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4	Japanese monkeys (Macaca fuscata) quickly detect snakes but not spiders: Evolutionary origins of
5	fear-relevant animals
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1 Running head: EVOLUTIONARY ORIGINS OF THREAT ANIMALS

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Abstract

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21 Humans quickly detect the presence of evolutionary threats through visual perception. Many 22 theorists have considered humans to be predisposed to respond to both snakes and spiders as 23 evolutionarily fear-relevant stimuli. Evidence supports that human adults, children, and 24 snake-naive monkeys all detect pictures of snakes among pictures of flowers more quickly than 25 vice versa, but recent neurophysiological and behavioural studies suggest that spiders may, in fact, 26 be processed similarly to non-threat animals. The evidence of quick detection and rapid fear 27learning by primates is limited to snakes, and no such evidence exists for spiders, suggesting 28 qualitative differences between fear of snakes and fear of spiders. Here, we show that snake-naive 29 Japanese monkeys detect a single snake picture among eight non-threat animal pictures (koala) 30 more quickly than vice versa; however, no such difference in detection was observed between 31 spiders and pleasant animals. These robust differences between snakes and spiders are the most 32 convincing evidence that the primate visual system is predisposed to pay attention to snakes but 33 not spiders. These findings suggest that attentional bias toward snakes has an evolutionary basis 34 but that bias toward spiders is more due to top-down, conceptually driven effects of emotion on 35 attention capture.

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Key words: macaque monkeys; snakes; spiders; evolutionarily fear-relevant animals; Snake
Detection Theory

39 Many anthropologists, neuroscientists, and psychologists have long considered both snakes 40 and spiders to be innate fear-relevant stimuli for humans (Öhman & Mineka, 2001; 2003). Humans form associations between pictures of snakes or spiders and electric shocks more 41 42 strongly than between pictures of guns or knives and shocks, despite the fact that, in modern 43 environments, guns and knives are more dangerous than snakes and spiders. Öhman and Mineka 44 (2001) postulated that humans are evolutionarily predisposed to process ancestrally fear-relevant 45 stimuli. This fear module hypothesis is also consistent with evidence that humans find pictures of 46 evolutionarily fear-relevant stimuli more quickly than those of neutral stimuli in visual search 47tasks. Öhman, Flykt, and Esteves (2001) demonstrated that adult humans more quickly detect a 48 deviant snake (or spider) picture in a complex array of neutral distracter stimuli (e.g. pictures of 49 flowers or mushrooms) than vice versa. In line with the evolutionary view (Öhman & Mineka, 50 2001; 2003), young children with relatively little prior exposure to snakes or their representations 51also react faster when identifying snakes than flowers (Hayakawa, Kawai, & Masataka, 2011; 52 LoBue & DeLoache, 2008; Masataka, Hayakawa, & Kawai, 2010), which suggests that prior 53 experience with snakes may not play a major role in enhanced human sensitivity (LoBue & 54 Rakison, 2013). These empirical studies suggest that evolution equipped our ancestors with a 55 readiness to easily associate fear with recurrent threats and with a visual system predisposed to 56 quickly detect dangerous animals (Öhman & Mineka, 2001; 2003; Shibasaki & Kawai, 2009). 57 Other researchers, however, have suggested that individuals may quickly learn to fear these 58 animals through observations, stories, and/or myths in the early stages of life (LoBue, Rakison, & 59 DeLoache, 2010).

The most convincing evidence for an evolved fear module comes from studies with macaque
 monkeys. For instance, Shibasaki and Kawai (2009) demonstrated that snake-naïve macaque
 monkeys (*Macaca fuscata*) more quickly identify a deviant snake picture among an array of

63 flower pictures than vice versa. Despite the fact that monkeys in this study were reared in 64 captivity and had never been exposed to real or toy snakes, these monkeys reacted to snake 65 pictures vigorously. Le et al. (2013) recorded the neural activity of the medial and dorsolateral 66 pulvinar from macaques' brains during exposure to four sets of pictures: snakes, angry monkey 67 faces, monkey hands, and geometric shapes. They found neurons that responded more rapidly and more strongly to snakes than to the other three stimuli, suggesting a neural mechanism for rapid 68 69 visual detection of snakes. In accordance with laboratory studies, many observations from a wide 70 variety of primate species in the wild have reported fear reactions to snakes (Bartecki & Heymann, 711987; Boinski, 1988; Seyfarth, Cheney, & Marler, 1980).

72 Nevertheless, it remains unclear whether spiders hold a special status in human and primate 73 perception. Although the fear module hypothesis suggests that both snakes and spiders may be 74prototypical evolutionarily threat-relevant stimuli (Öhman & Mineka, 2001), recent studies have 75 questioned whether spiders are processed preattentively in human visual perception. Studies with 76 visual search tasks have revealed a larger threat-detection advantage for snakes than for spiders 77 (Öhman, Soares, Juth, Lindstrom, & Esteves, 2012; Shibasaki & Kawai, 2011). Although human 78 adults have been shown to quickly detect deviant spider pictures among an array of mushroom 79 pictures, this attention bias disappeared when the deviant spider pictures were embedded among 80 animal pictures (LoBue, 2010; see also Öhman et al., 2012; Shibasaki & Kawai, 2011). Electroencephalogram studies using early posterior negativity (EPN), which reflects the early 81 82 selective visual processing of emotionally significant information, also suggest that the degree of 83 EPN for spider pictures was smaller than that for snake pictures and not different from 84 fear-irrelevant animals (He, Kubo, & Kawai, 2014). 85 It should be noted that, among non-human primates, quick detection (Shibasaki & Kawai,

86 2009) and vicarious fear learning (Cook & Mineka, 1990) are limited to snakes, and no such

evidence exists for spiders. Despite consistent results showing attentional bias toward snakes by
humans and non-human primates, the inconsistent data for spider detection suggests there may be
a difference between fear of snakes and fear of spiders (He, Kubo, & Kawai, 2014; Soares,
Esteves, Lundqvist, & Öhman, 2009). Empirical evidence is consistent with the Snake Detection
Theory (SDT) (Isbell, 2006), which proposes that the need to detect dangerous snakes provided
strong evolutionary pressure that resulted in the origin of primates via expansion of the visual
sense.

No studies have yet investigated whether monkeys more quickly detect a deviant picture of spiders among pictures of non-threatening animals. In this study, we compared reaction times for detecting deviant pictures of snakes and spiders in the background of non-threatening animal pictures (koala) as in a previous study of human adults (Shibasaki & Kawai, 2011). Based on the SDT (Isbell, 2006), we predicted that quicker detection would be observed only for snake pictures and not for spider pictures.

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Method

Subjects. Three female Japanese monkeys participated in this study. They were aged 3 years ('Pero' and 'Ume') and 5 years ('Shiba'). All were born in social groups and raised until the age of 3 at the Primate Research Institute of Kyoto University. They were then housed individually in cages with ad libitum water access. Daily food requirements (biscuits and vegetables) were delivered after each experimental session. All procedures were approved by the ethics committee of the Primate Research Institute of Kyoto University and were in accordance with the Guide for the Care and Use of Laboratory Primates.

Apparatus. The experimental tasks were performed in an operant box (700 mm × 610 mm ×
 700 mm) with acrylic panel walls (Shibasaki & Kawai, 2009). A 15-inch touch-sensitive LCD

screen was mounted on one side of the experimental box. A universal food dispenser was placedon the experimental box to provide a piece of food reward.

Stimuli. Two different kinds of visual stimuli were used in Experiment 1: grey scale images of nine snakes and nine koalas in naturalistic situations. The size of each picture was 320×240 pixels, and all were matched for luminance (Figure 1a, b). The images of snakes were replaced by nine images of spiders in Experiment 2 (Figure 1c). The size and averaged luminance of each stimulus were the same as in Experiment 1.

117 *Procedure*. The three monkeys performed a visual search task. The monkeys were already 118 experienced in the visual search task with conspecific faces (Kawai, Kubo, Masataka, & 119 Hayakawa, submitted). The basic procedure was similar to previous studies using visual search 120 tasks with pictures of snakes (Shibasaki & Kawai, 2009). The monkey initiated a trial by touching 121 a grey rectangle (i.e. start key) at the centre of the monitor. This rectangle disappeared, and after 3 122 s, a nine-picture matrix appeared. The monkey was required to touch the one deviant picture (e.g. 123 the fear-relevant animal) on the touch-sensitive monitor from among eight pictures of a different 124 category (e.g. fear-irrelevant animal) to receive a reward. Pictures were presented as a 125 nine-picture matrix in blocks of either fear-relevant or fear-irrelevant targets. A block consisted of 126 72 trials comprising a quasi-random sequence, altered each day. The criterion was set at a 127 performance rate of more than 95% in three consecutive blocks for each target condition. After 128 each monkey reached the target accuracy, data were collected for six consecutive days (a total of 129 432 trials per subject).

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Results

132Experiment 1: Snakes versus Koalas. Incorrect responses were classified as errors and 133 excluded from the following analyses. The percentages of errors were 0.5% (Shiba), 2.8% (Pero), 134 and 0.5% (Ume). Figure 2 illustrates the median reaction times (RTs) for detecting the deviant 135 pictures by the three monkeys. The RTs for detecting deviant pictures of snakes were less than 136 those for detecting deviant pictures of koalas (Mann-Whitney U tests: Shiba, U = 19341.0, Z =137 3.07, p = .002, r = .17, 95% CI [1054.1, 1129.5]; Pero, U = 19933.0, Z = 2.62, p = .009, r = .23, 138 95% CI [785.7, 855.3]; Ume, U = 17873.0, Z = 4.20, p < .001, r = .15, 95% CI [1109.5, 1269.7]). 139 Experiment 2: Spiders versus Koalas. The percentages of errors were 0.9% (Shiba), 1.9% 140 (Pero), and 0.4% (Ume). The median latencies for detecting deviant pictures of spiders did not 141 differ from those for detecting deviant pictures of koalas (Shiba, U = 22309.5, Z = 0.785, p = .432, r = .04, 95% CI [1069.6, 1141.3]; Pero, U = 22292.5, Z = 0.798, p = .425, r = .02, 95% CI [911.9, 142 143 1029.3]; Ume, U = 22824.5, Z = 0.39, p = .697, r = .04, 95% CI [1075.2, 1155.0]). 144 Across the two experiments, the RTs were significantly less for snake-target matrices than for 145 spider-target matrices for all three monkeys (Mann-Whitney U tests: Shiba, U = 20654.5, Z = 2.06, p = .039, r = .11, 95% CI [1029.8, 1092.7]; Pero, U = 15349.0, Z = 6.15, p < .001, r = .34, 95% CI 146 [851.7, 967.1]; Ume, U = 20037.5, Z = 2.54, p = .011, r = .14, 95% CI [1049.2, 1182.1]). The RTs 147148 for identifying deviant koala pictures in the two experiments, however, did not differ for Shiba (U149= 22821.0, Z = 0.39, p = .696, r = .02, 95% CI [1094.8, 1177.2]) and Ume (U = 22420.5, Z = 0.70, Z = 0p = .484, r = .04, 95% CI [1129.0, 1249.1]). For Pero, however, the RTs for identifying koala 150 151targets was less among pictures of snakes than those among pictures of spiders (U = 20151.0, Z =1522.45, p = .014, r = .14, 95% CI [844.0, 919.6]).

Discussion

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154The present study clearly demonstrates that macaque monkeys detect deviant pictures of 155snakes among distracting koala pictures faster than vice versa. This result is consistent with 156 previous work showing that macaque monkeys detect a deviant picture of snakes among flower 157 pictures faster than vice versa (Shibasaki & Kawai, 2009). In the present study, however, we 158 demonstrated for the first time that macaque monkeys found snake pictures more quickly even 159 when the deviant snake pictures were surrounded by pictures of fear-irrelevant animals (koalas). 160 This result is consistent with a previous study of young children using a similar visual search task (LoBue & DeLoache, 2008). This result is also consistent with previous studies that reported how 161 162 monkeys respond to snakes (Mineka, Keir, & Price, 1980). Macaque monkeys are predisposed to learn by observation to fear snakes (Cook & Mineka, 1990). Macaques can also assess the level of 163 164 threat by the snakes' postures (Etting & Isbell, 2014). These studies suggest that monkeys are 165 specifically sensitive to snakes, providing strong support for the SDT.

166 Most importantly, however, the same macaque monkeys did not show a search advantage for 167 spiders among fear-irrelevant animals, suggesting that spiders are not evolutionarily relevant 168 threat stimuli. This pattern of results is partly consistent with a study by LoBue (2010), which 169 showed that attentional bias toward spiders by human adults was not observed when a target 170 picture of spiders was embedded in pictures of non-threatening animals. It is unknown whether 171 monkeys can quickly find the target pictures of spiders embedded in pictures of mushrooms. If 172monkeys detect spider pictures efficiently among mushroom pictures, it does not mean that 173 spiders are evolutionarily fear-relevant animals, because pictures of fear-irrelevant animals were 174also quickly found among flower or mushroom pictures by humans (Lipp, Derakshan, Waters, & 175Logies, 2004). These results do not support the notion that spiders are processed pre-attentively in visual systems. Soares et al. (2009) compared spider- and snake-fearful human participants using 176 177 a visual search task. Although spider-fearful participants more quickly detected their feared

178 stimuli (spiders) against a background of fruit pictures than fear-relevant but non-feared stimuli 179 (snakes), there was no significant difference between the detection latencies of the feared stimuli 180 (snakes) and the fear-relevant but non-feared animal stimuli (spiders) for participants fearful of 181 snakes. The authors' interpretation of these results was that the detection of snakes is more 182 dependent on bottom-up, stimulus-driven processes, whereas the detection of spiders seems to be 183 less dependent on attentional efficiency, is highly selective in fearful participants, and is therefore 184 based on top-down, conceptually driven processes. Supporting the results of these visual search 185 tasks (Shibasaki & Kawai, 2011), Van Strien et al. (2014) have also shown that the degree of EPN 186 was the largest for snake pictures, intermediate for spider pictures, and the smallest for bird 187 pictures, and subjective spider fear was associated with EPN amplitude for spider pictures, whereas snake fear was not associated with EPN amplitude for snake pictures (see also He et al., 188 189 2014).

In the present study, the RTs of the three monkeys varied. They were, however, relatively
stable for each monkey. In two monkeys, reaction times to the koala targets did not differ across
the experiments. The RTs for snake pictures were less than those for spider and koala pictures for
the three monkeys. The RTs did not differ between spider targets and koala targets. In other words,
monkeys were selectively sensitive to snakes and not to spiders and koalas.

A field study in Senegal, West Africa, reported that primatologists encountered venomous snakes frequently (McGrew, 2015). In contrast, only about 0.1% of all spider species (30,000) are dangerous to humans, and many venomous species live hidden and scarcely come in contact with humans (Cartwright, 2001; Schmidt, 1985). To our best knowledge, there have been no reports of primates being afraid of spiders in the wild. Not only have there been no reports of non-human primates being afraid of spiders, but also several taxa perceive them as food. Cheirogaleidae, Callitrichidae, Cebidae, and Cercopithecidae are all reported to eat spiders (see Ullrey, 1986).

202	Therefore, primates do not seem to be predisposed to fear spiders predominantly. If primates have
203	a visual sensitivity to spiders, it is likely restricted to human primates and, thus, would be more
204	evolutionarily recent than the sensitivity to snakes (New & German, 2015). Our results suggest
205	that spider fears may be limited to humans and may be acquired through learning.

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Figure Captions

- *Figure 1*. Stimuli used in the experiments. The koala target is presented among snake distracters (a)
- and among spider distracters (c). The snake target is presented among koala distracters (b).
- 285 Figure 2. Median reaction times for locating discrepant target picture among distracter pictures. The
- 286 horizontal bars represent significant differences.