Great apes make anticipatory looks based on long-term memory of single events.

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Highlights

- We developed a novel eye-tracking task to examine great apes' memory skills
- Apes watched the same videos twice across 2 days, with a 24-hr delay
- Apes made anticipatory looks based on where-what information on the second day
- Apes thus encoded ongoing events into long-term memory by single experiences

Summary

Everyday life poses a continuous challenge for individuals to encode ongoing events, retrieve past events, and predict impending events [1–4]. Attention and eye movements reflect such online cognitive and memory processes [5, 6], especially through "anticipatory looks" [7–10]. Previous studies have demonstrated the ability of nonhuman animals to retrieve detailed information about single events that happened in the distant past [11–20]. However, no study has tested whether nonhuman animals employ online memory processes, in which they encode ongoing movie-like events into long-term storage during single viewing experiences. Here, we developed a novel eye-tracking task to examine great apes' anticipatory looks to the events that they had encountered one time 24 hr earlier. Half-minute movie clips depicted novel and potentially alarming situations to the participant apes (six bonobos, six chimpanzees). In the experiment 1 clip, an aggressive ape-like character came out from one of two identical doors. While viewing the same movie again, apes anticipatorily looked at the door where the character would show up. In the experiment 2 clip, the human actor grabbed one of two objects and attacked the character with it. While viewing the same movie again but with object-location switched, apes anticipatorily looked at the object that the human would use, rather than the former location of the object. Our results thus show that great apes, just by watching the events once, encoded particular information (location and content) into long-term memory and later retrieved that information at a particular time in anticipation of the impending events.

Keywords

anticipatory look; eye tracking; great ape; long-term memory; movie viewing

Results and Discussion

When we watch a movie (imagine *Alien* in 1979 by Ridley Scott), we spontaneously encode events into long-term memory [1, 2]. When we watch the same movie again, we often recall many details about particularly unusual or shocking events and even anticipate the outcomes [3, 4] (at what moment and from which actor was Alien born?). Attention and eye movement reflect such online cognitive and memory processes [5, 6], especially through "anticipatory looks"; people tend to look at the right place or object just before an anticipated event happens, based on their memories [7, 8, 10]. Currently unclear is whether nonhuman animals also employ such memory processes: online encoding of movie-like events into long-term memory, after single viewing experiences, and later retrieval of information in anticipation of the impending events. Great apes are well studied for their long-term memory skills. They recall the locations and types of hidden foods after a single exposure to such information [18, 21], even after delays of several years [20]. Recent advances in noninvasive eye-tracking technology have made it possible to track the eye movements of great apes. Several studies have demonstrated that apes anticipatorily look at the goal of an agent's reaching action based on memory of the same agent's previous actions [8, 9]. Thus, in this study, we devised a novel eye-tracking task that elicited great apes' anticipatory looks to impending events based on the long-term memory of single events.

We made half-minute movie clips depicting novel and potentially alarming situations for the participant apes. To enhance their understanding about the scenarios, we created the movies by combining novel scene elements with a familiar environment (Table 1). As the previous studies showed that apes better engage in, and encode, emotional (aggressive) stimuli than neutral ones [22, 23], we created situations in which the critical test events were contextualized within emotional events. In the movie used in experiment 1, an actor wearing a King Kong (KK) suit came out from one of two identical doors (the target door) and attacked a human actor (Figure 1; Movie S1). To elicit the explicit looks toward either of the doors (similar to the method used by [10]), warning lights attached above the doors flashed several times before KK came out. We presented this movie to each participant once on the first day and again on the second day, 24 hr later. In each case, we measured their viewing time toward the target and distractor doors during the critical pre-event period (i.e., just before KK appeared from the target door). 9 of 12 apes (Table S1) made explicit looks toward one of the doors during the critical pre-event period on the second day. Results showed that in the critical pre-event period, apes spent more time looking toward the target door (than the distractor door) on the second day compared to the first day (Figure 2): a repeated-measures ANOVA with areas of interest (AOIs; target, distractor) and day (first, second) as factors showed a significant interaction effect between these two factors ($F(1, 8) = 10.92$, $p = 0.011$, partial $\eta 2 = 0.57$; no significant main effects). Importantly, this effect was observed in the pre-event period, but not in overall presentation time; a repeated-measures ANOVA with AOI, day, and time (from the start to the post-event period; i.e., the horizontal axis in Figure 3) as factors revealed no interaction effect of AOI and day ($F(1, 8) = 2.25$, $p = 0.17$, partial $\eta 2 = 0.22$). Thus, the observed effect is explained by anticipatory looks toward the target door rather than by an overall preference for the target door on the second day.

Therefore, experiment 1 showed that apes encoded information about an event's location into long-term memory, as indicated by their anticipatory looks to that location. However, it remains unclear whether their anticipatory looks can also be directed at the content of a scene element rather than the location ("what" rather than "where" information). To examine this, we used the well-established Woodward [25] paradigm in experiment 2. This procedure was originally used in a habituation-dishabituation paradigm with human infants [25] but later also in an anticipatory-looking paradigm, with both human infants [7] and great apes [9]. In the anticipatory-looking studies, an actor reached to one of two different objects several times and thereby familiarized that action to participants. On the next action (after a short delay), when the location of objects was switched, participants anticipated that the actor's reach would be directed to the same (familiarized) object rather than to the same location.

In the movie used in experiment 2, the human actor grabbed one of two different objects (the target object) and attacked KK with it (Figure 1; Movie S2). On the second day (24 hr later), apes viewed the same movie again but with object-location switched. We measured apes' viewing time toward the target and distractor objects during the critical pre-event period (i.e., just before the human actor made an attempt to reach toward the object, i.e., before any directional signals were given). 9 of 12 apes (Table S1) made explicit looks to one of the objects during the critical pre-event period on the second day. Results showed that in the critical pre-event period, apes' gaze was biased more toward the target object (than the distractor object) on the second day compared to the first day (Figure 2): a repeated-measures ANOVA with AOI and day as factors revealed a significant interaction effect ($F(1, 8) = 7.43$, $p = 0.026$, partial $\eta 2 = 0.48$; no significant main effect). Importantly, as in experiment 1, this effect was observed in the pre-event period, but not in overall presentation time; a repeated-measures ANOVA with AOI, day, and time as factors revealed no interaction effect of AOI and day ($F(1, 8) = 0.29$, $p = 0.86$, partial $\eta 2 = 0.004$; Figure 3). Thus, the observed effect was explained by anticipatory looks to the target object rather than by an overall preference to the target object on the second day. Therefore, experiment 2 showed that apes made anticipatory looks to an object (even in a new location) based on their memory of a single event 1 day before, extending the results from experiment 1.

Thus, we have shown that apes encoded particular information (location and content) into long-term memory, just by watching the movies once, and later retrieved that information in anticipation of the impending events. Simple procedural learning (e.g., classical or operant conditioning, habituation or sensitization, and item-based familiarity recognition [26]) cannot explain our results. First, apes' long-term memories were formed after single events, excluding the possibility that their memory was based on multi-trial learning. Second, our movies depicted a novel situation to the participant apes, excluding the possibility that their memory was based on the learned rules acquired through extensive training prior to the tests. Third, we examined the apes' anticipatory looks, not their reactive looks, to the critical events (the appearance of KK in experiment 1 and the grabbing of an object in experiment 2). In addition, the apes' anticipatory looks were observed just before the critical events but not throughout the presentation time. Therefore, any recognition-memory process that acted on individual scene elements cannot explain our results. Our results are best explained by a memory process that acted on the relationship between events, that is, the spatial and temporal relations between the critical events and the preceding events (e.g., the actors' movements, light flashes). Lastly, a similar eye-movement-based memory process has previously been documented in humans [27, 28]; in one study [27], shortly after being presented scenes with target objects, participants saw the same scene without the target objects and tended to fixate on the location where those objects were previously observed. It was shown that this effect is dependent on hippocampal (as well as prefrontal) activities in humans and absent in amnesia [27, 28]. It was also shown that this eye-movement-based memory effect does not require explicit awareness in humans; therefore, it does not necessarily indicate the occurrence of episodic (conscious) recalls, although certain similarities exist in the pattern of neural activities between these memory processes [27, 28].

One important difference between this and previous studies is that our apes encoded information about novel events into long-term memory, just by watching those events once, while most of the previous studies relied on explicit behavioral training of apes prior to the tests. Thus, in our study, we can exclude the possibility that apes updated their knowledge within already-established rules that they had acquired through training; rather, they indeed encoded and retrieved the information that they had encountered only once and in a novel context. Another difference is that our paradigm allowed apes to retrieve the information based on several cues preceding the critical events. Therefore, our apes did not have to retrieve the information regarding when the critical events occurred. In this regard, our study differs from several previous studies that showed what-where-when or episodic-like memory in nonhuman animals [29]. Our study is rather consistent with several other studies that showed cued recalls in human and nonhuman animals [20, 30], in which the retrieval of information is facilitated by the (task-irrelevant) cues that existed with the critical information at the time of encoding.

Finally, our results highlighted a potentially important function of memory-based anticipatory looks. We have shown that great apes encode and retrieve significant events, such as an appearance of an agent's opponent and an agent's choice of a tool, just by watching those events. Such online memory processes should help animals to avoid impending dangers, enhance social learning, and navigate competitive and cooperative social environments. Given the known function of gaze in communicating about locations and objects to other individuals ("gaze following" [31, 32]), apes' memory-based anticipatory looks may also help a group of conspecifics to store shared memories.

Experimental Procedures

Participants

A total of 12 great apes (6 bonobos, Pan paniscus, and 6 chimpanzees, Pan troglodytes) participated in this study (Table S1). They lived with conspecifics in Kumamoto Sanctuary [33] with environmental enrichments (as described in [34]). They have some experience watching commercially available films and TV programs since youth for enrichments, although they were never language trained or explicitly trained for their gaze behavior. Three apes were excluded from the analysis respectively in experiment 1 (Misaki, Connie-Lenore, Lolita) and in experiment 2 (Misaki, Lolita, Zamba) because they exhibited no explicit look at the target or distractor during the critical 3 s pre-event period on the second day (Table S1). Animal husbandry and research protocol complied with the Guide for the Animal Research Ethics provided by Wildlife Research Center, Kyoto University (No. WRC-2014KS001A).

Apparatus

We used the setups that we previously established to record apes' eye movements accurately but non-invasively without a head-restraint devise [8, 9, 31]. Briefly, apes' eyes were imaged using an infrared eye-tracker (300 Hz; X300; Tobii Technology AB). Their heads were positioned either directly by the hands of the experimenter (Movie S1) or by the apes themselves as they sucked a nozzle through which they could drink juice (Movie S2). Apes were allowed to chew fruits or drink juice during the recording irrespective of their gaze behavior. See Supplemental Experimental Procedures and also [8, 9, 31] for details. Stimuli were presented at a viewing distance of 70 cm with a resolution of 1,280 × 720 pixels on a 23-in LCD monitor (43° × 24°) with Tobii Studio software (version 3.2.1).

Stimuli and Procedure

We prepared two scenarios respectively for experiment 1 and 2 (Figure 1). Apes watched the same scenario twice across 2 days, with a 24-hr delay. Experiment 1: in a 32-s movie, at the critical test moment (18 s), a costumed KK appeared from one of the two doors. After that, KK attacked one of the actors and then ran through a nearby door. We counterbalanced the side of the target door (left or right) across participants and thus prepared two movie clips that were the same except in that respect. Experiment 2: in a 36-s movie, at the critical test moment (24 s), the actor reached to one of the two objects (a red hammer or a yellow sword). After that, the actor grabbed the object and attacked KK with it. On the second day, the location of two objects (left or right) was switched in the movie scene (from the beginning). We counterbalanced the target objects (hammer or sword) and the locations of the target object (left or right) across participants and thus prepared four movie clips that differed in those respects.

Data Analysis

Polygon-shaped AOIs were defined on the doors and objects (see Figure 1). The eye-movement data were filtered using a Tobii fixation filter. The viewing-time scores to AOIs were then calculated in Tobii Studio software (version 3.2.1). A time-series analysis was conducted by first setting the zero point for the critical moments (18 and 24 s for experiment 1 and 2, respectively), then segmenting the presentation time using 3-s time bins relative to the zero points (as in Figure 3). The critical pre-event period was defined as the time bin prior to the zero point, i.e., −3~0 s.

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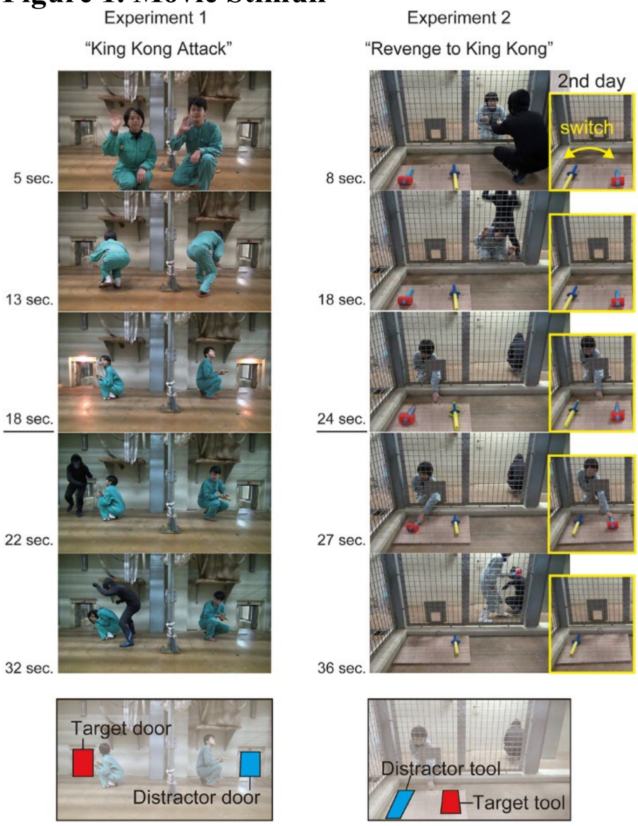
Table 1. Constructing Novel Situations in a Familiar Environment Using Familiar and Novel Scene Elements

Scene Element	Familiarity
Experiment 1	
Background (room)	familiar
Human actors	familiar
Doors	familiar
Lights	novel
KK	novel
Experiment 2	
Background (room)	familiar
Human actor	familiar
Objects	novel
KK	novel[a]

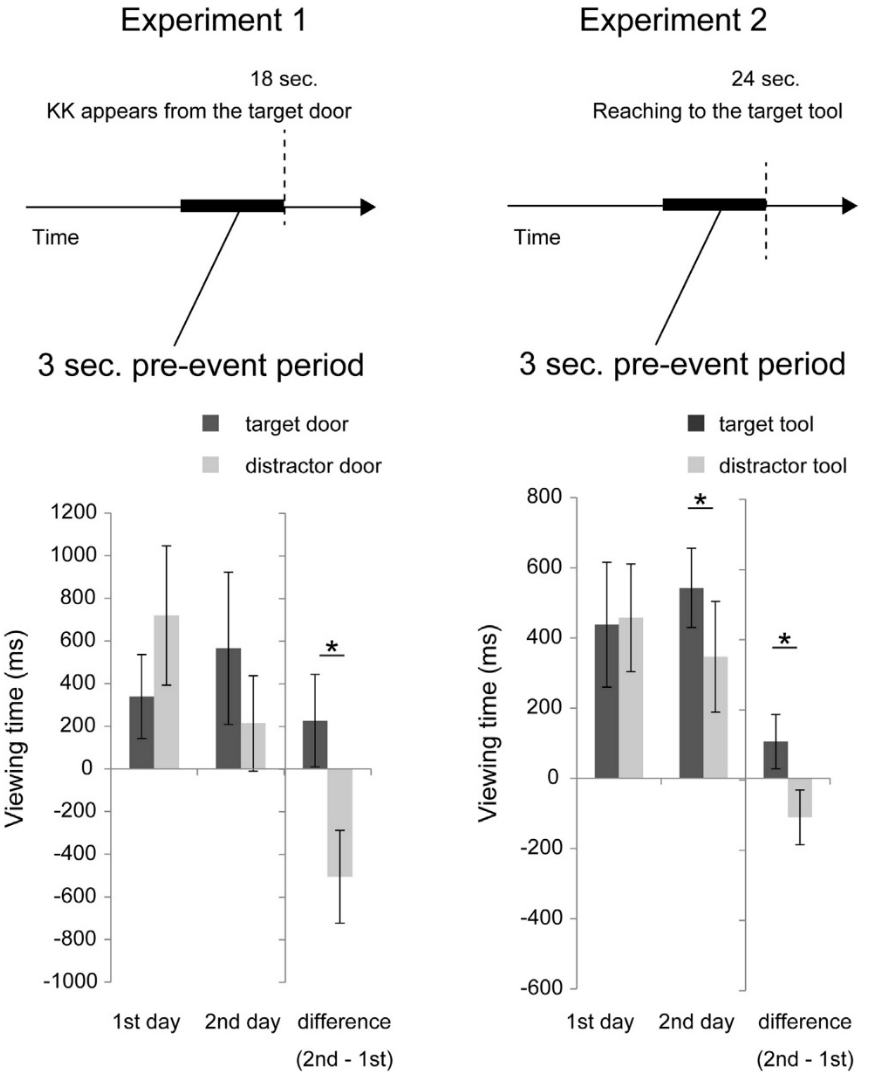
[a] Except that the participants saw him in experiment 1

Figure 1. Movie Stimuli



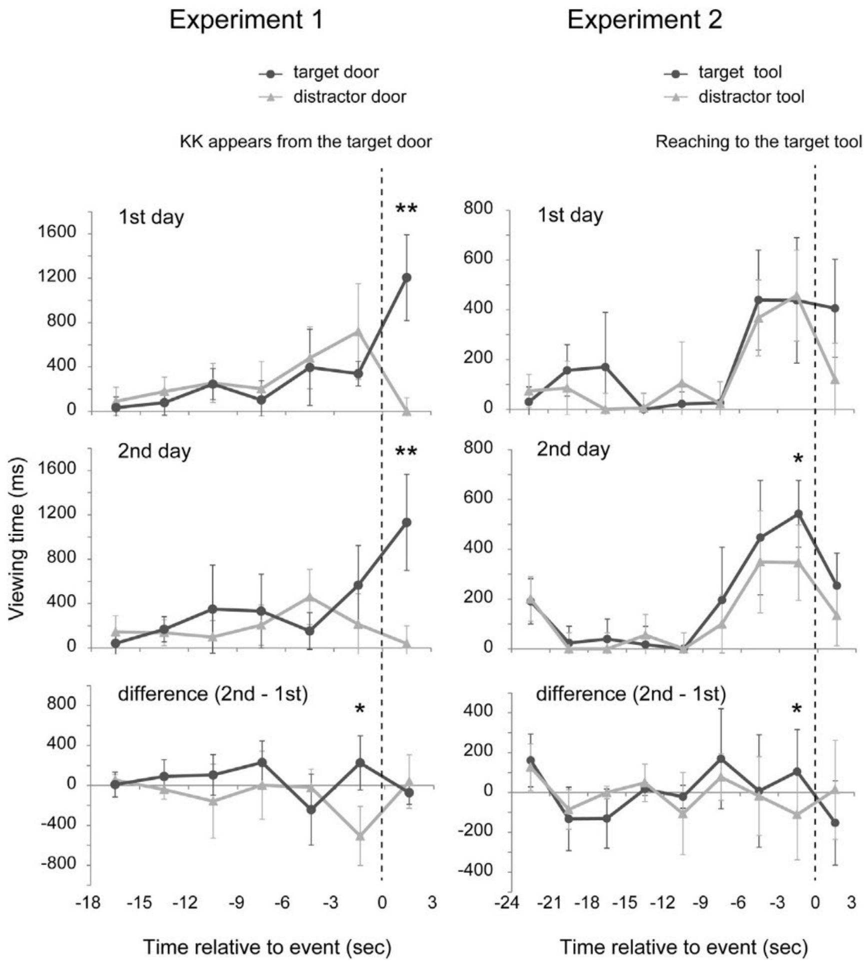
In experiment 1, two human actors waved hands at the camera (~5 s) and walked respectively to the left and right doors (~13 s). After the lights above the doors flashed several times (~18 s), the costumed King Kong (KK) appeared from one of the doors (counterbalanced across participants) and showed off in front of the camera (~22 s). KK then hit one of the actors, robbed bananas from the actor, and ran through a nearby door (~32 s). The target and distractor doors refer to the door through which KK appeared on both days and the other irrelevant door, respectively. Also shown are the areas of interest (AOIs) defined for the doors. In experiment 2, KK suddenly opened the door and came out from the room (~8 s). KK then hit the actor and sat down in the corner, facing away from the camera (~18 s). The actor then moved to a hole in the mesh, reached her left hand through the hole, attempted to grab the edge of a plate (equidistantly from the two objects) several times, then grabbed the edge, and pulled the plate and the objects on it (a red hammer and a yellow sword) (~24 s). The objects flashed several times during this period. The actor then reached for and grabbed one of the objects (the location and content were counterbalanced across participants) and took the object out through the hole (~26 s). The actor then hit KK with the object, and KK ran through the door (~36 s). On the second day of presentation, the location of the objects was switched. The target and distractor objects refer to the object that the actor used on the first day and the other irrelevant object, respectively. Also shown are AOIs defined for the objects.

Figure 2. Memory-Based Anticipatory Looks



Viewing times (ms) to the target and distractor during the 3-s pre-event period on each testing day, averaged across participants. The 3-s pre-event period refers to the period before KK appeared from the target door in experiment 1 (i.e., before any sign of KK was seen over the door) and the period before the human actor reached for the target object in experiment 2 (i.e., before any left or right directional movement of hand was given). Error bars indicate 95% confidence intervals corrected for within-subject design [24]. We also show the difference scores to visually represent the change in viewing times from the first to the second day. Asterisks indicate $p < 0.05$ in paired t tests (experiment 1 difference: $t(8) = 3.30$, $p = 0.011$; experiment 2, second day: $t(8) = 2.73$, $p = 0.026$; difference: $t(8) = 2.72$, $p = 0.026$; see ANOVA results in the main text). See Figure S1 for a higher time resolution.

Figure 3. Viewing Patterns Relative to the Critical Events



Viewing times (ms) to the target and distractor as a function of time relative to critical events (set to the zero points) on each testing day, averaged across participants, for each 3-s time bin. Error bars indicate 95% confidence intervals corrected for within-subject design [24]. Asterisks indicate $p < 0.05$ ($*$) or $p < 0.01$ ($**$) in paired t tests conducted for each time bin. See Figure S2 for the viewing times to KK and the actors.