Rapid Development of Feature Binding in Visual Short-Term Memory

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ABSTRACT—The binding of object identity (color) and location in visual short-term memory (VSTM) was examined in 6.5- to 12.5-month-old infants (N = 144). Although we previously found that by age 6.5 months, infants can represent both color and location in VSTM, in the present study we observed that 6.5-month-old infants could not remember trivally simple color-location combinations across a 300-ms delay. However, 7.5-month-old infants could bind color and location as effectively as 12.5-month-old infants. Control conditions confirmed that the failure of 6.5-month-old infants was not a result of perceptual or attentional limitations. This rapid development of VSTM binding between 6.5 and 7.5 months occurs during a period of rapid increase in VSTM storage capacity and just after a period of dramatic neuroanatomical changes in parietal cortex. Thus, the ability to bind features and the ability to store multiple objects may both depend on a process that is mediated by posterior parietal cortex and is perhaps related to focused attention.

Visual short-term memory (VSTM) plays a central role in cognition, allowing one to integrate views of the world separated by saccades and blinks (Hollingworth & Henderson, 2002; Irwin, 1991) and to discover relationships among objects that cannot be foveated simultaneously (Pomplun, Reingold, & Shen, 2001). Although different populations of neurons code the different features of an object, VSTM can bind multiple features into an integrated object representation (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001; Wheeler & Treisman, 2002; Xu, 2002). The problem of binding features together in VSTM poses a serious computational challenge to the brain (Feldman, 1985; Raffone & Wolters, 2001; Roskies, 1999), and researchers can gain insight into this problem by examining the developmental transition from unbound representations to bound representations and by determining how this transition corresponds to known neuroanatomical changes.

Previous studies have revealed that VSTM capacity for single-feature objects develops dramatically between 6 and 10 months of age, possibly approaching the adult capacity of three or four objects within the first year of life (Rose, Feldman, & Jankowski, 2001; Ross-Sheehy, Oakes, & Luck, 2003). However, little is known about infants’ ability to bind features in VSTM. Previous research using habituation and familiarization has revealed that from an early age, infants have impressive abilities to bind object features in long-term memory (LTM). For example, newborn infants can remember the correspondence between two object-identity features (e.g., color and shape—see Slater, Mattock, Brown, Burnham, & Young, 1991). In addition, the ability to bind two object-identity features in LTM emerges developmentally before the ability to bind an object’s identity to its location. Even 4- to 5-month-old infants fail to remember the correspondence between location and object identity (Mareschal & Johnson, 2003; Newcombe, Huttenlocher, & Learmonth, 1999), remembering such correspondences only after extensive familiarization (Catherwood, Skoien, Green, & Holt, 1996). Thus, although infants can bind object-identity features together from birth, the ability to bind identity and location in habituation and familiarization tasks emerges in the middle of the first year of life. This developmental ordering may reflect the fact that object-identity features are represented together within the ventral stream, making binding relatively easy, whereas binding identity with location may require communication between the anatomically separate dorsal and ventral streams (Ungerleider & Mishkin, 1982).

The results just summarized come from studies in which infants were tested using some form of habituation or familiarization. Such procedures are often used to test memory over
relatively short retention periods (e.g., a few seconds), but they likely involve LTM as well as VSTM. Specifically, infants typically accumulate tens of seconds of viewing time for a given stimulus during familiarization—plenty of time for forming an LTM representation. Moreover, the memories thus formed can persist for minutes, hours, or even days (see Rose, Feldman, & Jankowski, 2004, for a review).

In contrast, VSTM representations are created very quickly: Adults can form a robust VSTM representation in 50 ms, but they require 500 to 1,500 ms to form a robust visual LTM representation (Hollingworth & Henderson, 2002; Vogel, Woodman, & Luck, in press). In addition, whereas LTM representations are very durable, VSTM representations begin to fade immediately (Kikuchi, 1987), can be displaced as new objects are fixated (Hollingworth, 2004), and require active processing to avoid being overwritten. To unambiguously isolate VSTM in infants, it is therefore necessary to use a single brief exposure to a given stimulus (≤ 500 ms) followed by a brief retention interval (≤ 1,000 ms). Note that these timing parameters are not just a laboratory contrivance, but instead reflect the time course of fixating an object in a natural scene and then shifting fixation to another object.

In addition, LTM and VSTM representations are thought to rely on different neural substrates, with LTM but not STM being dependent on medial temporal lobe structures (Squire, 1987; Varga-Khadem et al., 1997). Thus, the developmental time course for creating LTM bindings in tasks with long stimulus exposures may differ from the developmental time course for creating VSTM bindings in tasks with brief stimulus exposures.

The only prior study of binding in infant memory using a task that minimized the influence of LTM, conducted by Kaldy and Leslie (2003, in press), suggests that binding of object identity and location emerges late in the first year of life. Kaldy and Leslie presented infants with a single exposure of two shapes at separate locations, occluded the shapes briefly, and then removed the occluders. On some trials, the objects switched locations when the occluders were removed (e.g., circle on the left and triangle on the right before occlusion; triangle on the left and circle on the right after the occluders were removed). Kaldy and Leslie (2003) found that infants between 8 months 15 days and 9 months 15 days looked longer on such trials than on trials in which the objects were in the “expected” locations, showing evidence of binding. Using a somewhat different procedure, Kaldy and Leslie (in press) found little evidence of binding of shape to location in infants 6 months 0 days to 6 months 30 days in age. Note, however, that in each procedure used by Kaldy and Leslie, the stimuli were visible for well over 4 s before being occluded (long enough for infants to have formed a long-term memory for the objects), and the retention interval was well over 4 s (long enough for VSTM representations to have faded considerably). In addition, even the older infants were unable to bind color and location in this paradigm, even though color is often the easiest feature for adults to store in VSTM (Luck & Vogel, 1997; Wheeler & Treisman, 2002). Therefore, although this procedure involves some form of working memory, the results do not provide clear evidence regarding developmental changes in the ability to bind objects to locations in VSTM. Nonetheless, on the basis of these studies, one might predict that the ability to bind object identity and location in VSTM develops between 6 and 9 months.

Neuroanatomical maturation also suggests that the ability to bind object identity and location in VSTM might develop during this period. Given that the storage of information in VSTM appears to depend on posterior parietal cortex (Todt & Marois, 2004), the emergence of binding in VSTM may follow periods of development in the parietal cortex. Although little is known about the development of specific parietal subregions, parietal cortex as a whole appears to undergo dramatic development between 3 and 6 months postnatally (Chugani, 1998; Greenough, Black, & Wallace, 1987). Thus, on the basis of neuroanatomical maturation, one might predict that the ability to bind object identity and location develops shortly after 6 months of age.

The present investigation tested infants’ binding of color and location in VSTM using a procedure we previously developed to examine infants’ VSTM capacity (Ross-Sheehy et al., 2003). This procedure was based on the change-detection task used by Luck and Vogel (1997) to assess VSTM in adults. In our procedure, infants are presented simultaneously with changing and nonchanging stimulus streams. In each stream, an array of colored squares cycles on and off, appearing for 500 ms, disappearing for 300 ms, and so on (see Fig. 1a). In changing streams, one or more of the items changes in some way from cycle to cycle. In nonchanging streams, all of the items remain the same from cycle to cycle. Infants’ visual preference for the changing stream on each trial is assessed. Only if they can remember the items across the 300-ms blank interval will they be able to detect the changes and prefer the changing side. Therefore, this procedure more clearly isolates VSTM than do the familiarization and habituation procedures used in previous studies; infants must form representations quickly (within 500 ms), and they need to remember information only over an extremely short retention interval (300 ms).1

1These parameters are based on the literature on adult VSTM, and it is important to consider whether they are appropriate for isolating VSTM in infants. In the present study, we chose to use an array duration of 500 ms. This duration should be long enough to allow the formation of robust VSTM representations in infants, but not robust LTM representations. Adults require 150 ms to form a VSTM representation of three simple objects (Vogel et al., in press), and our 500-ms exposure time was more than three times this duration, presumably providing sufficient time for infants to form a VSTM representation. If they could not form a VSTM representation in this amount of time, then VSTM would not be very useful to them in real-world situations. This 500-ms duration is shorter than the typical LTM encoding time in adults (see Hollingworth & Henderson, 2002), so it should minimize LTM encoding in infants. We used a 300-ms retention interval, which should be short enough to avoid substantial decay in infants, but should not make it possible for them to use iconic memory because the iconic memory of one array is erased by the onset of the next array even when the delay is as short as 16 ms (Becker, Pashler, & Anstis, 2000). For a more extensive discussion, see Ross-Sheehy et al. (2003).
Using this procedure, we previously established that by age 6 months, infants detect a change in color or location only when each stream contains a single item, whereas between ages 10 and 12 months, infants detect a change in color (with location held constant) or location (with color held constant) when each stream contains up to three to four items (Ross-Sheehy et al., 2003; Ross-Sheehy, Oakes, & Luck, 2004). Thus, our previous results suggest that the ability to represent color and location individually in VSTM develops during the second half of the first year of life. The present study assessed when infants develop the ability to bind these features together into a single VSTM representation.

GENERAL METHOD

Participants
Participants were 144 healthy, full-term infants with no history of birth complications, vision problems, or family history of color blindness. They included eighty 6.5-month-olds, forty-eight 7.5-month-olds, and sixteen 12.5-month-olds (77 girls and 67 boys). The infants were predominantly from White, middle-class families and were recruited using our standard procedures (Ross-Sheehy et al., 2003). An additional 10 infants were tested but were excluded from the final analysis because of fussiness (six 6.5-month-olds, two 7.5-month-olds, and one 12.5-month-old) or experimenter error (one 6.5-month-old).

Procedure
Infants sat on a parent’s lap 100 cm in front of two video monitors (viewable region = 18.26° × 13.50°) positioned side by side with a 24-cm gap (13.5°) between them. On each trial, infants were presented with two arrays (one on each monitor) consisting of three colored squares (2.9° × 2.9°) presented on a gray background. The colors of the squares were selected from a set of eight highly discriminable values (red, green, cyan, white, yellow, black, brown, and blue).

In each experiment, infants received two practice trials and four test trials. Except as noted, on each trial a changing stream was presented on one monitor, and a nonchanging stream was presented on the other; the side of the changing stream was counterbalanced across trials. During each 20-s trial, the array of colored squares on each monitor appeared and disappeared (visible for 500 ms, off for 300 ms, visible for 500 ms, and so on). The infants were free to look at the two monitors as much as they wished. A trained observer (unaware of the location of the changing stream) recorded the looking time to each monitor online, and a second trained observer recorded the looking time off-line for a randomly chosen 25% of the infants in each experiment. The average correlation between the two observers’ looking times was very high (\( r = .97 \)), with an average difference of 0.54 s. We calculated a change-preference score for each trial (duration of looking to the changing stream/total duration of looking to the two monitors; this calculation excludes time not spent looking at the two monitors). Our criterion for reliable change detection was an average preference score (across trials) significantly greater than chance (.50), as assessed by two-tailed \( t \) tests.

EXPERIMENT 1

Experiment 1 examined 12.5-month-old infants’ ability to bind color to location. Previous work indicates that the ability to use color as a feature in forming an object representation does not emerge until the end of the first year of life (Wilcox, 1999). One might therefore predict that the ability to bind color to location would emerge relatively late. Thus, in this first experiment, which was designed to show for the first time that infants can bind object identity to location in VSTM, we assessed the ability to bind color to location at age 12.5 months.
In the changing stream in this experiment, the same three colors and three locations were present on each cycle, but the colors switched locations from cycle to cycle (see Fig. 1a). Thus, the color at every location changed on every cycle, which should make the detection of changes trivial if color-location correspondences are stored in VSTM.

Sixteen 12.5-month-old infants \((M = 12\) months 20 days, range: 12 months 4 days to 12 months 23 days) were presented with a changing stream on one monitor and a nonchanging stream on the other monitor. The infants significantly preferred the changing stream, \(t(17) = 2.48, p = .025, d = 0.62\) (see Fig. 1b). In other words, 12.5-month-old infants detected a change in the combination of color and location, indicating that they could rapidly bind location and color in VSTM.

**EXPERIMENT 2**

Evidence from normal adults and patients indicates that parietal regions of the brain are involved in binding information represented by the dorsal and ventral streams (Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997; Shafritz, Gore, & Marois, 2002). We therefore predicted that the ability to bind object identity and location emerges shortly after the rapid period of parietal development that occurs between ages 3 and 6 months (Chugani, 1998; Greenough et al., 1987). This is also a time when the ability to bind object identity and location appears to emerge in tasks that presumably involve LTM (Catherwood et al., 1996; Kaldy & Leslie, 2003, in press).

In Experiment 2, we tested this prediction by examining the development of VSTM binding between ages 6 and 8 months. We assessed forty-eight 6.5-month-old infants \((M = 6\) months 16 days, range: 6 months 1 day to 6 months 29 days) and forty-eight 7.5-month-old infants \((M = 7\) months 12 days, range: 7 months 1 day to 7 months 28 days) using the same stimuli as in Experiment 1. The average change-preference scores are presented in Figure 1b. Mean change preference was near chance for the 6.5-month-old infants, \(t < 1\), but the 7.5-month-old infants significantly preferred the changing stream, \(t(47) = 3.04, p = .004, d = 0.44\). Moreover, the change-preference scores were significantly greater for the 7.5-month-old infants than for the 6.5-month-old infants, \(t(94) = 2.27, p = .025, d = 0.46\). Notably, the mean change-preference score of the 7.5-month-old infants was nearly identical to that of the 12.5-month-old infants in Experiment 1.

This experiment indicates that the ability to encode combinations of location and color in VSTM emerges between the ages of 6 and 8 months. Despite using a large sample size, we found no evidence that 6.5-month-old infants consistently preferred the changing stream to the nonchanging stream. However, the 7.5-month-old infants significantly preferred the changing stream (and did so at approximately the same level as the 12.5-month-old infants in Experiment 1). Moreover, the preference scores of the 7.5-month-old infants were significantly greater than those of the 6.5-month-old infants. Experiment 2 therefore demonstrates that the ability to bind color to location emerges at exactly the time suggested by the limited literature on the cytoarchitectural development of parietal cortex (Chugani, 1998; Greenough et al., 1987).

The failure of the 6.5-month-old infants to detect a change cannot be explained by a general inability to use VSTM at this age, because we have previously observed that 6.5-month-old infants can store object color and location individually in VSTM (Ross-Sheehy et al., 2003, 2004). Moreover, infants could have detected a change in the present task by simply remembering a single color-location combination on each cycle of the stream, so limitations in VSTM storage capacity cannot explain the failure of the 6.5-month-olds to prefer the changing stream to the nonchanging stream. Thus, the failure of the 6.5-month-old infants to bind color and location in VSTM is quite remarkable, particularly given that each individual object in the changing stream changed color on every cycle.

Does this failure reflect a general inability to represent multiple objects, rather than a specific inability to bind color and location? In a previous study, when the delay interval was removed so that no memory was required, we found that 6.5-month-old infants could detect a change in one of three simultaneously presented objects (Ross-Sheehy et al., 2003). Thus, the present results cannot be explained by a general inability to show a preference for changes when presented with multiple objects. In Experiments 3 and 4, we tested infants in two control conditions to further support our claim that the failure of the 6.5-month-old infants in Experiment 2 was truly a failure to bind color and location in VSTM and not a failure due to perceptual or attentional limitations.

**EXPERIMENT 3**

In Experiment 3, we tested sixteen 6.5-month-old infants \((M = 6\) months 15 days, range: 6 months 3 days to 6 months 22 days) in a control condition designed to assess the ability to detect changes in multiple-object displays. Each trial began with three identical squares on each monitor. On one monitor, the colors of the objects stayed the same from cycle to cycle (e.g., always three yellow objects), and on the other monitor, all three squares underwent the same color change on each cycle (e.g., three red objects were replaced by three blue objects, and so on; see Fig. 2a). If 6.5-month-old infants failed to prefer the changing stream in Experiment 2 because they were overloaded by the presence of multiple objects, then infants of this age should have difficulty detecting a change even when all the objects in a display are the same color. If, however, 6.5-month-old infants can detect changes when multiple objects are present, then they should detect a change in homogeneous multiple-object displays such as those in this experiment. Indeed, the 6.5-month-old infants in Experiment 3 did prefer the changing stream under these conditions, \(t(15) = 2.90, p = .011, d = 0.73\) (see Fig. 2c). Thus, the
failure of 6.5-month-old infants to prefer the changing stream in Experiment 2 was not caused by a general inability to detect changes in the context of multiple objects.

EXPERIMENT 4

To confirm that 6.5-month-old infants can actually perceive multiple different-colored objects in this procedure, we tested an additional group of sixteen 6.5-month-old infants (M = 6 months 18 days, range: 6 months 0 days to 6 months 29 days). Both stimulus streams were changing streams in which the colors of all three objects changed from cycle to cycle. In the heterogeneous stream, the three objects were different colors, and these three colors were replaced with three new colors on each cycle (e.g., a display of a red, a blue, and a black object was replaced with a display of a yellow, a green, and a brown object, and so on). The homogeneous streams were the changing streams from Experiment 3 (see Fig. 2b). If 6.5-month-old infants in Experiment 2 failed to prefer the changing stream because they were unable to perceive multiple colors in a single display, infants of this age would not be expected to prefer the heterogeneous over the homogeneous displays. However, if 6.5-month-old infants can perceive multiple simultaneous colors, then they should prefer the heterogeneous streams to the homogeneous streams because of their general preference for more complex stimuli (Brennan, Ames, & Moore, 1966). Indeed, the infants in Experiment 4 significantly preferred the heterogeneous streams, t(15) = 2.19, p = .044, d = 0.55 (see Fig. 2c), demonstrating that 6.5-month-olds’ lack of preference for the changing streams in Experiment 2 was not due to an inability to perceive object colors in a multiobject display.

GENERAL DISCUSSION

The present results demonstrate that the ability to bind object identity and location in VSTM develops rapidly between 6 and 8
months of age. Although 6.5-month-old infants can show preferences for some types of changes in arrays containing three simultaneously presented objects, they cannot detect changes in color-location combinations in such arrays, even though each object changes its color on each cycle. In contrast, 7.5-month-old infants show just as strong a preference for changes in color-location combinations as 12.5-month-old infants. Thus, the ability to rapidly bind color and location—prototypical ventral-stream and dorsal-stream features, respectively—develops rapidly between 6 and 8 months of age.

This developmental change occurs during a general time period in which infants’ ability to represent object identity and location separately in VSTM also changes (Rose et al., 2001; Ross-Sheehy et al., 2003, 2004). It appears, therefore, that the ability to represent multiple items in VSTM and the ability to bind features in VSTM emerge during the same time period. Raffone and Wolters (2001) developed a neural network model of VSTM in which the abilities to maintain multiple objects and to bind features together in VSTM depended on the same mechanism, namely, synchronized neural firing. The finding of the same developmental time course for the ability to store multiple objects in VSTM and the ability to bind features in VSTM is broadly consistent with this hypothesis.

Moreover, this is the same time period when infants apparently become able to bind object features to locations in procedures that provide the opportunity for involvement of LTM (Catherwood et al., 1996; Kaldy & Leslie, 2003, in press). The present results provide a demonstration that such binding emerges in VSTM between ages 6 and 8 months, whereas the developmental change demonstrated in previous studies may have occurred either in VSTM or in LTM. Thus, previous results may reflect the developmental change in binding in VSTM documented here or may document a different process. Indeed, binding appears to depend on different neural substrates in STM and LTM, so it would not be surprising if binding in these different memory systems had different developmental time courses.

The development of VSTM binding follows a period of apparent substantial cytoarchitectural development in parietal cortex (Chugani, 1996; Greenough et al., 1987). Representing multiple object identities appears to depend on a region of cortex in the intraparietal sulcus, part of the dorsal stream (Todd & Marois, 2004). In addition, binding object identity and location involves integrating information in widely separated brain regions in the dorsal and ventral streams, and creating bindings involving spatial information appears to involve the posterior parietal lobe. For example, Robertson et al. (1997) found that a patient with bilateral parietal damage was unable to bind features under contexts that required the use of spatial information (i.e., when multiple objects were presented simultaneously). Similarly, Shafritz et al. (2002) observed increased activity in posterior parietal cortex when subjects were required to bind features of objects at different locations. Thus, studies of functional neuroanatomy are also consistent with the proposal that the ability to represent multiple object identities and the ability to bind object identity to location are linked and may emerge during the same time period. Posterior parietal cortex also plays a well-known role in attention (Posner & Peterson, 1990), and attention may play a key role in creating VSTM representations of multiple single-feature objects (Vogel et al., in press) and in binding features together (Treisman, 1999). It is quite plausible that the developmental trends we have observed in infants’ VSTM are a consequence of the development of parietal-lobe attentional systems. A stronger link, however, will require more detailed studies of the structural and functional development of posterior parietal cortex in human infants.

In summary, the present experiments provide the first unambiguous evidence that infants can bind object identity and location in VSTM. In addition, we observed rapid development of this ability between the ages of 6 and 8 months, a time period predicted by both anatomical and behavioral developmental changes. The present results are broadly consistent with evidence that the ability to represent multiple single-feature objects and the ability to bind features together may be consequences of the same underlying neural mechanism (Raffone & Wolters, 2001), perhaps involving posterior parietal cortex (Todd & Marois, 2004). Thus, the present results bring researchers one step closer to understanding the neural bases and functional development of a fundamental cognitive process.

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REFERENCES


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