Research Report

Dynamic Object Individuation in Rhesus Macaques

A Study of the Tunnel Effect

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ABSTRACT_A manual-search experiment with rhesus monkeys (Macaca mulatta) explored dynamic object individuation in the tunnel effect: Subjects watched as a lemon rolled down a ramp and came to rest behind a tunnel (Occluder 1) and then as a kiwifruit emerged and became occluded at the end of its path behind a screen (Occluder 2). When the kiwifruit emerged at about the time that the lemon should have (had it continued its motion), subjects searched for food only behind Occluder 2—apparently perceiving the lemon to have transformed into a kiwifruit on the basis of spatiotemporally continuous motion. In contrast, when a brief pause interrupted the occlusion of the lemon and the emergence of the kiwifruit, monkeys searched for food behind both occluders. With further control conditions, this experiment demonstrates a spatiotemporal biassimilar to a bias found in adult visual perception—in the computation of object persistence in the context of a dynamic correspondence problem.

A central project in several areas of cognitive science is to uncover the rules that guide the perception of an object as the same enduring individual across time and motion. Without such a process, visual experience would be incoherent. Existing work in both adult vision (e.g., Scholl, 2001) and cognitive development (e.g., Carey & Xu, 2001; Scholl & Leslie, 1999) has uncovered one especially powerful factor that seems to guide the perception of object persistence: the principle of spatiotemporal priority. In many situations (e.g., in apparent motion; Burt & Sperling, 1981; Schecter, Hochstein, & Hillman, 1988), the visual system is faced with a correspondence problem— "which went where?" Potential solutions to such problems that satisfy certain spatiotemporal criteria (e.g., proximity or temporal synchrony) will often dominate or trump other possible solutions, even when they involve seemingly impossible featural transformations (e.g., changing from a circle into a square).

Perhaps the most direct demonstration of spatiotemporal priority is observed in a visual phenomenon called the *tunnel* effect (Burke, 1952; Flombaum & Scholl, 2004; Michotte, Thinès, & Crabbé, 1964/1991). This effect is found when an object moves behind an occluder (the "tunnel"), and then a different object emerges from the other side of the occluder and continues moving. When the second object emerges at about the time and place that one would expect the first object to emerge, people tend to perceive the event in terms of a single object undergoing continuous motion behind the occluder. This percept obtains even when the second object differs from the first object in its surface features (e.g., turning from red to green; Burke, 1952; Michotte et al., 1964/1991) or its kind (e.g., turning from a ball into a box; Carey & Bassin, 1998; Carey & Xu, 2001). In contrast, if the second object emerges after an extended temporal delay, subjects perceive the event as involving two different objects, the first remaining behind the occluder when the second emerges.

Thus, the tunnel effect constitutes an elegant demonstration of vision's reliance on spatiotemporal properties in weaving together a coherent phenomenological experience. For this reason, the tunnel effect may be an especially fertile test bed for studying the nature of persisting object representations. A limitation of previous work, however, has been the dependent measure used to study the tunnel effect: Typically, subjects are asked to judge whether the event appears to involve one or two objects, or even just to describe the event. Such measures are notoriously susceptible to higher-level response biases and pose a serious challenge to the study of the tunnel effect in nonverbal populations.

In the present study, we developed a paradigm for studying the tunnel effect using a manual-search method in which this illusion determines subjects' real-world behavior. Our use of manual search builds on the pioneering studies of Hauser and

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his colleagues, who developed this dependent measure for exploring monkeys' object representations across a variety of domains (e.g., Hauser, 2001; Hauser, Carey, & Hauser, 2000). In the present experiment, free-ranging rhesus monkeys (*Macaca mulatta*) watched as a kiwifruit or a lemon rolled down a short ramp and behind a tunnel (Occluder 1). A second fruit then rolled out from behind the other end of the tunnel, down the rest of the ramp, and behind a final screen (Occluder 2). The monkeys were then allowed to search for the hidden foods. We reasoned that the monkeys' search behavior would reflect both the number of perceived objects in the display and their locations. In several conditions, we varied both the objects' surface features and the timing of the emergence of the second object, to explore their influence on the number of perceived objects in the display.

METHOD

Subjects

We tested free-ranging adult rhesus macaques at the Cayo Santiago field station (Rawlins & Kessler, 1987), home to a population of 800 individuals, all well habituated to human experimenters. Similar paradigms have been used with this population in a number of previous studies (e.g., Hauser, 2001; Hauser et al., 2000; Santos, 2004; Santos, Hauser, & Spelke, 2001). Our experiment involved four conditions, as described in Procedure; the final sample included between 18 and 20 individuals in each condition. A total of 82 monkeys were tested. Attempts were made to test another 164 monkeys, but these tests were not completed because of interference, inattention, or lack of approach, or because the monkeys had been tested previously. Of the monkeys that were tested, 5 were excluded at coding because of poor video quality or disagreement among coders.

Apparatus and Stimuli

Subjects observed displays consisting of fruit objects (lemons and kiwifruits, roughly 6 cm in diameter) that rolled down a ramp constructed of foamcore, a plastic channel, duct tape, and cloth (see Fig. 1). The ramp (122 cm long) was at a 14° angle. A foamcore tunnel (20 cm \times 25 cm, Occluder 1) was centered 61 cm down the ramp, and a second similar foamcore tunnel (Occluder 2) was centered 112 cm down the ramp. Foamcore runners along the ramp (3 cm high) allowed the fruit to roll smoothly and continuously. A small wall inside each tunnel stopped the fruit when it rolled in, and a releasing mechanism inside Occluder 1 allowed the experimenter to control the release of the second fruit object. All studies were videotaped with a Sony Hi-8 camera and analyzed later off-line.

Procedure

The four conditions consisted of the same event sequence, differing only in the nature of the fruit objects and in the presence of a temporal delay. (In conditions involving both a lemon and a kiwifruit, the order of presentation was always counterbalanced across subjects, though in this report we



Fig. 1. Sample stills from a trial of the tunnel-effect condition. The subject watches as a lemon rolls down the ramp (Frames A–B) and becomes concealed by Occluder 1 (Frame C), and then as a kiwifruit rolls down the remainder of the ramp (Frames D–E) and becomes concealed by Occluder 2 (Frame F). Finally, the experimenter walks away, and the subject is given the opportunity to search (Frame F).

describe these conditions as involving a lemon first and a kiwifruit second.) As in previous studies using similar methods, experimenters chose subjects opportunistically by locating lone individuals seated in a flat, clear area. Two experimenters (a presenter and a cameraperson) ran each session. Each subject participated in only a single trial, testing one of four conditions. A sample trial movie of each condition can be viewed on-line at http://www.yale.edu/perception/tunnel/.

Condition 1: The Tunnel Effect

In this condition, the presenter began by drawing the subject's attention to the apparatus. He then removed a lemon from his waist pouch and drew the subject's attention to it, while surreptitiously loading a kiwifruit into the releasing mechanism behind Occluder 1. The monkey next watched as the presenter placed the lemon at the top of the ramp and released it so that it rolled down and became concealed behind Occluder 1. The experimenter then surreptitiously and immediately released the kiwifruit, which rolled down the remainder of the ramp, eventually becoming concealed by Occluder 2. (Human observers reliably perceived the tunnel effect with these motions.) At this point, the experimenter surreptitiously removed the lemon from within Occluder 1 and walked away from the display with his back to the apparatus. Subjects then approached the display and were allowed to search for the fruit for as long as they liked. The cameraperson indicated that a trial was over when the monkey moved 3 m away.

Condition 2: Temporal Gap With Featural Change

This condition was identical to Condition 1, except that the kiwifruit emerged from behind the first occluder 3 s after the lemon became occluded.

Condition 3: Temporal Gap Without Featural Change

This condition was identical to Condition 2, except that we used two featurally identical objects—either two lemons or two kiwifruits (counterbalanced across subjects).

Condition 4: Simultaneous Presentation

This condition was identical to Condition 1, except that the experimenter did not surreptitiously load the kiwifruit into Occluder 1 at the start of the experiment. Rather, he held up both the lemon and the kiwifruit, drawing the monkey's attention to both. The experimenter then placed the lemon in position at the top of the ramp while at the same time holding the kiwifruit within the monkey's view, just below Occluder 1. When the lemon rolled behind Occluder 1, the experimenter simply released the still-visible kiwifruit to let it roll down the remainder of the ramp and disappear behind Occluder 2. This is the only condition in which subjects ever saw two food objects simultaneously.

RESULTS

Four independent off-line coders scored Conditions 1, 2, and 4, and four different coders scored Condition 3, indicating which occluders subjects searched. (Only 2 trials resulted in a discrepancy; both were dropped from the final analysis.) All subjects searched for fruit behind Occluder 2. Because subjects in this environment are wary of interference from other (possibly higher-ranking) individuals, they will often retrieve only a single object before moving away; therefore, we did not expect all monkeys in any condition to search behind both occluders, but it was still possible to observe significant differences in the proportion of monkeys who searched behind both occluders in different conditions.

Figure 2 reports the results of each condition in terms of the proportion of subjects who searched behind Occluder 1 (in addition to Occluder 2). Fewer monkeys searched behind Occluder 1 in the tunnel-effect condition than in either the temporal-gap-with-featural-change condition (Fisher's exact test, p = .02; all tests two-tailed) or the simultaneous-presentation condition (p < .01). In the temporal-gap conditions, more monkeys searched behind Occluder 1 when there was a featural change than when the objects were featurally identical (p < .01). There was no difference, however, between the searching rates for the tunnel-effect and temporal-gap-without-featural-change conditions (p = .69).

DISCUSSION

These results constitute the first demonstration of a nonhuman animal perceiving the tunnel effect, and of this percept guiding search behavior. When monkeys were given unambiguous featural and spatiotemporal cues for two objects in the simultaneous-presentation condition, they were likely to search behind both occluders-providing initial evidence that they would search behind multiple screens thought to contain food. Individuation of two distinct objects on the basis of their featural differences was also observed when the two objects were seen successively: Monkeys tended to search behind both occluders in the temporal-gap-with-featural-change condition. This searching behavior clearly required the featural difference, as monkeys tended to search behind Occluder 2 only in the otherwise identical temporal-gap-without-featural-change condition. The tunnel-effect condition then provides evidence that monkeys perceive-and act on the basis of-the tunnel effect. This condition differed from the temporal-gap-withfeatural-change condition only in that the kiwifruit appeared immediately after the disappearance of the lemon, yet monkeys searched significantly less often behind Occluder 1 in the tunnel-effect condition-apparently often perceiving the lemon transform into a kiwifruit on the basis of spatiotemporally continuous motion.



Fig. 2. Schematic diagrams (not to scale) of the events observed during all four conditions, along with the proportion of monkeys who searched behind Occluder 1 (in addition to Occluder 2) in each condition. For on-line demonstrations of the conditions, see http://www.yale.edu/perception/tunnel/.

These findings make several methodological and theoretical contributions to the study of dynamic object individuation:

Dynamic Amodal Integration and Spatiotemporal Biases in a Nonhuman Primate

Previous work has shown that the tunnel effect is perceived by adults (e.g., Burke, 1952; Carey & Bassin, 1998; Flombaum & Scholl, 2004; Michotte et al., 1964/1991) and perhaps also by human infants (Carey & Bassin, 1998; Wilcox & Chapa, 2004). This experiment constitutes the first demonstration of the tunnel effect in a nonhuman primate-and thus, to our knowledge, the first behavioral demonstration in a nonhuman species of dynamic visual amodal integration, wherein an object maintains its identity through only certain types of spatiotemporal gaps (cf. Assad & Maunsell, 1995, for related physiological work). The fact that monkeys perceive the tunnel effect is especially striking because many experiments have shown that they will use featural differences to individuate objects (albeit in static displays, and in the absence of unambiguous spatiotemporal information; e.g., Munakata, Santos, Spelke, Hauser, & O'Reilly, 2001; Santos, Sulkowski, Spaepen, & Hauser, 2002; Uller, Xu, Carey, & Hauser, 1997). These results make the tunnel effect all the more striking in rhesus monkeys because it shows a discounting of information that these animals normally use in similar foraging situations.

A New Implicit Measure of the Tunnel Effect

This is the first experiment to measure the tunnel effect with an implicit measure. Previous work has relied on perceptual reports in which subjects simply describe what they see, and experimenters sort these descriptions in various ways. Such reports may reflect robust visual percepts, but they are notoriously susceptible to contamination by higher-level biases. This is more than a minor methodological concern. Indeed, such ambiguities have fueled substantial confusion and debate regarding the tunnel effect in other contexts.

For example, several infant cognition researchers have recently debated whether or not certain object-individuation results reflect the tunnel effect, and this debate has remained difficult to resolve because different researchers ask different questions and interpret verbal reports in different ways (Carey & Bassin, 1998; Carey & Xu, 2001; Wilcox, 1999; Wilcox & Baillargeon, 1998; Wilcox & Chapa, 2004; Xu & Carey, 2000). The manual-search method employed here could potentially help to resolve this debate if adapted for use with infants, because it unambiguously signals how many objects the subjects perceive as being involved in the events, without relying on verbal reports, and it allows for a more precise quantitative comparison of the magnitude of the effect across different conditions.

Effects on Search Behavior: Beyond Fleeting Visual Impressions

The manual-search method may be a particularly useful tool for studying these issues in nonverbal populations, but it might not be a useful test for adults, at least in this form. Why? Adults, though they *perceive* the lemon turn into a kiwifruit, will still know that such a transformation is unlikely or impossible, and could thus still search on the basis of this knowledge. In general, many visual illusions may be perceptually compelling, yet the observer never truly believes them. Indeed, most illusions are striking precisely because one knows that there must be some distortion involved: One does not truly believe that a friend has shrunk in half while in the Ames room, that a twodimensional stereogram has true three-dimensional structure, or that a pole has truly bent when half-submerged in water. As a result, most tests of visual illusions require some method of directly tapping perception, because most of subjects' actual behavior will be controlled instead by their beliefs.

Our subjects, however, not only perceived the tunnel effect, but also acted on its basis. In this way, the results show that the tunnel effect need not be only a fleeting visual impression, discarded or ignored by higher-level cognition and in actual behavior. The percept of one object changing into another featurally distinct object on the basis of spatiotemporal continuity seems to be strong enough, at least in monkeys, to guide foraging behavior. Thus, the tunnel effect may be more than an artifact of visual processing—it may be a reflection of a critical spatiotemporal heuristic used to guide object perception.

Conclusions

In this study, we demonstrated the tunnel effect—and its associated spatiotemporal bias—for the first time in a nonhuman primate. In doing so, we also measured it for the first time using an implicit dependent variable, in a situation in which the tunnel effect directly influenced foraging behavior, and was not simply a fleeting, powerless visual impression. Though the tunnel effect has received relatively little empirical attention since the seminal experiments of Burke and Michotte (Burke, 1952; Michotte et al., 1964/1991), we suggest that it may be a particularly useful tool with which to study aspects of dynamic object individuation.

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