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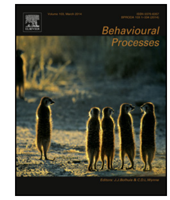

Enhanced visual exploration for real objects compared to pictures during free viewing in the macaque monkey

Faiz Mustafar[a,b,1], Paolo De Luna[a,b], Gregor Rainer[a,b,*]

[a] Visual Cognition Laboratory, Department of Medicine, University of Fribourg, Chemin du Musée 5, Fribourg CH-1700, Switzerland
[b] Swiss Non-Human Primate Competence Center for Research, Switzerland

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ABSTRACT

The question of whether animals perceive pictures as representation of real objects remains still unsolved. Object-picture perception is generally studied requiring animals to learn some information about real objects and transfer that knowledge to the pictorial domain, or vice versa. Here, we tackle the issue of object-picture perception from a different perspective, examining visual exploration behavior of two naïve macaque monkeys during free-viewing of objects and pictures of these objects on a computer monitor. Our main finding is that monkeys looked spontaneously longer at object rather than picture stimuli. However, we find striking similarities in temporal dynamics of gaze allocation within the time course of a single stimulus presentation, as well as in habituation rates within and across behavioral sessions. We also highlight differences between stimulus types in terms of spatial gaze patterns and looking strategies. Stimulus features that attract overt attention during spontaneous visual exploration are thus better predicted for object stimuli by a visual saliency model. Moreover, we provide evidence for a consistency in stimulus preference for objects and pictures, suggesting a correspondence of in how macaques perceive objects and their pictorial stimuli. Taken together, our data suggest that macaque monkeys exhibit evidence for correspondence between objects and pictures. This validates spontaneous visual exploration as a method for studying object-picture correspondence without a need for extensive behavioral training. We discuss the potential advantages of using object over picture stimuli in the context of studies on visual cognition.

1. Introduction

The degree to which animals can recognize pictorial representations of objects is a subject of current interest (Bovet and Vauclair, 2000; Fagot et al., 2010). A widely used approach to study this question relies on examining transfer effects in learning paradigms, where animals are trained on a task involving objects and then tested with the corresponding pictures or vice versa. A considerable literature has examined object-picture perception in birds (Fagot and Parron, 2010) including chicken (Railton et al., 2014) and pigeon (Cabe, 1976; Spetch and Friedman, 2006; Watanabe, 1997) as well as other species such as tortoise (Wilkinson et al., 2013). These studies have revealed different degrees of transfer, usually partial transfer, from objects to pictures, in dependence on task and stimulus variables.

Object-picture perception has also been studied in different primate species. For example, capuchin monkeys trained in an object matching task are able to transfer this knowledge to correctly match objects to pictures (Truppa et al., 2009). By showing that capuchin monkeys are able to match objects to objects when a matching picture is used as a distractor, these authors also provide evidence that transfer is not simply due to confusion between objects and pictures. The results by Truppa and colleagues reveal a large degree of transfer between objects and pictures, and thus suggest a close correspondence between objects and pictorial representations. Other studies have shown that transfer can often be more limited. Thus, macaque monkeys require considerable training to learn that selecting the picture of a preferred food item results in the delivery of that food as a reward (Judge et al., 2012). This study has highlighted large inter-individual differences between participant macaques, with the fastest learner requiring only about 15% of the training needed by the slowest learner to achieve criterion behavioral performance. Similarly, another study demonstrated

* Corresponding author at: Visual Cognition Laboratory, Department of Medicine, University of Fribourg, Chemin du Musée 5, Fribourg CH-1700, Switzerland. Tel.: +41 26 300 8689; fax: +41 26 300 9734.
E-mail address: gregor.rainer@unifr.ch (G. Rainer).

[1] These authors contributed equally to this work.

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partial transfer between objects and pictures in marmoset monkeys, in that animals pre-exposed to a real snake model showed enhanced fearful responses to a picture of the same snake (Emile and Barros, 2009). In related work, it was shown that baboons and gorillas, but not chimpanzees that have been trained to select real bananas over stone pebbles tend to choose bananas over pebbles when confronted with their pictures (Parron et al., 2008), thus, demonstrating transfer from the object to the picture domain. In fact, the animals frequently ate the banana pictures, which the authors interpreted as evidence for confusion between objects and pictures. The observation that animals reliably chose the real banana over the banana picture however suggests that the transfer of task-related behavior (that is, eating) from the object to the picture situation might be an alternative explanation. Curiously, object-picture perception has been only rarely studied in macaques, for example (Zimmerman and Hochberg, 1970), despite the fact that this species is used so extensively in visual neuroscience investigations.

The existing literature on object-picture perception can be broadly classified into two cases: some studies have first trained animals on tasks involving objects, such as the stimulus matching paradigm, and then tested their performance with pictures of the same objects to estimate transfer (Truppa et al., 2009; Wilkinson et al., 2013). Other studies have relied on spontaneous behaviors elicited by certain objects, such as approach behaviors for preferred fruits or fearful behavior for snakes, and tested how these behaviors transfer to picture stimuli (Emile and Barros, 2009; Judge et al., 2012; Parron et al., 2008). In both cases, animals are required to transfer acquired or innate knowledge about objects to pictures. Such transfer is likely to depend heavily on cognitive abilities and flexibility, as animals with extensive previous experience on task-related behaviors appear to perform better on transfer to pictures than naïve animals. An alternative to studying the transfer between objects and pictures would be to compare the spontaneous behaviors elicited by both stimulus types when not associated with emotional content or foraging behavior. Similarities in such spontaneous directed behaviors for objects and pictures provide evidence for correspondence in their mental representations, in analogy to high transfer performance from objects to pictures on the transfer tasks. Visual explorative behavior is an example of this kind of spontaneous behavior directed toward elements of the visual environment.

Visual exploration has been studied extensively, and can provide a wealth of information about which aspects of visual scenes attract overt attention, and what kinds of information subjects are extracting from the visual environment (Gottlieb et al., 2013; Gunhold et al., 2014; Schutz et al., 2011). In visual exploration studies, subjects are generally not rewarded for fixating on particular visual scene elements, to avoid biasing the gaze patterns toward these rewarded locations. A part of the visual exploration literature focuses on gaze patterns during free-viewing of ethologically or socially relevant stimuli, such as faces or body parts of conspecifics or other species (Dal Monte et al., 2014; Ghazanfar et al., 2006; Gothard et al., 2004; Kano and Tomonaga, 2009, 2010; Sigala et al., 2011). In this context, gaze patterns are thought to be driven by the need to make predictions about the intentions of other agents (Cannon et al., 2012; Kano and Call, 2014; Southgate et al., 2007), which might be relevant for guiding future behaviors. This can be considered as a form of top-down gaze control, because it is primarily the information requirements of the observer that determines which scene elements are fixated. By contrast, a largely separate body of work has examined bottom-up contributions to gaze control, by attempting to predict gaze patterns based on local statistical properties of image patches in natural scenes (Berg et al., 2009; Berger et al., 2012; Einhauser et al., 2006). In this context, the gaze patterns are determined exclusively on the properties of the visual input, without considering the information requirements of the observer. An emergent concept in this research area is the saliency map, which is computed by combining various low-level statistical image properties and can be compared to the experimental eye fixation map to determine how well it can predict the allocation of overt attention for a particular visual stimulus (Hou et al., 2012; Itti and Koch, 2000; Koehler et al., 2014; Tatler et al., 2011).

A pertinent property of primate visual explorative behavior is that it tends to habituate with repeated exposure to stimuli, such that less time is spent on successive viewing periods (Butler and Alexander, 1955; Humphrey, 1972, 1974; Jutras and Buffalo, 2010). Habituation has been observed to occur at different timescales of separation between observation periods, ranging from minutes to 24-h intervals (Gammon et al., 1972; Rabedeau and Miles, 1959; Wilson and Goldman-Rakic, 1994). Habituation is generally stimulus specific, and thus not a consequence of general fatigue resulting from repeated exposure. It reflects reduced allocation of overt attention, because there is a reduced need to gather information about stimuli that have been previously explored. Habituation is thought to depend on implicit memory formation, and can thus be used to study recognition memory, as is typically done in novelty preference paradigms (Antunes and Biala, 2012; Hannula et al., 2010; Snyder et al., 2008).

Thus, previous studies on object-picture perception in non-human primates have generally employed manual interactions with the stimuli as well as substantial behavioral training. Here, we address the issue of object-picture perception using gaze fixation instead of manual interaction as a behavioral measurement and rely on the inherent motivation of the animals for visual exploration rather than a trained behavior that results from operant conditioning. This approach can complement existing literature and provide important evidence for perceptual correspondence between objects and pictures in non-human primates. Specifically, we have compared the spontaneous visual exploratory behavior of task-naïve monkeys for sets of arbitrary three dimensional shapes and the corresponding pictures presented on a computer monitor. The use of arbitrary shapes ensured that monkeys had no relevant semantic knowledge that might bias their behavior during free-viewing, thus, emphasizing bottom-up saliency as the main factor determining gaze control.

2. Material and methods

2.1. Subjects

Experimental subjects were two male macaque monkeys (*Macaca fascicularis*), aged of 12 years and referred to as monkey C (7.5 kg) and monkey D (8.4 kg). The monkeys lived within the same social group, in an enriched environment with indoor residence and outdoor compound. They were maintained on a diet of fresh fruit, vegetables, and monkey chow with water available ad libitum. The monkeys were familiar with the behavioral setup but they had not been trained on any behavioral task, except brief fixation on flashed light spots during eye tracker calibration (De Luna et al., 2014). They had never encountered the stimuli in the laboratory or in their home-cage. To perform good quality gaze tracking, monkey's head movements were non-invasively restrained using a helmet made of thermoplastic material (Uni-frame Thermoplastics MTAPUI2232, Civco Medical Solutions), that was manually shaped to achieve a comfortable fit for each animal (De Luna et al., 2014; Machado and Nelson, 2011). All experimental procedures and protocols were in fully compliance with Swiss and European Union animal experimental regulations and approved by the Fribourg cantonal veterinary authorities.