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Neural Mechanisms of Attention and Memory in Preferential Looking Tasks

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The Visual Paired Comparison Task: A Measure of Explicit Memory?

The term *preferential looking* refers to a class of behavioral methods that rely on an infant's inherent preference for viewing novel stimuli (i.e., novelty preferences) to provide evidence for learning, memory, or discrimination. Despite wide use of these tasks across different domains of development, there is a long history of debate about how to interpret infants' performance in preferential looking tasks (e.g., Bogartz, Shinskey, & Speaker, 1997). For instance, to what extent do novelty preferences reflect knowledge that the infant has brought to the experiment versus knowledge acquired during the course of the experiment? What is the nature of this knowledge? Is the infant conscious or aware of such knowledge? Does the infant have access to this knowledge for further reasoning and reflection? How flexible is this knowledge, and to what extent can the infant generalize this knowledge across different contexts? One approach to resolving this debate has been to investigate whether the neurobiology underlying novelty preferences reflects brain systems involved in explicit or implicit memory.

The task most widely investigated using this approach has been the visual paired comparison (VPC). By current accounts, the VPC is considered a measure of infants' visual recognition memory (see chapter 7, this volume). I refer to this as the explicit memory hypothesis of novelty preferences. This view holds that there is a one-to-one mapping between the task (VPC) and a

competency (i.e., recognition memory), such that infants' performance in the VPC reflects memory per se. That is, despite the fact that look duration is an indirect measure of memory, and memory for a familiar stimulus is most often inferred from longer looking at a novel stimulus, visual preferences are treated as a direct measure of memory (i.e., recognition of the familiar stimulus), and null preferences (equal looking at the novel and familiar stimulus) are treated as failures of memory. As a consequence, developmental differences in infants' performance in the VPC are typically attributed to the development of a single underlying competency, namely recognition memory. Since the VPC can be used with both adults and preverbal infants, such a one-to-one mapping between the VPC and recognition memory would provide researchers with a procedure in which memory could be studied across the life span.

In this chapter, I would like to propose an alternative way of thinking about infants' performance in the VPC. Specifically, instead of interpreting visual preferences as a direct measure of memory, and recognition memory in particular, I would like to propose that infants' performance in the VPC reflects the interaction between visual attention and memory. This view differs from the former in several respects. First, memory is viewed as only one of many processes that may influence infants' performance in the VPC. The implication here is that memory interacts with other processes (e.g., goals, affect, etc.) in guiding visual attention, and so may not always determine visual preferences. Second, the term *memory* in this view does not refer to a specific memory subsystem, such as recognition or explicit memory, but memory in a broader sense as it is implemented in different ways throughout the brain. Thus, while top-down, goal-directed processes over which we have deliberate and voluntary control may guide visual attention in some circumstances, so do bottom-up, automatic processes of which we may be unaware and do not have voluntary control. Third, the goals of the visual attention system are considered to provide an important constraint on the extent to which memory, and indeed what kind of memory, guides visual attention in any particular situation. Thus, in contrast to the explicit memory hypothesis of novelty preferences, I propose that repetition suppression in the visual processing pathway, a phenomenon thought to underlie implicit memory, may direct visual attention toward novel stimuli in preferential looking tasks.

Forms of Memory or Memory Systems?

Graf and Schacter (1985) originally used the terms *explicit* and *implicit* to refer to different forms of memory, as well as the tests that were used to measure them. Explicit memory refers to the ability to deliberately retrieve, or consciously recollect, facts, events, and prior experiences, and is measured by direct tasks that require intentional retrieval such as recall and recognition tests. Implicit memory, on the other hand, refers to facilitation or changes in behavior resulting from involuntary retrieval of prior experience in the absence of conscious awareness and is usually measured by indirect

or incidental tests such as word stem completion and repetition priming. It is important to note that these two different forms of memory may simply differ in different retrieval circumstances and do not necessarily imply multiple memory systems in the brain (Schacter & Tulving, 1994).

The task demands of the VPC would appear to make it an implicit memory task, for the simple reason that subjects are not instructed to refer back to a prior study episode, yet prior experience clearly influences their response. There is no evidence that subjects' performance in the task requires deliberate or intentional behavior of any kind, nor is there a way of testing whether infants experience conscious awareness during the test phase of the task. Of course, the lack of evidence for deliberate or intentional retrieval is not itself evidence for the absence of such a phenomenon. This leads us to a problem at the heart of much research in memory development: Could the VPC measure deliberate, conscious retrieval of information despite the absence of instructions to do so? If so, how can we determine if this is the case? One approach that researchers have used to resolve this problem is to take a memory systems approach to understanding infants' performance in the VPC.

According to most contemporary views of memory, memory consists of multiple systems (but see Roediger, Weldon, & Challis, 1989). The most common nomenclature proposes a primary distinction between explicit (or declarative) and implicit (or nondeclarative) memory systems (e.g., Nelson, 1995; Squire, 1994). The explicit or declarative memory system comprises both semantic (memory for facts) and episodic (memory for personal experiences) memory and is thought to be subserved by a cortico-limbic-diencephalic circuit that includes the hippocampus, entorhinal cortex, anterior and medial-dorsal nuclei of the thalamus, mamillary bodies, ventromedial prefrontal cortex, and modality-specific higher-order areas of the cortex such as visual area TE. The implicit or nondeclarative memory system, on the other hand, comprises multiple independent processes and neural subsystems. Perceptual priming, for example, is thought to reflect experience-induced changes in a cortically based, presemantic perceptual representation system (PRS; e.g., Schacter, Wagner, & Buckner, 2000), whereas procedural memory is thought to depend on a cortical-striatal system.

Evaluation of the Explicit Memory Hypothesis of Novelty Preferences

At the heart of the distinction between explicit and implicit memory is the issue of conscious awareness (Schacter, 1998). Despite researchers' lack of agreement on how to define consciousness (see Willingham & Preuss, 1995), adults' ability to accurately report whether an item occurred during a prior study episode is generally accepted as evidence of conscious awareness and distinguishes explicit from implicit forms of memory. This presents a formidable challenge for the study of early memory development, since infants cannot understand verbal instructions to report their recollective experiences.

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Thus, researchers must employ other criteria for distinguishing between explicit and implicit memory in infants. One approach, therefore, has been to focus on the dissociation between brain systems that support explicit and implicit memory in adults.

Using this approach, several researchers have proposed that the VPC is a measure of explicit/declarative or preexplicit memory (McKee & Squire, 1993; Nelson, 1995; Pascalis & Bachevalier, 1999; but see Schacter & Moscovitch, 1984). Evidence from several sources has appeared to support this view, including studies involving amnesic patients, lesion studies of nonhuman primates, and behavioral studies of adults. Much of this evidence has been interpreted as providing support for the view that performance in the VPC depends disproportionately on the hippocampus (see Nelson, 1995; Pascalis & Bachevalier, 1999). A critical evaluation of the evidence from these studies, however, suggests that the hippocampus may not be critical for successful performance in the task.

Neuropsychological Evidence

McKee and Squire (1993) were the first to report that amnesic patients with medial-temporal lobe damage were impaired in the VPC. They found that amnesic patients were impaired, relative to controls, in the VPC at delays of 2 minutes and 1 hour,¹ and concluded that performance in the VPC likely reflects a form of declarative memory mediated by the medial-temporal lobe memory system.

One problem in concluding, from this study, that infants' performance in the VPC is mediated by the hippocampus is that neurological damage in these patients was not confined to the hippocampus. Of the 11 patients tested in this study, only 4 had some degree of hippocampal damage. Four other patients had Korsakoff's syndrome, resulting in damage to the mammillary nuclei, thalamus, and frontal lobes; one patient had bilateral damage to the thalamus; and the remaining two patients were never scanned and so had damage of an unknown locus. Thus, the pattern of impairment observed in these patients cannot be specifically attributed to the hippocampus.

In a more recent study, Pascalis and colleagues tested a patient with discrete hippocampal damage (patient YR) in the VPC at delays of 0, 5, and 10 seconds. YR performed as well as controls at the 0-second delay but was impaired relative to controls at delays of 5 and 10 seconds (Pascalis, Hunkin, Holdstock, Issac, & Mayes, 2004). In a forced-choice recognition memory test, however, YR performed as well as controls at all delays.² Based on these findings, the authors argued that performance in the VPC depends on the integrity of the hippocampus, and that the VPC may "provide an indirect index of the ability to show *aware* recognition of studied stimuli" (Pascalis et al., 2004, p. 1294).

The finding that YR was impaired in the VPC at 5-second delays is puzzling given that amnesic patients in McKee and Squire's (1993) study exhibited significant novelty preferences after a 2-minute delay, and recent lesion

studies in nonhuman primates (reviewed in the next section) have shown that discrete hippocampal damage does not produce impairments in the VPC at delays less than 1 minute. One possibility is that YR's hippocampal damage was significantly more extensive than that of amnesic patients and nonhuman primates in other studies, and that spared hippocampal tissue in the latter two groups accounts for their enhanced performance relative to YR. Another possibility, however, is that YR's impairment in the VPC is the result of her parietal lobe atrophy. An important function of the parietal lobe is the integration of perceptual information with eye movement plans (Colby, Duhamel, & Goldberg, 1996), a function that may be particularly important for guiding visual attention in the VPC. Considering that YR had no trouble verbally identifying the familiar stimuli in the recognition task, it is possible that YR's impairment in the VPC was the result of disruptions in the integration of stimulus information and visual attention caused by the damage to her parietal lobe.

An important question about the studies reviewed above is whether findings about the neural basis of adults' performance in the VPC generalize to infants. Inferences about the neural basis of infants' performance on the VPC from studies of adults depend on the assumption that the VPC measures the same process in both infants and adults. This assumption is only warranted if (a) the task used with infants and adults is equivalent, and (b) the performance of infants and adults on the task is comparable. Otherwise, there is no reason to suppose that infants and adults are engaging the same cognitive processes, and hence neural circuits, to perform the task.

The task used in the adult studies reviewed above, however, differs from the infant version of the VPC in several respects that may be especially important for interpreting effects of medial-temporal lobe lesions. First, there are differences in the number of items that must be encoded in the infant and adult versions of the VPC. Infants are typically familiarized to a single stimulus, whereas McKee and Squire (1993) required participants to encode 24 different stimuli during the encoding phase of the task. Similarly, Pascalis et al. (2004) tested subjects in 72 trials administered in four sessions over a 1-month period. Thus, the procedures that have been used with adults are much more susceptible to proactive and retroactive interference than the procedure typically used with infants. Second, adults were exposed to each stimulus for a brief period of time (i.e., 5 seconds), whereas the encoding phase in many VPC studies with infants is longer (e.g., 10–20 seconds) and can be as long as several minutes. Third, differences in semantic memory between adults and infants likely affect the way that stimuli are encoded in the first place. Infant studies have used stimuli ranging from abstract patterns to photographs of faces and everyday objects. Depending on the age and experience of the infant, the infant may not have encountered the stimulus before participating in the VPC. In any case, the infant does not likely have a rich semantic representation for the stimulus that would include things such as verbal labels, functions, relations to other

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objects, and so on. The stimuli used in the adult studies reviewed above, on the other hand, have been pictures of everyday scenes or common objects that adults can readily name, and for which adults have rich semantic representations. Since semantic memory is considered a form of explicit memory, this may represent another fundamental difference in the kinds of processes and representations available to adults compared to infants during encoding.

Thus, differences in the number of stimuli encoded, familiarization times, and semantic memory likely make the nature of the encoding tasks fundamentally different for adults and infants. Critically, encoding in the adult studies but not the infant studies appears to involve (a) interleaved learning (i.e., concurrent learning of multiple stimuli); (b) rapid, single-trial learning (due to the very brief study times); and (c) interactions with pre-existing semantic representations. These encoding circumstances are consistent with proposed hippocampal functioning, which may explain findings that amnesic patients or patients with hippocampal damage are impaired in the adult VPC task. The typical infant VPC, on the other hand, does not seem to require interleaved or rapid, single-trial learning. It is possible, therefore, that the processes and neural circuits underlying infant performance in the VPC may be different from the processes and neural circuits that underlie adults performance in studies using variants of the VPC procedure. Thus, the results of neuropsychological studies of adults may not generalize to infants.

Evidence from Lesion Studies in Nonhuman Primates

Evidence for the explicit memory hypothesis of novelty preferences has also come from lesion studies in nonhuman primates. Early studies showed that large medial-temporal lobe lesions led to impaired performance in the VPC in both infant and mature monkeys at short delays (e.g., Bachevalier, Brickson, & Hagger, 1993), leading to the hypothesis that novelty preferences depend on the hippocampus. It is important to note, however, that the lesions in these early studies encompassed the entire medial-temporal lobe system (i.e., hippocampal formation, entorhinal cortex, perirhinal cortex, and parahippocampal gyrus), as well as the amygdala, so the impairments observed in these animals may not have been caused by damage to the hippocampus *per se*.

Further studies initially appeared to support the hypothesis that performance in the VPC depended on the hippocampus. Pascalis and Bachevalier (1999) reported that adult monkeys with neonatal aspiration lesions of the hippocampal formation (including the hippocampal cell fields, dentate gyrus, subicular complex, and portions of the parahippocampal gyrus) showed intact performance in the VPC at short delays (10 seconds) but impaired performance relative to controls at longer delays (from 30 seconds

to 24 hours). In addition, Zola, Squire, Teng, Stefanacci, and Buffalo (2000) reported that adult monkeys with selective hippocampal lesions (including the hippocampal cell fields, dentate gyrus, and subiculum) showed intact performance in the VPC at 1-second delays but impaired performance relative to controls at delays of 10 seconds, 1 minute, and 10 minutes.³ One problem with the latter study, however, was that these animals sustained unintended damage to the caudate nucleus that was significantly more extensive (i.e., 38–73%) than the intentional damage to the hippocampus (24% and 33%). This is a critical confound since it raises the question of whether deficits in these animals can be attributed to the medial-temporal lobe system or a cortical-striatal circuit supporting implicit memory.

More recently, Nemanic, Alvarado, and Bachevalier (2004) reported that lesions to different structures within the medial-temporal lobe system impair performance in the VPC in a delay-dependent manner. In this study, perirhinal lesions impaired performance at delays greater than 10 seconds, and parahippocampal lesions impaired performance at delays of 30 seconds or more, but hippocampal lesions did not produce deficits until delays reached 60 seconds. These findings may help explain impairments observed at short delays in the studies reviewed above. For instance, the lesions produced in very early studies encompassed all of these structures (hippocampus, perirhinal cortex, parahippocampal gyrus), suggesting that the impairments observed at short delays were most likely due to damage to perirhinal cortex and not the hippocampus. Similarly, since hippocampal lesions do not appear to create deficits at delays shorter than 60 seconds, the impairment observed at 30-second delays by Pascalis and Bachevalier is most likely due to the inclusion of the parahippocampal area in the lesion and not the hippocampus *per se*.

Thus, it appears that damage to medial-temporal lobe structures does impair performance in the VPC in adult monkeys, but that the hippocampus is only critical at longer delays. This raises an important point: Performance in the VPC under different delay conditions may be supported by different neural structures. Furthermore, lesions to medial-temporal lobe structures do not impair performance in the VPC at immediate or very short delays. The implication for infant memory research is that immediate performance in the VPC may not depend on the medial-temporal lobe at all. Although damage to visual area TE, a structure implicated in visual perceptual processing, produces impairments in the VPC at very short delays in adult monkeys, the same lesion has no effect on infant monkeys' performance in the VPC (Buffalo et al., 1999; Haggar, Brickson, & Bachevalier, 1985). Thus, there are currently no data regarding the neural structures that may support immediate performance in the VPC in infants.

Given the findings that damage to the medial-temporal lobe system does impair performance in the VPC in adult monkeys, it is tempting to conclude that novelty preferences do, in fact, reflect some form of explicit memory, at least when a long enough delay is imposed between study and test.

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Before reaching this conclusion, however, another point is worth consideration: This evidence is based on studies of adult animals. Given changes in the anatomical and functional maturity of many of the medial-temporal lobe structures during development, as well as changes in connections between medial-temporal lobe and other cortical structures, the circuits (and hence processes) underlying performance in the VPC may change with development. Thus, lesion studies in adult animals ultimately may not inform our understanding of the neurobiology underlying novelty preferences in infants.

Unfortunately, very few studies have examined the neurobiology of VPC performance in infant monkeys. Early lesion studies reported that infant monkeys with bilateral medial-temporal lobe lesions failed to show novelty preferences at short delays (10 seconds) (Bachevalier et al., 1993; Saunders et al., 1991). The lesions in these early studies, however, encompassed the entire medial-temporal lobe system as well as the amygdala. Unfortunately, there have been no studies examining the specific role of these structures in infant monkeys' performance in the VPC.

Behavioral Evidence

A final source of evidence for the explicit memory hypothesis comes from a single behavioral study in human adults. Manns, Stark, and Squire (2000) investigated the relation between preferential looking in the VPC and recognition memory in healthy adults. They found that preferential looking scores 5 minutes after encoding were correlated with confidence ratings of recognized items after a 24-hour delay, and concluded that the VPC is a measure of recognition memory. Note, however, that the task used in this study had many of the same problems noted earlier. That is, subjects were given 5 seconds of exposure to each of 24 different colored pictures of common objects during the encoding phase, after which they were tested for their memory of all 24 objects. Thus, the encoding demands of this task may reflect processes related to explicit encoding, explaining the correlation between VPC performance and recognition memory.

An important question about this experiment is the extent to which the relation between preferential looking and confidence judgments can be attributed to recognition memory, given that neither recognition accuracy nor response times were correlated with visual preferences. Snyder (2003) examined the relation between preferential looking scores and confidence judgments in an implicit memory task (i.e., a preference judgments) and found that preferential looking scores were correlated with confidence judgments in this task as well. Thus, the relation between preferential looking scores and confidence judgments may not reflect any particular kind of memory.

In contrast to the evidence for a relation between preferential looking and recognition memory reviewed above, there is evidence to suggest that adults recognize stimuli for which they fail to show a novelty preference. For example, McKee and Squire (1993) found that healthy adults did not show novelty preferences after retention intervals longer 1 hour, yet Manns et al. (2000)

found high recognition accuracy (approximately 84%) for stimuli encountered during the study phase of the VPC after a 24-hour delay. Snyder (2003) examined this pattern directly and found high recognition accuracy (85%) after a 24-hour delay despite no preference in looking behavior in adults. If novelty preferences reflect explicit recognition of the familiar stimulus, then why would novelty preferences and recognition accuracy be dissociated by delay interval? These observations make an explicit memory account of novelty preferences difficult to reconcile with conventional views of recognition memory.

Summary

In summary, the neuropsychological and behavioral evidence from human adults does not fully support the hypothesis that novelty preferences reflect a form of explicit memory dependent on the hippocampus. Patients with amnesia and nonhuman primates with damage to the hippocampus succeed in the VPC when the delay is short. Since damage to the hippocampus in these populations is never absolute, one possibility is that novelty preferences obtained under these conditions are supported by spared tissue. Another possibility is that novelty preferences per se do not depend on the hippocampus, and so the hippocampus is not necessary for novelty preferences. In addition, since adult monkeys with cortical but not hippocampal lesions are also impaired in the VPC, it would appear that the hippocampus is also not sufficient for novelty preferences. These observations argue against a primary role for the hippocampus in preferential looking.

Repetition Suppression in the Occipitotemporal Visual Processing Pathway and Its Role in Visual Attention

Earlier I proposed that the bias toward novelty in preferential looking paradigms reflects an interaction between visual attention and memory. In fact, the preferential processing of new or not recently seen stimuli appears to be an inherent bias of the visual system (Desimone & Duncan, 1995). This bias appears to be mediated by a reduction of neuronal responses in the occipital-temporal visual processing pathway with stimulus repetition, a phenomenon known as repetition suppression. Repetition suppression appears to be an intrinsic property of the visual cortex, as repeated exposure to the same visual stimulus leads to both short- and long-term suppression of neuronal responses to the stimulus (Desimone, 1996). Repetition suppression has been observed in cellular recordings in nonhuman primates (Fahy, Riches, & Brown, 1993; Li, Miller, & Desimone, 1993; Miller, Gochin, & Gross, 1991; Riches, Wilson, & Brown, 1991), as well as event-related potential (ERP) studies (e.g., Begleiter, Porjesz, & Wang, 1993) and brain imaging studies (e.g., Squire et al., 1992) in humans.

Desimone (1996) has proposed that repetition suppression reflects learning about the critical features of a stimulus. As a stimulus is repeated, the population of neurons responding to the stimulus becomes smaller. This decrease in the population of neurons activated by a repeated stimulus reflects a reduction in the responses of cells that were initially activated but were not selective for the features of the stimulus (Li et al., 1993). Thus, repetition suppression may reflect neuronal "tuning" to stimulus features. This type of stimulus memory is considered to be independent of hippocampal functioning and has been found to be long lasting (Fahy et al., 1993; Li et al., 1993), thus providing a plausible alternative to the hypothesized role of the hippocampus in visual preferences. Repetition suppression also occurs during passive fixation (Miller, Gochin, et al., 1991) and in anesthetized monkeys (Vogels, Sary, & Orban, 1995), suggesting that deliberate or voluntary control over visual attention is not necessary for learning to occur. Furthermore, brain imaging studies of humans suggest that repetition suppression plays a role in repetition priming, a form of implicit memory (Buckner et al., 1995; Squire et al., 1992; Ungerleider, 1995).

This model of how memory and visual attention interact suggests a plausible alternative to the hypothesis that novelty preferences depend on the hippocampus and reflect a form of recognition memory. In theory, the reduction in activation to a repeated stimulus would bias the competition for visual processing resources, and hence visual attention, toward a novel stimulus. This is supported by evidence that repetition suppression is sufficient to produce orienting to a novel stimulus in monkeys (Desimone, Miller, Chelazzi, & Lueschow, 1994; Li et al., 1993). Furthermore, since repetition suppression is thought to occur independently of the hippocampus, and has been implicated in perceptual priming, it may account for the observation that patients with amnesia and nonhuman primates with lesions of the medial-temporal lobe succeed in the VPC when the delay is short. Thus, novelty preferences may reflect the effects of repetition suppression on visual attention, independent of the hippocampus.

An important implication of this model is that longer looking to a novel stimulus is merely a consequence of reduced neural responses to previously encoded elements; it does not require explicit awareness, voluntary or deliberate control, or even a comparison between new and previously encoded elements. Thus, memory for a familiar stimulus may influence visual attention in a very indirect sense (i.e., in that the neural activity elicited by the familiar stimulus is reduced, and hence loses the competition for visual attentional resources). In this model, then, memory is an indirect, incidental influence on visual preferences.

The Functional Significance of Preferential Looking

Earlier I proposed that the goals of the visual attention system are an important constraint on the extent to which memory guides visual attention

in preferential looking tasks. Understanding these goals may help us to understand otherwise puzzling findings. For instance, if we assume that preferential looking is a direct measure of either memory or discrimination, as most research using the VPC appears to, then the observation that adults show null preferences in the face of intact memory is puzzling. In contrast, if we view preferential looking as merely influenced by memory, but not determined by it, then these findings do not appear contradictory. One implication of this latter view is that the primary function of look duration in preferential looking tasks is not memory or discrimination *per se*.

Roediger (2003) has argued that although a system may exhibit characteristics of memory, it does not necessarily mean that memory defines the function of the system. An example proposed by Roediger may help clarify this idea: The immune system exhibits characteristics of memory (broadly defined) that are important to the operation of the system, but this does not lead to the conclusion that the immune system exists to perform memory. Instead, the goal of the immune system is to mount a defense against disease. Consequently, one would not consider measures of the relative amounts of antibodies in blood serum a direct measure of memory, since other factors would also contribute to antibody production. Thus, while visual attention in preferential looking tasks clearly exhibits characteristics of memory, it may not be appropriate to define the function of preferential looking in terms of memory *per se*.

This leads to the question, what are the goals of the visual attention system? As a starting point, it seems reasonable to suppose that the goals of the visual attention system are linked to survival. In order to survive, an organism must be able to interact with and respond to its environment in appropriate ways. At the very least, it must be able to obtain food and avoid harm or predators. This requires the ability to detect (or possibly seek out) things in the environment, make appropriate evaluations (is this food or enemy?), and execute (or fail to inhibit) an appropriate response (eat or run). In this context, it is interesting to note that change is an inherent property of the visual environment, and preferential processing of new or not recently seen stimuli (i.e., change) is an inherent bias of the visual system. Thus, orienting to novel stimuli and the decrement in visual fixation following sufficient exposure to a stimulus that underlies both habituation and novelty preferences may function to distribute attention across events in the environment (for similar arguments, see also Sokolov, 1963). This has clear and obvious adaptive value in that it enables an organism to disengage from irrelevant events in order to alert and respond to relevant ones (e.g., a predator nearby).

Thus, one goal of the visual attention system may be to direct our processing of environmental input to objects and events that have behavioral significance. This suggests an answer to the question posed earlier. That is, adults may fail to show a preference in the VPC despite intact memory for the familiar stimulus because the familiar stimulus has no particular biological significance or relevance to ongoing behavior. This suggests that unlike a recognition memory task, in which the mnemonic status of the stimulus is

most relevant in guiding the response, the recency of the information is more relevant in guiding visual attention when there are no explicit task demands (such as in the VPC) and the stimuli are of no inherent interest.

Preferential Looking Procedures: Challenges, Limitations, and Recent Advances

There are two basic preferential looking procedures: habituation-dishabituation, and the VPC. These procedures both rely on the infant's inherent preference for viewing novel stimuli to provide evidence for learning, memory, or discrimination (for a detailed description of these procedures, see chapter 7, this volume). Due to the difference in the test phases of the two procedures, however, the VPC is generally considered to be (a) more sensitive to subtler differences between the familiar and novel stimuli, since the infant may actively compare the two stimuli simultaneously (Cohen & Gelber, 1975); and (b) an easier test of recognition memory since it provides perceptual support for the comparison process. Thus, despite the fact that both paradigms rely on the same dependent measure (i.e., proportion of looking to a novel stimulus) to provide evidence for memory, it is not clear that they engage the same exact cognitive processes. Furthermore, all of the research examining the neural basis of novelty preferences has used the VPC. Thus, our understanding of the neurobiology underlying preferential looking from these studies may not generalize to infants' performance in the habituation-dishabituation procedure.

Challenges and Limitations

One important limitation of preferential looking procedures for the study of infant memory is that there does not appear to be an unambiguous measure of forgetting. Null preferences do not necessarily reflect memory loss since (a) null findings are inconclusive, and (b) memory is confounded with novelty preference in these procedures: The infant must both remember the familiar stimulus and prefer to fixate the novel stimulus (Sophian, 1980). Thus, developmental or group differences in performance may result from differences in either memory or interest, or both. Similarly, null preferences following a delay may result from renewed interest in the familiar stimulus rather than memory loss, and age-related differences in retention may result from changes to preferences as well as memory. Despite these observations, most of the research on age-related differences in memory, as well as recent research on the neural correlates of performance in the VPC involving amnesic patients and nonhuman primates, assumes that null preferences reflect memory loss or impairment.

A significant challenge in using these procedures to study memory development is that many of the parameters, such as length of familiarization

and complexity of the stimuli, interact such that certain values of these parameters may be optimal for producing novelty preferences with infants at different ages. For this reason, spurious trends may result when using the same parameter values with infants of different ages, or the same length of familiarization with different stimuli in infants of the same age (Clifton & Nelson, 1976). Thus, our use of these procedures to study change across development is limited, in part, by our lack of knowledge about the relation between procedural parameters, stimulus conditions, and infant variables.

Recent Advances: Electrophysiological Studies with Infants

It is very difficult to dissociate explicit and implicit memory in infants since (a) measures that dissociate these forms of memory tend to rely disproportionately on verbal abilities not present in infants, and (b) brain imaging techniques with the requisite spatial resolution (e.g., fMRI) to assess the participation of neural structures that dissociate different forms of memory (e.g., the hippocampus vs. the striatum) are not feasible for use with infants participating in visual paradigms at this time. One brain imaging method that is appropriate for use with young infants, however, is ERPs.

ERPs reflect the synchronous firing of neuronal populations in response to a discrete event (such as the presentation of a stimulus). They are recorded from electrodes placed on the scalp, are derived from the electroencephalogram, and provide excellent temporal resolution (on the order of milliseconds) of ongoing cognitive processes. There are numerous advantages to using ERPs to study cognitive development. They are noninvasive, do not require the subject to remain motionless for long periods of time, and do not require a behavioral response by the subject. Furthermore, the spatial and temporal information provided by ERPs permits the differentiation of cognitive processes that may not be directly reflected in behavior.

Two major components are typically observed in the infant ERP (see Figure 8.1): a middle-latency negative component (Nc) that peaks between 400 and 800 milliseconds following stimulus onset and is commonly observed over frontocentral scalp regions, and a long-latency slow-wave component that begins around 1,000 milliseconds following stimulus onset and is commonly observed to be maximal over temporal scalp regions. The Nc is thought to reflect aspects of attention and orienting, and the slow wave is thought to reflect aspects of memory (see Nelson, 1994, for review). Since looking time measures reflect the influence of memory on visual attention, ERPs may be especially useful in investigating the neural basis of infants' performance on preferential looking tasks.

Effects of Repetition on Infant Brain Activity

Given the hypothesis that novelty preferences reflect the influence of repetition suppression in the visual processing pathway on visual attention, one

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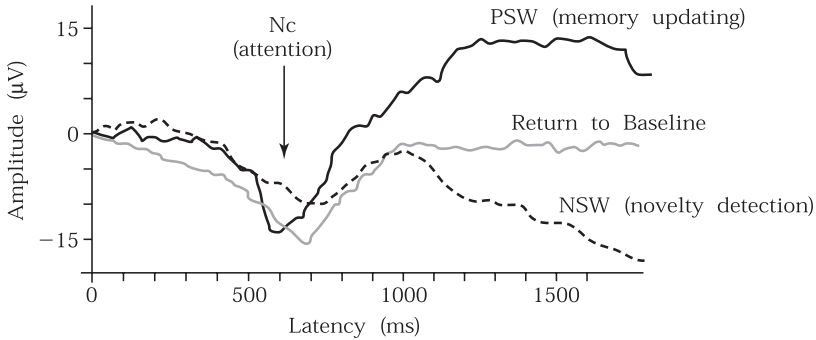


FIGURE 8.1 Illustration of the major ERP components observed in previous ERP studies with infants. Nc, negative component; NSW, negative slow wave; PSW, positive slow wave. Adapted from de Haan and Nelson (1997).

starting point is to examine the effects of stimulus repetition on infant brain activity. Thus, we contrasted the repetition of a familiar stimulus with the repetition of a novel stimulus (Snyder, Webb, & Nelson, 2002). One goal was to see if we would find evidence of repetition suppression using ERPs, and whether repetition effects would be different for familiar versus novel stimuli.

In this study, 6-month-old infants passively viewed alternating pictures of their mother's face and a female stranger's face on a computer screen while their brain activity was recorded. We compared infants' brain activity in response to the first 15 presentations of each face (Block 1) and the second 15 presentations of each face (Block 2). This design allowed us to dissociate memory (i.e., novel vs. familiar) from stimulus repetition (i.e., Block 1 vs. Block 2). We found that the amplitude of the slow wave decreased with repetition for both the familiar and novel face (see Figures 8.2 and). Thus, repetition of both familiar and novel faces resulted in the reduction of brain activity over temporal scalp regions, a finding consistent with the phenomenon of repetition suppression in the visual processing pathway.

Intracellular recordings in nonhuman primates have shown a functional distinction between repetition suppression in different parts of the visual processing pathway. Specifically, lateral inferotemporal cortex (e.g., visual area TE) exhibits reduced responses for both novel and highly familiar stimuli, whereas perirhinal cortex exhibits reduced responses for novel stimuli only (Baylis & Rolls, 1987; Li et al., 1993; Miller, Li, & Desimone, 1991). Based on these findings, Desimone and colleagues have suggested that lateral inferotemporal cortex may encode and maintain a representation of the immediate visual environment, whereas perirhinal cortex may primarily encode new information. The finding that repetition resulted in reduced brain activity over temporal regions for both novel and familiar faces is consistent

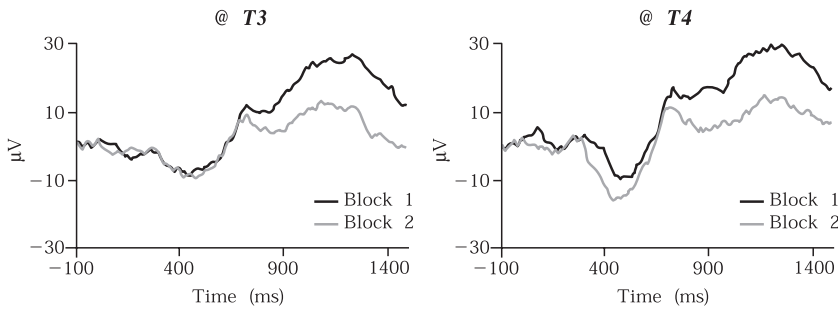


FIGURE 8.2. Grand mean ERP waveforms for Block 1 and Block 2 illustrating the reduction in amplitude of the positive slow wave with repetition. Responses to the familiar and novel face are combined for each block.

with observations of repetition suppression in lateral inferotemporal cortex, suggesting that this effect may reflect the incidental encoding of the visual scene into a perceptual store rather than the encoding of new information per se. This would explain why responses to the mother’s face, for which the infant already has extensive experience, exhibited the same effect of repetition as the stranger’s face.

Relation Between Infant Brain Activity During Encoding and Preferential Looking at Test

The results of Snyder et al. (2002) reviewed above help to establish evidence of repetition suppression in infants. In a recent study, we examined the relation between infant brain activity during the encoding of a novel stimulus and looking behavior at test (Snyder, Stolarova, & Nelson, 2006).

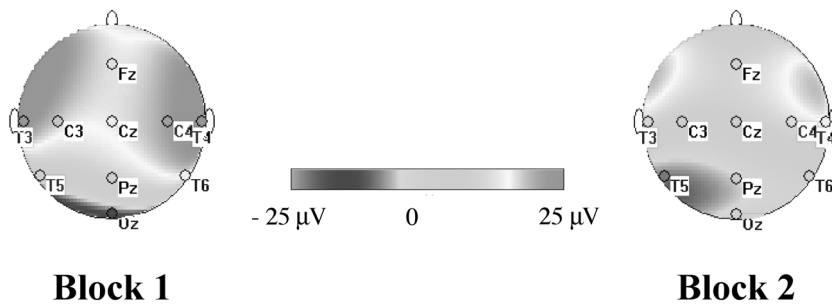


FIGURE 8.3. Topographic plots showing the scalp distribution of the positive slow wave (PSW) for Block 1 and Block 2. The PSW is shown as patches of red over the left and right temporal regions when it is maximal (at 1,250 ms).

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In addition, we examined whether this relation would be the same or different for faces and objects. This study allowed us to test hypotheses about the neurobiology underlying infant novelty preferences, since the explicit memory hypothesis and repetition suppression hypothesis make different predictions about the observed relation between brain activity during encoding and preferential looking at test.

Both intracellular recordings in nonhuman primates and neuroimaging studies in human adults have shown that recognition is associated with an increase in neural responses in the medial-temporal lobe and prefrontal cortex, whereas priming is associated with a decrease in neural responses in posterior visual areas (Buckner et al., 1998; Schacter & Wagner, 1999; Wagner, Gabrieli, Desmond, & Glover, 1998). Thus, the explicit memory hypothesis would predict that novelty preferences would be associated with increased amplitudes of ERP components over temporal and frontal regions, whereas the repetition-suppression hypothesis would predict that novelty preferences would be associated with decreased amplitudes of components located over posterior and occipitotemporal regions.

In this study, 6-month-olds' brain activity was recorded using a high-density electrode cap during the encoding of a novel object. At test, the familiar and a novel stimulus were presented serially, and the infant was allowed one continuous look at each stimulus. The relation between brain activity at encoding and preferential looking was examined by comparing the ERPs of infants who showed a novelty preference at test (i.e., novelty score $\geq 55\%$) and infants who showed a familiarity preference at test (i.e., novelty score $\leq 55\%$). Too few infants showed a null preference for further analysis.

The ERP components that showed effects of preference differed for faces and objects. Novelty preferences for faces were associated with a reduction in the amplitude of neural activity over temporal scalp regions (see Figure 8.4),

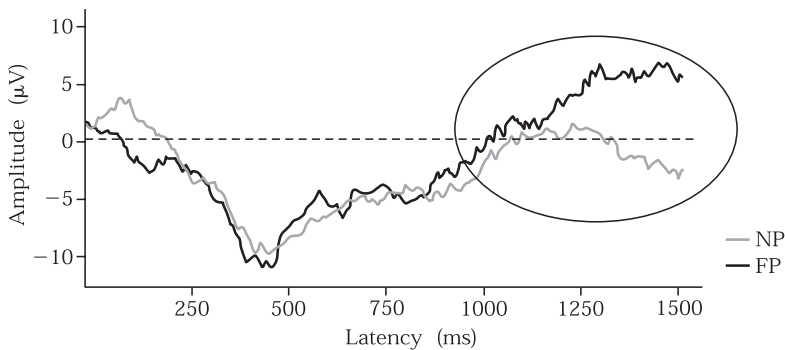


FIGURE 8.4. Grand mean ERP waveforms for infants who showed a novelty preference at test (NP) and infants who showed a familiarity preference at test (FP) at a representative temporal electrode in the vicinity of T3.

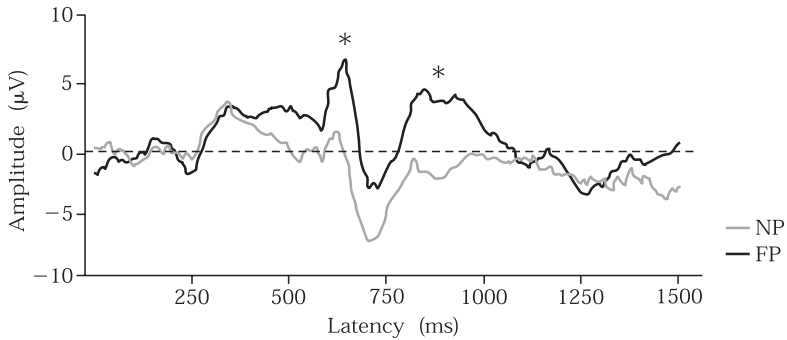


FIGURE 8.5. Grand mean ERP waveforms for infants who showed a novelty preference at test (NP) and infants who showed a familiarity preference at test (FP) at a representative occipitotemporal electrode. Asterisks are shown directly above components that are significantly different between conditions.

and novelty preferences for objects were associated with a reduction in the amplitude of neural activity over occipital-temporal scalp regions (see Figure 8.5). The observed reduction in neural activity over temporal and occipital scalp regions associated with novelty preferences is consistent with the hypothesis that novelty preferences reflect the influence of repetition suppression in the visual processing pathway on visual attention in infants and may thus reflect a form of implicit memory.

Null Preferences Do Not Reflect Memory Loss

Just as novelty preferences are typically interpreted as evidence for recognition of the familiar stimulus, null preferences are typically interpreted as a failure of memory or discrimination. As I noted earlier, however, a null preference may not reflect memory loss, since memory and interest are confounded in preferential looking procedures. Thus, another focus of my research has been to investigate whether null preferences do, in fact, reflect memory loss or an inability to discriminate. One approach I have used is to investigate possible dissociations between looking behavior in the VPC and infant memory as assessed by ERPs. Another approach I have used is to investigate the relation between adults' looking behavior in the VPC and other measures of explicit and implicit memory.

In one study, 6-month-old infants' memory for an object was assessed after a 24-hour delay using two different measures: the VPC and ERPs (Snyder, 2003). Infants who exhibited a null preference in the VPC nevertheless exhibited memory for the familiar stimulus when ERPs were used as the measure of retention. A large negative ERP component observed over posterior scalp regions, putatively labeled the N700, showed this memory

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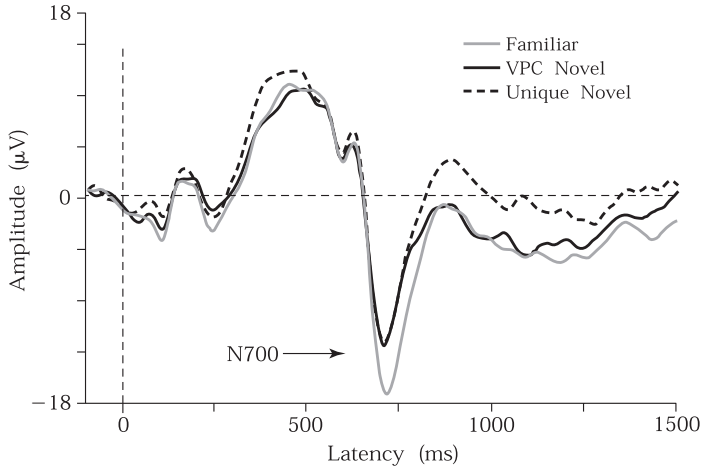


FIGURE 8.6. Grand mean ERP waveforms from a representative posterior electrode showing the effect of familiarity at the N700 component. The N700 peaks earlier to the familiar stimulus (shaded line), compared to the two novel stimuli (black dotted and black solid lines).

effect and peaked later in response to the familiar object compared to two novel objects, but did not differ in latency for the two novel objects (see Figure 8.6).

Since we used a within-subject design in which infants were first tested in the VPC and then the ERP task at the 24-hour delay, it is possible that the dissociation between looking behavior and ERPs was due to reactivation of the memory for the familiar object in the VPC. To examine this possibility, we tested a second group of infants using the same procedures, except that the VPC contained two completely novel objects. Thus, the infant was not reexposed to the familiar stimulus prior to the ERP task. We observed the same effect of familiarity on the N700 in this second group of infants. The ERP effect observed in the second group of infants could not be due to reactivation of the familiar stimulus, making a stronger case for the argument that the ERP effects observed in the first group reflected residual memory for the familiar stimulus that the VPC was not sensitive enough to detect. Thus, this study provides a source of positive evidence that null effects in the VPC do not reflect memory loss or an inability to discriminate.

The dissociation between VPC performance and infant memory reported here is consistent with previous findings using other measures of retention. For example, Gross, Hayne, Herbert, and Sowerby (2002) reported that infants exhibited retention in a mobile conjugate reinforcement task and a deferred imitation task but showed null preferences for the familiar stimuli from each task in the VPC. Likewise, Wilk, Klein, and Rovee-Collier (2001) compared 3-month-olds' memory in the VPC and mobile conjugate

reinforcement paradigm, and found evidence for retention in the mobile conjugate reinforcement measure despite null preferences in the VPC. Thus, there is converging evidence from behavioral and ERP measures that null preferences in the VPC do not necessarily reflect failures of memory or discrimination.

I have also investigated the relation between adults' looking behavior in the VPC and measures of explicit and implicit memory. In one study, adults' memory for an object was assessed following a 24-hour delay using one of three different measures: the VPC, a forced-choice recognition memory task, or a preference task in which participants were asked to indicate which of the two stimuli they liked better (Snyder, 2003). Despite a null preference in the VPC following the 24-hour delay, adults' recognition memory for the familiar stimulus was very high (85%). In addition, adults preferred the novel and familiar objects equally often. The observation that adults exhibited a null preference and equivalent liking of the familiar and novel stimuli provides some support for the idea that null preferences may reflect an intermediate state of memory in which interest in the familiar and novel stimuli are roughly equivalent. Most important, though, adults clearly recognized the familiar object despite exhibiting a null preference. Thus, null preferences in this study clearly do not indicate memory loss or an inability to discriminate.

In summary, the studies reviewed above provide converging evidence for the idea that null preferences do not reflect memory loss or lack of discrimination. Following a long delay, infants still exhibited ERP evidence of memory and adults exhibited highly accurate recognition despite null preferences in the VPC. Converging evidence from these and other studies suggests that null preferences do not provide a measure of memory failure.

Summary

The major findings that have emerged from the work reviewed above are that (a) repetition of a stimulus results in a reduction of neural activity over temporal scalp regions in 6-month-old infants, (b) infant novelty preferences are associated with a reduction in the amplitude of neural activity over temporal and occipital scalp regions during encoding, and (c) both infants and adults show evidence of memory for the familiar stimulus despite exhibiting null preferences when measures other than looking time are used as the measure of retention.

The pattern and topography of the ERP effects observed in the experiments reviewed above are consistent with observations of repetition suppression in inferotemporal cortex from electrophysiological recordings in nonhuman primates and brain imaging studies of human adults, and suggest a common mechanism underlying both repetition of stimuli and novelty preferences. These observations help to establish a possible role for repetition suppression in mediating preferential looking in infants.

Mechanisms of Change in Infants' Performance in Preferential Looking Tasks

Infants' performance in preferential looking tasks changes dramatically during the first year of life. Changes have been observed in infants' ability to encode stimuli of increasing complexity, speed of encoding, retention, and flexibility of the representation (for reviews, see chapter 7, this volume; Bornstein, 1985; Cohen & Gelber, 1975). Changes in infants' performance in preferential looking tasks likely result from complex interactions between neurobiological development and the experience of the infant. Given the enormous changes in the brain during the first few years of life, a complete neurobiological model of memory development must go beyond systems involved in memory and also consider the contribution of systems involved in sensory input, storage, and motor output. Thus I will briefly consider the development of parts of the brain involved in the creation and storage of visual representations (i.e., the visual processing pathway), as well as control over eye movements and their implications for how change occurs.

Visual Processing and Cortical Development

Visual information is processed sequentially along the ventral occipitotemporal pathway. Visual information enters through the retina, travels along the optic nerve to the thalamus, and is then sent on to primary visual cortex (in the occipital lobe), which is the first cortical area to receive visual information. From primary visual cortex, visual processing proceeds sequentially through secondary, tertiary, and association processing areas in the occipital lobe, and then descends through the temporal lobe, culminating in the inferotemporal cortical areas TEO and TE. At each stage in the ventral pathway, the receptive field size of neurons increases, the visual information becomes more highly integrated, and the representation is more complex. Thus, whereas neurons in primary visual cortex have receptive fields restricted to small portions of the retina and are simple edge detectors, a complete representation of a stimulus is synthesized in area TE.

The immaturity of the cortex early in development likely plays a role in age-related changes in infants' performance in preferential looking tasks. For instance, since the visual cortical areas appear to develop hierarchically, with areas earlier in the processing stream (e.g., TEO) developing sooner than areas later in the processing stream (e.g., area TE), the complexity of the information that an infant is able to encode, store, and retrieve is likely to increase with age. The findings that stimulus properties affect rates of habituation and that older infants can detect more subtle differences in change to stimuli, provide some support for this proposal. For example, infants appear to habituate more slowly to more complex stimuli (e.g., Caron & Caron, 1969), suggesting they require more time to adequately encode the stimuli and show larger novelty preferences when the novel and familiar stimuli are more dissimilar looking. Furthermore, these effects interact with age in that

young infants (e.g., 3- and 4-month-olds) require a change in more than one dimension (e.g., color, shape) of the familiar stimulus to exhibit a novelty preference at test, whereas by 8 to 12 months a change in one dimension is sufficient (e.g., Cohen, Gelber, & Lazar, 1971; Cohen, 1973). This suggests that either the kind or amount of information that infants encode in preferential looking tasks changes with age, as would be predicted by changes in the visual processing stream with development.

In addition, information stored in the cortex may be especially vulnerable to decay, interference, or retrieval failure during periods of cortical development. Since representations for both explicit and implicit forms of memory are stored in the cortex, one implication of cortical development is that some forms of explicit and implicit memory (e.g., perceptual priming) are equally likely to be affected.

Development of Voluntary Control Over Eye Movements

An important difference between explicit and implicit memory tasks is that subjects deliberately attempt to match their response (either verbal or motoric) with retrieval of prior study items in an explicit memory task, but are not required to do so in an implicit task. In an implicit task, although subjects may deliberately or voluntarily control their responses (by pushing buttons or speaking), they do not deliberately attempt to use memory to guide these responses. Thus, memory may guide responses in a top-down manner in explicit tasks, whereas it only biases responses in implicit tasks. This raises the question of whether infants have voluntary or deliberate control over their responses (i.e., eye movements) in the VPC task, and whether memory exerts top-down control over looking or simply influences looking in a bottom-up, automatic manner.

In the VPC, eye movements are used to orient toward and visually explore stimuli. Thus, preferential looking behavior relies on the oculomotor system for both sensory input and motor output. Voluntary eye movements, in particular, involve the participation of structures in the frontal cortex that appear to be later developing. The point in development when eye movements come under voluntary control has important implications for preferential looking behavior. If visual fixation and exploration is primarily reflexive, preferential looking behavior may simply reflect the influence of bottom-up, automatic processes (of which novelty is an inherent bias). If eye movements are under voluntary control, on the other hand, infants may be able to use recollective experiences to deliberately guide their looking behavior. Thus, changes in preferential looking behavior with age may reflect, in part, the development of voluntary control over eye movements rather than the infant's ability to encode, remember, and recognize a stimulus.

Visual exploration depends critically on saccadic eye movements, and saccades can be either voluntary or involuntary. The speed, duration, and direction of a saccade are coded by populations of neurons in the brain stem,

which project directly to the oculomotor nuclei, controlling the muscles of the eyes. Determining the target location of a saccade and voluntary control over eye movements, on the other hand, involves neurons in the parietal cortex, basal ganglia, and frontal eye fields. Neurons in these three areas project directly to brain stem nuclei, enabling them to initiate or inhibit saccades. The parietal cortex is thought to be critical for determining the target location of the eye movement, whereas the frontal eye fields can override reflexive mechanisms, suggesting it is the critical structure for control of voluntary eye movements.

There is some debate in the literature regarding the age at which voluntary control over eye movements emerges. It has historically been assumed that saccades in young infants are reflexive and not under voluntary control (as cited in Richards, 2001a). Evidence for this view comes primarily from anatomical information and behavioral evidence. Anatomically, the layers of visual cortex mediating voluntary eye movements are relatively immature at birth and undergo significant development over the first 6 months of life (Richards, 2001a). This anatomical information coincides with behavioral evidence that infants between the ages of 2 and 6 months show little to no development in involuntary saccades used for visual tracking, but a significant increase in attention-directed saccades and smooth-pursuit eye movements over this same time period (Richards & Holley, 1999). In contrast to this view, infants as young as 2 to 3 months will make anticipatory eye movements in the visual expectation procedure. Haith, Canfield, and colleagues (Canfield, Smith, Brezsnayak, & Snow, 1997; Wentworth & Haith, 1998) have argued that infants' predictive saccades in this procedure reflect voluntary eye movements and hence the involvement of the frontal eye fields.

Recently, evidence from ERP studies has attempted to resolve this debate, although results have been mixed. Using the spatial cueing task, Richards (2001b) reported saccade-related ERPs over frontal scalp regions in 4.5- and 6-month-old infants, but not in 3-month-olds, and concluded that only in the older infants did saccades involve the frontal eye fields and were, therefore, voluntary. Using the visual expectation procedure, on the other hand, Wentworth, Haith, and Karrer (2001) and Csibra, Tucker, and Johnson (2001) both reported a negative potential over frontal leads in 3- and 4-month-olds that appeared to resemble a negative saccade-related potential observed in adults. In adults, this negative potential is thought to reflect activation of the frontal eye fields or motor potentials in the supplementary eye fields, and hence voluntary eye movements. Thus, these authors concluded that saccades are under voluntary control in 3- and 4-month-old infants.

Development of the Medial-Temporal Lobe System

Although Nelson (1995) has suggested that novelty preferences obtained under immediate test conditions in young infants likely depend disproportionately on the hippocampus, the results of neuropsychological studies

and lesion studies in nonhuman primates has shown that damage to the medial-temporal lobe (including the hippocampus) does not impair performance in the VPC at very short delays. Thus, infants' performance in the VPC under immediate test conditions may not depend on the medial-temporal lobe at all.

In general, the observation that older infants require less familiarization time to encode stimuli than younger infants may reflect the contribution of the medial-temporal lobe structures later in development to the encoding portion of the task. This is based on findings that the medial-temporal lobe system is critical for rapid acquisition of information during memory tasks. Note, however, that involvement of the medial-temporal lobe system during encoding does not imply involvement of the system during retrieval. Words activated during a priming task (e.g., word stem completion), for example, may have been initially encoded via the medial-temporal lobe system at some earlier point in time, but successful retrieval during the priming task does not require the medial-temporal lobe. This reflects an additional limitation of lesion studies for investigating the neurobiology underlying performance in the VPC: It is not possible to determine whether the lesion impaired encoding or retrieval. More systematic research examining the interaction of age, familiarization time, length of delay, and location of lesions in infant monkeys is needed to disentangle these issues.

Effects of Experience

Finally, the experience of the infant likely plays an important role in the encoding, storage, and retrieval of information in preferential looking tasks. Earlier I argued that an important difference between the task used with infants and the task that has been used with adults involves semantic memory. By semantic memory, I am referring to perceptual representations of the physical structure of the world, as well as conceptual representations regarding the function, use, and relations between objects. An important difference between adults and infants is that adults have already accumulated a great deal of perceptual and conceptual information about the world, while infants are only beginning to do so. These preexisting perceptual and conceptual representations play a critical role in priming in adults. By several accounts, exposure to a stimulus during the study phase of a priming task results in small changes to a preexisting representation via modifications to connection weights or synaptic efficacies. This helps explain why priming effects seem to last over very long periods of time. When the stimulus is then reencountered during the test phase of the task, the stimulus is processed more fluently (due to stronger connections), resulting in increased reaction time or enhanced likelihood of producing the prime. Thus, priming involves reactivation of a preexisting representation.

Contrast this with an infant's experience in a preferential looking task. Depending on the age of the infants and the stimulus used, infants may not

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have encountered the stimulus before participating in the task, and may thus have no preexisting perceptual representation for the stimulus. Even if they have, it is unlikely that their perceptual or conceptual representation is adultlike, given the immaturity of the cortex that is thought to store such representations. Thus, the familiarization phase may be more similar to initial learning than to reexposure.

Questions and Issues on the Horizon

The primary goal of this chapter was to examine the hypothesis that infants' performance in the VPC reflects explicit recognition of a familiar stimulus, and that changes in infants' performance in the VPC result from the development of a single underlying competency (i.e., recognition memory). Given the interactions reviewed earlier between age, delay, and location of lesion, a one-to-one mapping between performance on the VPC and a single underlying competency seems unlikely. Instead, it was argued that infants' performance in the VPC reflects the interaction between visual attention and memory, and that memory is but one process that guides visual attention in these tasks. Repetition suppression in the visual processing pathway was proposed as the mechanism that guides visual attention toward a novel stimulus in these tasks. The implication of this latter view is that memory may be an incidental influence on visual attention, and that infants need not be aware that they have seen the familiar stimulus before in order to look longer at a novel stimulus.

It is my hope that the arguments and evidence presented here will reinvigorate the debate about whether infants' performance in preferential looking tasks reflects a form of explicit or implicit memory, since the way we interpret preferential looking is critical to the kinds of knowledge and abilities we ascribe to young infants. Investigating the neurobiology underlying performance on these tasks is one approach to resolving this debate, but many questions remain to be answered. For instance, given the argument that lesion studies in adult animals ultimately may not inform our understanding of the neurobiology underlying novelty preferences in infants, we need more research examining the neurobiology of VPC performance in infant monkeys. In addition, examining interactions among stimulus properties, length of familiarization, delay, and location of lesion could help us understand age-related changes in human infants' performance on preferential looking tasks.

Results from lesion studies provide a good starting point, but converging evidence from additional methodologies is also needed if we wish to provide a full explanatory account of infants' performance in preferential looking tasks, and hence memory development. As was noted earlier, lesion studies may confound processes involved in encoding, storage, and retrieval. It is possible, for example, that medial-temporal lobe structures are involved in the initial encoding of stimuli when study times are brief but are not required

for the retrieval of information that produces longer looking toward a novel stimulus during the test phase. Neuroimaging methods, on the other hand, would allow investigators to examine the contribution of different structures during encoding and retrieval, and have been successful in dissociating such processes in other types of memory tasks.

Despite the promise of a neurobiological approach to understanding infants' performance in preferential looking tasks, there remains a very difficult inferential issue that must be addressed. That is, in addition to mapping out the specific parts of the brain that appear to be critical for task performance, we must also figure out the function of these structures early in infancy. For example, the logic of the explicit-memory account of novelty preferences appears to hold that (a) the medial-temporal lobe is critical for explicit memory in adults; (b) the VPC seems to depend on medial-temporal lobe structures; and therefore (c) the VPC likely measures explicit memory. One problem with this line of reasoning is that it assumes that structures like the hippocampus are performing the same function early in infancy as in adulthood. Given changes in the anatomical and functional maturity of many of the medial-temporal lobe structures during development and, perhaps more critically, changes in connections between medial-temporal lobe structures and other cortical structures (e.g., prefrontal cortex), it is possible that the function of these individual structures early in life bears little resemblance to the integrated function of the complete circuit that underlies explicit memory later in life.

Figuring out the function of a structure early in infancy, however, will require going beyond a single task-structure mapping. Instead, studies examining the contribution of a particular structure to performance across different tasks, as well as a principled understanding of the task requirements of these tasks (i.e., what the tasks are actually assessing), are needed to develop an understanding of function. Importantly, without an independent analysis of task requirements, the mapping of structure to function is reduced to a mapping of structure to a bunch of tasks, leaving us with little more than a tautology. In other words, to say that the VPC is dependent on the hippocampus tells us little. What we really want to know is what kind of memory it measures. To answer this, we need to know the function of the hippocampus. If we base the function of the hippocampus on what we think the task measures (i.e., explicit memory), but we base what we think the task measures on the fact that damage to the hippocampus impairs performance on the task, then we are reduced to circular reasoning. Research examining the neurobiology of memory in adults has used multiple tasks, as well as task analysis, to investigate the function of particular brain structures. An understanding of the neurobiology of memory development would benefit greatly from the same approach, but must examine structure-function relations in developing animals and human infants.

Finally, the view that preferential looking reflects the interaction between memory and attention, and that memory is but one influence on looking

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behavior, raises the question of what other processes influence visual attention in these tasks. For example, the idea that memory for the familiar stimulus and interest in the novel stimulus are confounded in preferential looking paradigms suggests that affective processes may be another influence on visual attention. Thus, a full understanding of the changes in infants' performance in preferential looking tasks will likely involve an understanding of how systems involved in visual processing, oculomotor control, affective modulation of stimulus processing, novelty detection, and learning and memory interact during development.

Acknowledgments

The author wishes to thank Margarita Stolarova, Heather Whitney, Sara Webb, Sandi Wewerka, Alissa Westerlund, Betsy Meehan, Kari Barth, Emily Shunk, and Dana Keufner for help with data collection, Liza Zolot for help with manuscript preparation, and Chad Marsolek for his very helpful comments on an earlier draft of this manuscript.

Notes

1. It is important to note, however, that amnesic patients showed significant novelty preferences at the 2-minute delay and above-chance performance in the recognition memory task.
2. In a forced-choice recognition task, subjects are simultaneously presented with two stimuli, one familiar and one novel, and are asked to identify which stimulus was previously seen.
3. It is interesting to note, however, that animals with radio frequency lesions were impaired at delays of 1 minute and 10 minutes, whereas animals with neurotoxic lesions were impaired at delays of 10 seconds and 10 minutes but showed intact performance at 1-minute delays.

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