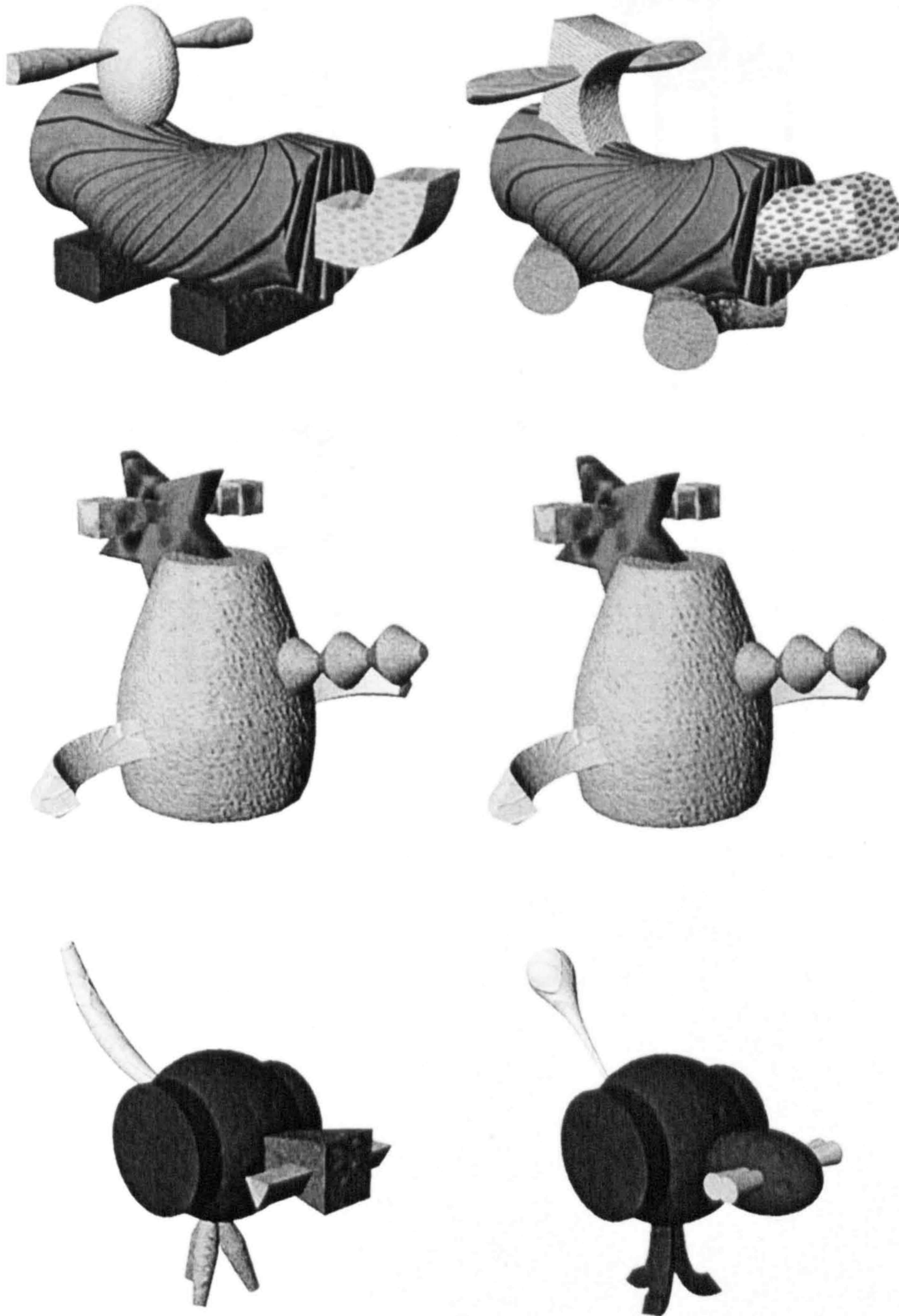




Appendix F – examples of greeble stimuli



Appendix 7 – examples of fribble stimuli



Appendix G – examples of forced-choice stimuli

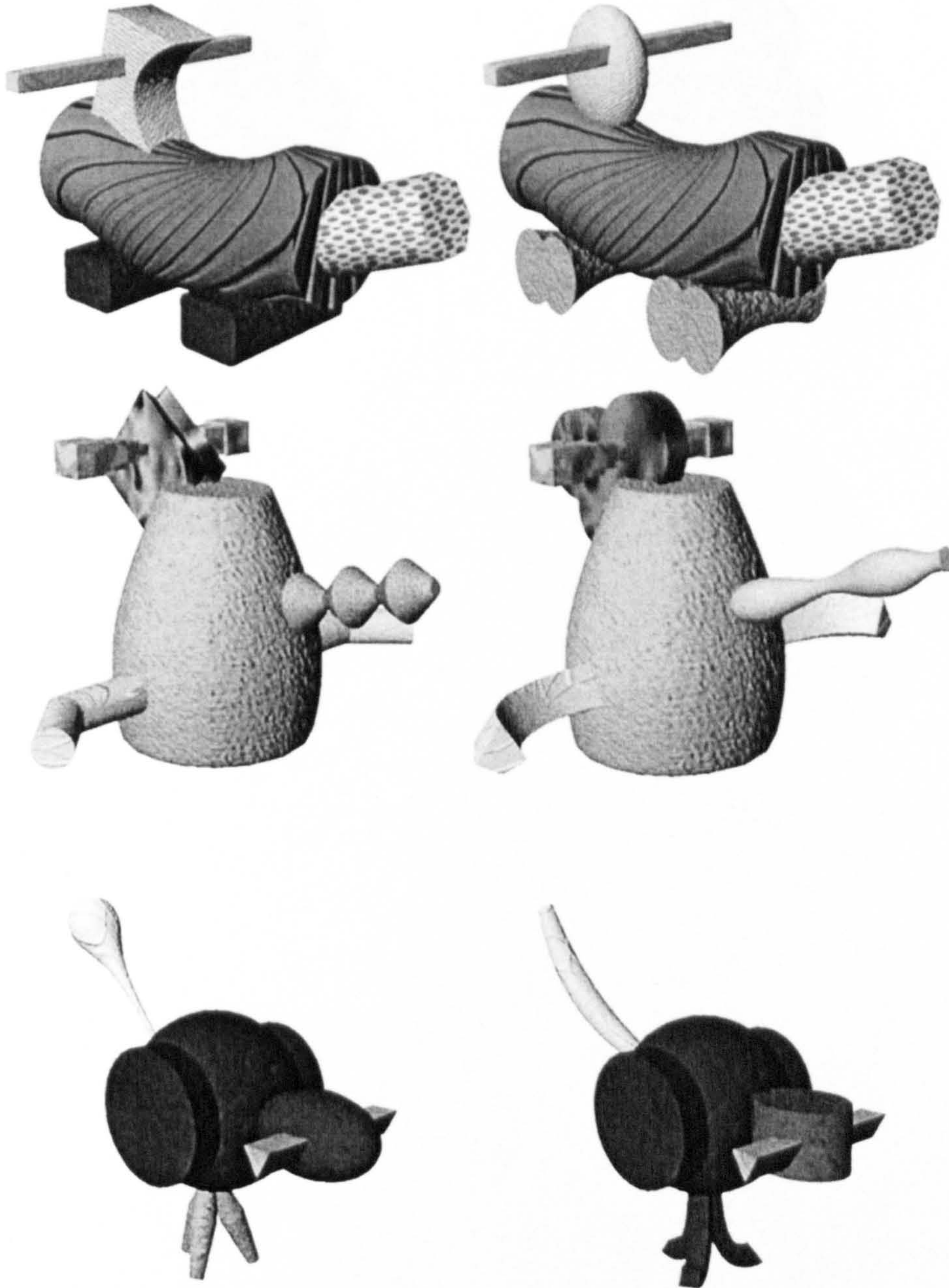
Chairs



Faces



Fribbles



Appendix G – examples of forced-choice stimuli

Greebles



Appendix H – face stimuli

