

# UC Davis

## UC Davis Previously Published Works

### Title

The influence of image salience on the artistic renditions of cave lions in the early Upper Paleolithic

### Permalink

<https://escholarship.org/uc/item/9zc4h4nz>

### ISBN

ISBN 978-3-030-46190-4

### Author

Coss, Richard G.

### Publication Date

2020-12-19

Peer reviewed

# The Influence of Image Saliency on the Artistic Renditions of Cave Lions in the Early Upper Paleolithic



Richard G. Coss

The heuristic aim in this chapter is evaluating the neurobiological and behavioral evidence suggesting that humans retain ecologically relevant elements of felid-predator recognition shaped by natural selection that could influence the portrayals of large-bodied cats in prehistoric art. Emphasis will be given to identifying the salient visual properties of extinct cave lions (*Panthera spelaea*) that likely influenced the anatomical accuracy of their renditions in cave drawings and mobiliary figurines in the early Upper Paleolithic of Europe.

Visual-image saliency emerges primarily from the ecological context in which it is perceived. Such distinctiveness requires the perception of difference between the target of visual fixation and the surrounding features (cf. Nothdurft, 2007; Simons, 2000). This figure-background contrast applies to both the lowest level of neural organization and the highest level of perceptual organization that shapes the interaction of the organism with its environment. However, perceptual contrast alone does not account for why some images “pop out” from background settings. When viewed from the perspective of perceivers, image saliency can be magnified by its meaningfulness in a particular setting that can reflect innate perceptual properties coupled with a history of prior exposure of its predictive properties in ecologically relevant circumstances. I will explore this conceptual framework of perceived context as I develop my argument for how salient visual features of dangerous felids influenced visual imagery, working memory, and artistic expression.

---

R. G. Coss (✉)  
University of California, Davis, Davis, CA, USA  
e-mail: [rgcoss@ucdavis.edu](mailto:rgcoss@ucdavis.edu)

## 1 The Implications of Innate Face Recognition and Contextual Assessment

Human neonates exhibit the innate ability to recognize schematic faces at close viewing distances shortly after birth (Goren, Sarty, & Wu, 1975; Jirari, 1970), indicating a “predetermined epigenesis” (see Gottlieb, 1973, p. 9) of functioning subcortical neural pathways directing visual attention. Subcortical face perception was inferred initially because the infant’s visual cortex is undeveloped at birth (Johnson, 2005; Johnson, Senju, & Tomalski, 2015). Human infants do exhibit a sparse pattern of synapses in visual cortex at 8 months of age, followed by synaptic overproduction by 500 days of age with slow pruning until age 11 years (Huttenlocher & Dabholkar, 1997, p. 170). Even with low synaptic density in visual cortex, infants are still capable of discriminating fearful faces at 7 months of age, an ability suggestive of subcortical facilitation (Peltola, Leppänen, Palokangas, & Hietanen, 2008). While the sparsely connected visual and temporal cortices might play a role in recognition processes, the most likely neurological source for face perception by newborn infants is visual input via the retinotectal pathway to the superficial layer of the superior colliculus (SC) (Rafal et al., 2015). Electrophysiological recordings have found that SC neurons in Japanese macaques (*Macaca fuscata*) respond to high-contrast face-like patterns including two-facing eyes (see Fig. 6A in Nguyen et al., 2014).

Visual-image stability is critical for pattern recognition. As recorded electrophysiologically in rhesus macaques (*M. mulatta*), stable visual images are perceived because the SC alerts the cortical frontal eye field that saccadic eye movements are about to occur, a process guided by the SC’s intermediate layer projecting to the cortical frontal eye field via the mediodorsal thalamus (Sommer & Wurtz, 2004, 2006). Functional maturation of this subcortical visual pathway for face recognition occurs prior to birth several weeks after fetal eye opening. During clinical evaluations, preterm infants have exhibited distress when looking at a human face (discussed in Coss & Goldthwaite, 1995). More specifically, research using upright and inverted triangular arrays of three light-emitting diodes placed on the mother’s abdomen recorded reliably greater fetal head orientation toward the upright face-like array of lights (Reid et al., 2017).

The superior colliculus is considered an essential neural structure for innate object recognition in early development (Sewards & Sewards, 2002). In fish, birds, and reptiles, the evolutionary homologue of the superior colliculus is the optic tectum, a phylogenetically ancient structure for regulating visual attention and action (Tamietto & de Gelder, 2010). Research on tectally dominant species, such as fish and birds, has shown that face-like patterns with two conspicuous eyes can be provocative and engender caution or rapid defensive behavior (reviewed by Coss & Goldthwaite, 1995).

While the superior colliculus plays a role in low-frequency (softly blurred) face perception, the higher level of cortical visual-pattern integration occurs within the occipitotemporal network. Electrophysiological recordings and functional magnetic

resonance imaging of the anterior portion (TE) of the inferotemporal cortex (IT) of macaques have revealed a mosaic of nonadjacent “face patches” that contribute to distinguishing faces with different orientations and non-face objects (Freiwald & Tsao, 2010; Moeller, Freiwald, & Tsao, 2008). Freiwald and Tsao (2010) suggest that the face-processing system “interdigitates with representations for other objects implementing the same three view stages” (p. 6). Rather than identifying specific faces, single neurons within face patches appear to use a coordinate system to measure facial structure for feature integration, a process likely applicable to non-face objects throughout the IT (Chang & Tsao, 2017). Similar to patches at a much smaller anatomical scale, clusters of axon terminals are evident in macaque IT in which pyramidal cells in layers 2 and 3 radiate collateral axons horizontally that terminate on layer 5 cells in nonadjacent neural columns (Fujita & Fujita, 1996). Humans also exhibit face patches in the fusiform gyrus that is anatomically equivalent to the macaque TE (Tsao, Moeller, & Freiwald, 2008).

While single-unit recordings of neurons in macaque TE face areas show broad tuning to schematic face-like patterns (Minami, Tamura, Fujita, & Tanaka, 1995; Tanaka, 1996), they also respond to photographs of unique macaque and human faces (Perrett, Rolls, & Caan, 1982). The human fusiform face area also responds similarly to faces in a manner that appears to be “genetically specified” (Kanwisher, 2010, p. 11165). Nevertheless, this ability to generalize to a variety of faces provides the neurological scaffold for observational learning of specific faces, and other familiar objects with face-like properties, such as automobile headlights and grills (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). Two examples relevant to my ensuing discussion of felid saliency were the maximum responses of a macaque TE neuron to a drawing of a striped cat and horizontal and vertical gratings and another neuron’s responses to a cat’s striped hind leg and a stripe-like vertical grating (Tanaka, Saito, Fukada, & Moriya, 1991; Tanaka, 2003, p. 91).

While the aforementioned processes of face perception by nonhuman primates would be essential for detecting the faces of partially concealed predators predominantly from the salient aspects of two-facing eyes (cf. Coss & Goldthwaite, 1995; Coss, Ramakrishnan, & Schank, 2005), there are complementary neurological processes that integrate the features of non-face patterns into recognizable *gestalts*. TE neurons can fire selectively to presentations of two-dimensional contours; but, more importantly, large numbers will fire to texture characteristics engendering three-dimensional selectivity for curved surfaces (Janssen, Vogels, Liu, & Orban, 2001). For example, texture-sensitive cells in macaque TE can respond to a single bar, multiple stripes, and dot patterns that could define a three-dimensional surface feature. Furthermore, cohesive bar-like contours can emerge from moving dot patterns, a process originating in early visual areas V1, V2, and V3 (Peterhans, Heider, & Baumann, 2005). In intermediate visual cortex, V4 cells respond to illusory figure-ground borders produced by groups of dots moving slowly in opposite directions (Roe et al., 2012) and arrays of dots moving unidirectionally that might reflect gradients of vertical shading of surface textures (Hanazawa & Komatsu, 2001).

## 2 Contextual Figure-Ground Segmentation

The response specificity of downstream TE neurons to specific shapes and their response generalization to similar-appearing shapes is important for understanding how objects embedded in larger, complex background images are recognized. One technique for examining this phenomenon in humans involves rapid presentations of natural scenes with embedded target images and the recording of event-related potentials with task-specific behavioral measures. Rousselet, Fabre-Thorpe, and Thorpe (2002) reported that one to two objects (animal/non-animal) presented to human subjects briefly (20 ms) in complex photographs of natural images could be identified without the need for focal attention.

In humans, natural-scene perception includes participation of the parahippocampal gyrus that evaluates peripheral spatial areas (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013) in a manner that could evaluate the contextual assessment of danger, notably the position of the body relative to immediately perceived and previously known refuge. For ancestral humans in natural settings, covert (non-foveal) attention would be very useful for the rapid detection of a single dangerous target in the peripheral field of view, such as a lurking felid predator. Evaluation of the spatial layout of the microhabitat by the parahippocampal place area, a subregion of the parahippocampal gyrus, is crucial for integrating the properties of objects and faces processed by the fusiform face area (Kanwisher, 2010).

From the perspective of neural-circuitry operations in the fusiform gyrus integrating contours, textures, and colors, a recognizable shape without a background pattern has limited meaningfulness to the perceiver until the meaningfulness of its background pattern is evaluated as a top-down process. For example, Bar et al. (2006) presented familiar objects followed briefly by an intermixture with other objects. To record rapid brain activity, magnetoencephalography (MEG) and behavioral tasks were employed, the results of which identified a downstream prefrontal site in the orbitofrontal cortex that facilitated top-down object recognition via contextual associations. In complex images with embedded targets, pattern recognition within the fusiform gyrus is integrated with scene-selective processing by the adjacent parahippocampal gyrus in the medial temporal lobe (Nasr et al., 2011). Related research into the contextual associations of objects and their spatial properties revealed a major contribution of the posterior region of the parahippocampal cortex (Bar, 2009; Mullally & Maguire, 2011), the retrosplenial complex, and the medial prefrontal cortex (Kveraga et al., 2011; Panichello, Cheung, & Bar, 2013). In particular, neural activity measured by MEG showed that the visual cortex, parahippocampal cortex, and retrosplenial complex was phase locked early during contextual processing of pictures of objects with later phase locking of the retrosplenial complex and the medial prefrontal cortex. Early phase locking was also evident for the visual cortex and orbitofrontal cortex followed by phase locking of the fusiform cortex and orbitofrontal cortex (Kveraga et al., 2011). Together, these findings support the argument that contextual information about object meaningfulness is extracted early during object recognition. In natural settings, the visual

saliency of a recognized object juxtaposed with background images emerges as a contextual relationship, both of which are subject to the effects of natural selection on perception and action. The next section focuses on the sources of natural selection shaping the visual saliency of felids and the significance of contextual association with appropriate defensive action patterns by prey.

### 3 Sources of Natural Selection Promoting Felid Recognition

For innate predator recognition to emerge in the evolutionary time frame, prey species need to have experienced a long history in which predators and the microhabitats in which they were encountered were perceived and acted upon consistently. As emphasized above, the neural underpinnings of face recognition can generalize face-processing operations to encompass similar visual schemata. Such face-generalization ability can thus be coopted by natural selection to share some of the same facets of neural organization, thus facilitating how selection from predation filters out failure to recognize predators in specific contexts. In shared perceptual processing, the ancient schema of two-facing eyes can metaphorically anchor surrounding facial structure for heterospecific face recognition. Like primates that rely on stereoscopy for distance estimation, felid predators have forward-facing eyes permitting three-dimensional judgments of prey distances for launching attacks. When monitoring prey from cover, their two eyes are generally exposed to view. Because of the long history of prey detecting predators based on this facing eye schema, a number of ambushing and coursing carnivores have evolved obliterative camouflage, such as vertical eye bars, horizontal masks, and facial patches that reduce the distinctiveness of two-facing eyes. Felids in particular have evolved short vertical bars above the eyes coupled with dark eyelids and white patches below the eyes (Ortolani, 1999, p. 454), and some felids have dark vertical stripes on their cheeks aligned with the upper eye bars that, as subjective contours, transect the inner elliptical edges of the two eyes. In other felids, the numerous flecks and spots near the eyes probably act as blending camouflage reducing eye-schema detection (see Mottram, 1915, 1916). At the larger scale of body coat patterns, such blending camouflage consists of spots, rosettes, and stripes (Allen, Cuthill, Scott-Samuel, & Baddeley, 2011) that interrupt the continuity of felid-body outline, a process also complemented by obliterative shading in which a darker back and lighter ventral pelage optically flatten felid cylindrical appearance generated by sunlight and shadow (Cott, 1941; Jarős, 2012).

The oldest fossil record of leopards (*P. pardus*) migrating from Africa to Europe is dated at circa 900 ka (1000 years ago) (Sala, 1990) whereas genetic-distance analyses suggest that leopards migrated further into southern and eastern Asia more recently, between 300–170 ka (Uphyrkina et al., 2001). Nonetheless, leopard-like rosettes appear to be the ancestral condition shared phylogenetically with lions and jaguars (Werdelin & Olsson, 1997) and were likely displayed by the primitive jaguar (*P. aff. gombaszoegensis*) that inhabited South Asia ~2 Ma (million years ago)

(Hemmer, 1976). As such, it is reasonable to argue that South Asian primates and ungulates had a much longer history of exposure to the rosette coat-pattern of this felid predator before the arrival of leopards.

Because of their consistent daytime appearance to prey engendering successful evasive behavior, the rosettes on the coats of leopards that putatively evolved as blending camouflage in dappled light now appear to be a salient predator-recognition cue for several species of primate and ungulate prey, such as muntjac deer (*Muntiacus reevesi*), sambar deer (*Cervus unicolor*), and chital deer (*Axis axis*) in South Asia (Ramakrishnan & Coss, 2000; Yahner, 1980). In addition, the yellowish background color for the rosette coat-pattern enhances leopard detection by macaques because their neurons in early vision are sensitive to yellowish hues (see Yoshioka & Dow, 1996; Yoshioka, Dow, & Vautin, 1996). To reduce detection, leopards have adopted the strategy of stealthy daytime and nighttime hunting (Isbell, Bidner, Van Cleave, Matsumoto-Oda, & Crofoot, 2018; Zuberbühler & Jenny, 2002).

For wild bonnet macaques (*M. radiata*) foraging on the ground in southern India, the sudden appearance of a leopard model can elicit fast (200–300 ms) flight-reaction times and similar reaction times for leopard-naïve monkeys on a park-like university campus in Bangalore city (Coss & Ramakrishnan, 2000). Moreover, the exposed forequarters and facing head of this leopard model partially concealed by vegetation engendered a much greater flight to trees than exposure of this model's hindquarters. These monkeys responded even less to presentations of the forequarters and facing head of a dark-leopard model without rosettes representing the dark melanistic morph, and were totally unresponsive to its dark hindquarters (Coss et al., 2005).

In a related study, Schel and Zuberbühler (2009) also found that leopard-naïve Guereza monkeys (*Colobus guereza*) in Uganda reacted promptly when they detected the back of a leopard-like model with conspicuous rosettes moving below them. Similarly in captivity, leopard-naïve sooty mangabeys (*Cercocebus atys*), pig-tail macaques (*M. nemestrina*), and rhesus macaques exhibited vigorous alarm calling to a leopard model derived from the model presented to wild bonnet macaques (Davis, Parr, & Gouzoules, 2006). Together, these studies of monkeys from field sites in Africa and India where leopards are absent along with inexperienced captive monkeys suggest that leopard recognition is mediated by innate perceptual processes.

Outside of heterospecific face-generalization that might promote leopard recognition, what is the likelihood that human ancestors experienced historical felid predation with the intensity of Old World monkeys that engendered leopard recognition? This question is relevant to the central premise of whether evolved perceptual processes for recognizing felid predators influence their artistic renditions. A review of the temporal coincidence of felid and hominin fossils in the same and nearby fossil assemblages clearly suggests the potential for predator–prey interactions.

During the Early Miocene epoch, widely distributed African barbourfelid cats (Morales & Pickford, 2018) would have been capable of taking large-bodied hominoids. The advent of bipedality in the Late Miocene of Africa would have permitted early hominins to forage well beyond the immediate refuge of trees (Richmond,

Begun, & Strait, 2001, p. 98). The earliest occurrence, circa 7 Ma, of the dirk-toothed cat, *Megantereon*, co-occurs with a larger *Machairodus* sp. in a fossil assemblage in Chad (Peigné et al., 2005; de Bonis et al., 2010, p. 225) not far from the fossil site of the oldest putative member of the hominid clade, and possible biped, *Sahelanthropus tchadensis* (Brunet et al., 2005; Zollikofer et al., 2005). With a jaguar-like morphology and presumed prey immobilization ability, *Megantereon* is thought to have been an ambush hunter that engaged in carcass dragging (Arribas & Palmqvist, 1999); albeit its short tail (Christiansen, 2013) is not indicative of arboreal hunting. Nevertheless, such felid agility might have posed considerable danger to early hominins not unlike that of ambushing leopards that hunt vervets, baboons, macaques, and larger langurs and chimpanzees (Boesch, 1991; Busse, 1980; Cowlshaw, 1994; Isbell et al., 2018; Ramakrishnan, Coss, & Pelkey, 1999). Emergency bipedal flight behavior with rapid assessment of potential refuge has arguably provided the most consistent context for selection to act on successful predator avoidance. It is reasonable to suggest that *Megantereon* provided one of the longest time frames of felid predation on hominins (Lee-Thorp, Thackeray, & van der Merwe, 2000) prior to its extinction during the Early Pleistocene (Treves & Palmqvist, 2007; Turner & Antón, 1998; Werdelin & Lewis, 2005).

Although tooth marks (punctures and pitting) on fossil bones are suggestive of predation, they also characterize scavenging activity, so interpretations of hominin predation by felids that are flesh specialists should be viewed cautiously. In the approximately 6 Ma fossil beds in the Rift Valley, Kenya, the femora of *Orrorin tugenensis*, another basal member of the hominin clade considered to be an habitual biped (Pickford, Senut, Gommery, & Treil, 2002; Richmond & Jungers, 2008), exhibits gnawing damage and tooth marks suggestive of possible predation by a leopard-sized felid that appears in the same fossil assemblage (Gommery, Pickford, & Senut, 2007; Pickford & Senut, 2001). About 2 Ma later, another habitually bipedal hominin, *Australopithecus anamensis*, is evident in northern Kenya (Haile-Selassie, Melillo, Vazzana, Benazzi, & Ryan, 2019; Ward, Leakey, & Walker, 1999) with a small percentage of the bone assemblage showing carnivore damage (Drapeau et al., 2014). Clearly, the shift from being a facultative biped and tree climber to a highly derived obligate biped by 3.6 Ma (Raichlen, Gordon, Harcourt-Smith, Foster, & Haas Jr., 2010) followed by a long period of stasis (Haile-Selassie et al., 2010) would have enhanced successful running to arboreal refuge from large-bodied felids.

The earliest felid (*P. aff. Gombaszoegensis* or *P. palaeosinensis*) resembling modern lions (*P. leo*) and a smaller, more definitive leopard (cf. *P. pardus*) appear in Laetoli, Kenya, about 3.6 Ma (Barry, 1987). True lions first appear in East Africa 1.8–1.9 Ma (Werdelin & Lewis, 2005) consistent with the appearance of *Homo erectus* whose highly mobile groups would have probably procured meat from partly consumed carcasses (Lewis, 1997). Successful competition with lions for scavenging kills would possibly include harassment with stone throwing and counteractive lion actions where *H. erectus* would be endangered and need to engage in evasive antipredator behavior (Willems & van Schaik, 2017). In South Africa, leopards would pose significant threats to hominins, especially at night (de Ruiter & Berger, 2000). Moreover, the accumulation of hominin fossil deposits in caves is



strongly suggestive of leopard predation (Brain, 1970, 1981). Leopards can drag large carcasses to caves so they are the most likely predator for the collection of hominin bones rather than alternative felid predators, such as *Megantereon* or the false saber-tooth felid, *Dinofelis* (de Ruiter & Berger, 2000).

During the Plio-Pleistocene, there is suggestive evidence that early *Homo* was already equipped with sufficient technology for ambush hunting 1.8 Ma (Bunn & Gurtov, 2014), thereby potentially changing the dynamics of competitive interactions with lions. Nevertheless, lions and leopards would have likely constituted the greatest predatory threat to hominins until the Middle Pleistocene when *H. erectus* would have employed both effective defensive and harassing tactics to dissuade lions and hyenas during confrontational scavenging at kill sites. With the advent of hand-delivered spears ~500 ka with hafted stone points (cf. Johnson & McBrearty, 2010; Shea & Sisk, 2010; Wilkins & Chazan, 2012; Wilkins, Schoville, Brown, & Chazan, 2012), competitive scavenging by late *H. erectus* and archaic humans would become exceedingly dangerous for lions. This technological development would begin to change the context of natural selection on this predator–prey interaction when humans as competitors changed into dangerous adversaries (see O’Connell, Hawkes, & Jones, 1988, p. 357). As a result, one can envision that daytime predation on human ancestors by leopards and lions slowly transformed into nocturnal situations where, most recently, predation occurs in small groups and while sleeping (cf. Corbett, 1947; Packer et al., 2019; Packer, Swanson, Ikanda, & Kushnir, 2011).

Lion predation on hominins led to lion infection by *Helicobacter pylori*, an old Gram-negative stomach bacterium in the human lineage. This bacterial jump from early humans to lions is estimated, based on a synonymous genetic distance, to have occurred maximally within the past 400k years (Eppinger et al., 2006). Despite occasional predation currently, the long period of dangerous interactions with humans has engendered considerable caution of humans on foot by African lions evidenced by lions fleeing from Maasai pedestrians (Packer & Clottes, 2000) and when Bushmen hunter–gatherers and herders chased away lions easily with commanding voices (Bauer & de Iongh, 2005; Thompson, 2003, p. 73).

#### 4 Effects of Prolonged Relaxed Selection on Felid Saliency

The proposed daytime shift in lion-predation threat to nighttime circumstances would initiate the onset of prolonged relaxed natural selection on the lion component of felid-predator recognition. Since the aforementioned neurological properties of pattern recognition affect rapid and meaningfully defensive behavior, relaxed selection might uncouple some facets of felid recognition and defensive behavior; that is, relaxed selection engendering genetic drift might weaken interneural connectivity between recognition processes and action coordination. For example in laboratory recreations of the historical context of snake–predator encounters, California ground squirrels (*Otospermophilus beecheyi*) living in snake-absent and

snake-rare habitats maintain innate recognition of their former rattlesnake and gopher snake predators for an estimated time frame of 300k years of relaxed selection; albeit, their defensive behavior is less coordinated (Coss, 1991a; Coss, 1999; Coss & Biardi, 1997). Neural systems are generally protected from disintegration under relaxed selection if they have multiple functions still under selection or their pattern of organization involves shared developmental pathways (Coss, 1999, p. 200; Lahti et al., 2009; Lehmann, Strauß, & Lakes-Harlan, 2007, p. 542; Moczek et al., 2011, p. 2710).

Outside of generalized face recognition processes still under selection in humans, if felid shape and coat patterns are also recognized innately, as documented in some monkeys, then the time frame for their complete disintegration under prolonged relaxed selection would likely span several million years. Such evolutionary persistence would reflect the much slower mutation rate in humans based on their estimated generation time of 29 years compared with 1–2 years in ground squirrels (cf. Coss & Goldthwaite, 1995; Langergraber et al., 2012, p. 15717). The persistence of defensive behavioral relicts under prolonged relaxed selection from felid predation, which includes higher-order cognition about habitat refuge (Coss & Moore, 2002), is also indicative of the historical consistency of successful evasive action in specific situations. Retention of rapid refuge assessment as a behavioral relict under relaxed selection does not appear to be costly and the neural processes for its expression might, like some aspects of predator recognition, be buffered from rapid disintegration due to their shared functionality in related situations (Blumstein, 2006; Coss, 1999; Lahti et al., 2009).

In modern humans, running from an attacking lion (see Patterson, 1907) powered by the uniquely large gluteus maximus muscles (Bartlett, Sumner, Ellis, & Kram, 2014, p. 130) is still adaptive. Similarly adaptive, emergency tree climbing is also reported when lions are encountered unexpectedly and there are several anecdotal cases on the web of incidences of tree climbing under predatory threat. Simulated climbing by preschool children of tree silhouettes using their fingers showed that young children without tree-climbing experience continued to recognize the historical utility of low weight-bearing branches by choosing refuge closer to the crown edges to feel safe from a lion (Coss & Moore, 2002). Follow-up research on preschool children using realistic leopard and deer models in a playground simulation of antipredator behavior provided further evidence of a sophisticated understanding of how a predatory threat could be monitored safely from a distance or from cover (Coss & Penkunas, 2016). Although conducted in truly safe contexts, these studies of preschool children are consistent with evidence observed in other species that innate antipredator behavior like that of face recognition can appear early in the developing brain (Coss, 1991a, 1991b).

The summarizing point of this discussion relevant to artistic behavior is that, unlike natural encounters with felids, representations of large-bodied felids in paintings and sculptures can be considered as simulations viewed in safe situations. Nevertheless, the viewing of dangerous felids in movies, photographs, and illustrative art works might still evoke preconscious echoes of ancient patterns of evasive behavior. Similarly, the earliest artistic depictions of felids by Upper Paleolithic

artists might have engendered mnemonic reminders of their threatening capabilities. The next section evaluates experimental evidence for the perceptual aspects of felid salience presented in safe laboratory settings.

## 5 Experimental Studies of Human Responses to Lion Images

Inspired by a Darwinian perspective of threat assessment, there is a growing literature on human responses to viewing dangerous animals, mostly using photographs of snakes and spiders known to engender phobic responses (see LoBue, Matthews, Harvey, & Stark, 2014). The experimental protocols used in these studies resemble those employed for face perception and typically evaluate subjective attitudes, viewer reaction times, and physiological measures (e.g., Berdica, Gerdes, Pittig, & Alpers, 2014). Controlled presentations of animal images in laboratory settings can provide information on the specific perceptual properties of these animals that attract attention and influence rapid decision making, including aesthetic preferences (cf. Blanchette, 2006; Landova et al., 2018).

Our initial research on children and adults employed multiple presentations of natural scenes to examine their ability to detect standing and reclining lion targets in arrays of eight randomly arranged antelope as distractors and vice versa using a visual-search protocol and touch-screen computer display (Penkunas & Coss, 2013a). We were particularly interested in determining whether the patterns of lion detection during childhood were also present in adulthood. Both American children and adults detected target lions in arrays of antelope distractors more quickly than target antelope in arrays of lion distractors, the results of which might reflect an evolutionary influence on threat assessment (Penkunas & Coss, 2013a). However, there were numerous opportunities for children to learn about lion dangerousness in books, movies, and on television, so a second study compared children living in a forested area of southern India inhabited by tigers and leopards with children from the nearby predator-free city of Bangalore. We found similarly faster reaction times for lion-target detection in arrays of antelope in both urban and rural children (Penkunas & Coss, 2013b) consistent with our initial study of American children. A follow-up study of adults employed eye tracking to measure the speed of detecting standing lions and impala (*Aepyceros melampus*) in natural scenes and found similarly higher attention-catching properties for lions (Yorzinski, Penkunas, Platt, & Coss, 2014).

While these studies of children and adults suggest that lions pop out from visual arrays of antelope, they did not reveal what features of lions were salient. Eye tracking was employed again using the same visual-array methodology, comparing standing lion targets with lion distractors and impala targets with impala distractors that were either facing or facing away. Both facing lion and impala targets were detected faster than when these target animals were facing away, although the latency to detect facing lion targets was faster than that of facing impala targets (Yorzinski, Tovar, & Coss, 2018). The standing posture of lions might be one

critical cue for assessing lion dangerousness so eye tracking was employed again to compare standing lions with reclining lions and standing impala with reclining impala. Counter to our predictions, we found that the standing postures of both species facilitated target detection (Yorzinski & Coss, 2019). Together, these studies of visual search for lions in natural scenes revealed that lions are relatively salient when they are compared directly with other nonthreatening species that are less relevant ecologically to perceivers. Not surprisingly, differences in body configurations, such as head orientation and body posture, are less distinguishable during visual search for targets in visual arrays of the same species; that is, the efficiency of visual search is hampered when these defining features are part of the visual schemata engendering species recognition and participants have adopted a “feature search mode” (see Folk & Remington, 2006, p. 463). Target-image saliency, however, still depends on the contextual relationship of these targets and distractors; for example, target snakes and spiders presented with threat-irrelevant distractors are not necessarily detected faster than technological threats, such as guns, knives, and syringes presented in arrays of threat-irrelevant distractors (cf. Blanchette, 2006; Fox, Griggs, & Mouchlianitis, 2007). It appears from these picture studies of biological and technological threats that the relevance of the image to perceivers is more important for guiding target detection than its historical importance from an evolutionary perspective.

Another approach to studying felid saliency is to consider that some innate behaviors with cognitive components are expressed early in human development prior to their obvious adaptive utility. Precocity of innate behavior results from the early installment of specific patterns of interneural connectivity on newly formed neurons with only initial dendritic branch outgrowth that resist the remodeling that occurs during “experience-dependent” dendritic growth and connectivity later in development (see Black & Greenough, 1986). Such innate precocity is quite apparent for California ground squirrel pups that can visually recognize their gopher snake predator and engage in adult-like antisnake behavior the first day they use vision for guiding locomotion (Coss, 1991a). Similar behavioral precocity is evident in nursing age infants that, on their hands and knees, mouth shiny plates as if drinking from a water hole at a much older age (Coss, Ruff, & Simms, 2003).

The important aspect of studying the precocious expression of recognition systems in young children is that it can reveal the adaptive defensive behavior of adult ancestors (Coss & Goldthwaite, 1995, p. 126) and might provide insight on the visual cues used to recognize ancestral predators or other dangerous species (for snake perception by infants, see Bertels, Bayard, Floccia, & Destrebecqz, 2018). For example, 7–15 month-old infants and toddlers in day-care playroom settings engaged in more exploratory poking of yellowish plastic jars displaying python scales and leopard rosettes compared with yellowish plaid and plain jars prior to picking them up (see Coss, 2003, p. 113). The saliency of leopard rosettes outside the context of observing leopards was examined further in adults using eye tracking (Shabbir, Zon, & Thuppil, 2018). These researchers found that small images of target people wearing clothing with leopard, floral, and camouflage prints were detected reliably faster in photographs of a crowded airport terminal than targets wearing nonpatterned shiny and plain clothing.

## 6 Cave Lion Portrayals in the Early Upper Paleolithic

This final section evaluates how image salience influences artistic expression. One method of measuring how salient images promote long-term memory and the generation of visual imagery is to evaluate the realism of human artifacts. I will emphasize the degree of morphological accuracy of early Upper Paleolithic drawings and figurines of European cave lions by Aurignacian artists.

The study of visual-image salience on the ability to recall various items from memory is an important area of memory research and highly imageable items are thought to be recalled most easily (e.g., Fletcher et al., 1995), especially if they are rated highly as pleasant or unpleasant (Bywater, Andrade, & Turpin, 2004). Based on brain-imaging studies, the parietal and frontal cortices appear to play an important role in the production of mental images (Ishai, Ungerleider, & Haxby, 2000), with the underlying long-term memory for its expression organized spatially by the topographical properties of area V1 in early vision (Pearson, Naselaris, Holmes, & Kosslyn, 2015). When the eyes are closed, the formation of mental images can activate the cortical frontal eye field regulating eye movement (Winlove et al., 2018) as if the mental images are being scanned overtly. Along with activation of the precuneus in the posterior-medial parietal region, the subjective vividness of mental imagery is also correlated positively with increased activation of the fusiform gyrus, posterior cingulate gyrus, parahippocampal gyrus and the retrosplenial cortex (Fulford et al., 2018). Both the parahippocampal gyrus, and retrosplenial cortex respond to landmark features relevant to mental-image vividness and contextual assessment (see Auger, Mullally, & Maguire, 2012; Mullally & Maguire, 2011). It thus appears from this brain-imaging research that mental images are evaluated by attentional processes almost as if they were real visual images (Amedi, Malach, & Pascual-Leone, 2005).

There are several aspects of artistic creation that need to be addressed in my discussion of the relationship of mental imagery and artistic production. I have argued previously (Coss, 2017, p. 26) that European Neanderthals (*H. neanderthalensis*) were not deficient in generating mental imagery useful for hunting, but they lacked the neurological ability of anatomically modern *H. sapiens* (AMH) to translate this imagery from working memory into drawing recognizable images. Neanderthals were capable of generating nonfigurative geometric images as evident from the red scalariform (ladder-like) image on the wall of La Pasiega cave, Spain, dated at ~65 ka (Hoffmann et al., 2018; Hoffmann et al., 2018; but see dating critique by Aubert, Brumm, & Huntley, 2018) and the multilined crisscross engraved on the floor of Gorham's Cave, Gibraltar, dated ~39 ka (Rodríguez-Vidal et al., 2014). Currently, the closest approximation to figural art by Neanderthals is relevant to my discussion of felid salience. A natural flint block roughly resembling a feline face caught the attention of Neanderthals at La Roche-Cotard, France ~76 ka (Marquet, Lorblanchet, Oberlin, Thamo-Bozso, & Aubry, 2016). Its coincidental cat-like appearance was enhanced further by deliberately removing flakes to flatten



**Fig. 1** Left: Natural flint stone reworked by Neanderthals to enhance its face-like appearance. Dimensions: 98–93 mm height, 105 mm width, with a 74 mm long bone sliver, dated at circa 76 ka. Photograph by Jean-Claude Marquet. Right: Female African lion, Kenya (Photograph by Richard Coss, 2013)

the head and define the nose and by inserting a bone splinter through a hole joining its illusory eye sockets (Fig. 1).

Unlike Neanderthals, AMH engaged in both abstract and realistic parietal depictions of animals and therianthrope representations (recognizable admixtures of humans and other species useful for shamanistic purposes, cf. Jolly, 2002; Leihitu & Permana, 2019). Abstract figural art in the Upper Paleolithic can reflect an undeveloped drawing ability that results in child-like renditions (Coss, 1968, p. 282). Distortion can also be deliberate “socio-sexual signalism” (Sütterlin, 2003, p. 153) as seems evident for the ~35 ka female figurine excavated at Hohle Fels Cave in southwestern Germany (Conard, 2009). For Southeast Asian rock art, a mildly distorted painting of a babirusa “deer-pig” (*Babyrusa* sp.) on Sulawesi, Indonesia, dated ~35 ka is among the earliest AMH recognizable animal depictions (Aubert et al., 2014). More relevant to the issue of felid saliency, an African example of a Late Stone Age therianthrope was discovered in the Apollo 11 rockshelter in southern Namibia consisting of a painted stone slab depicting the silhouette of a feline head and body adorned with oryx-like horns, ungulate forelegs, and human hind legs (Vogelsang et al., 2010, p. 195). These early examples of AMH art complement other realistic examples in which mental-image vividness likely played a role in artistic expression.

There are different situations in which Aurignacian hunter-gatherers would have acquired vivid episodic memories of cave lions behaving in nature as well as close-up inspections of cave-lion carcasses that were exploited systematically. Osteological evidence of cave-lion exploitation from the Aurignacian and Gravettian periods of

the Swabian Jura in southwestern Germany spanning around 40–27 ka indicates that Aurignacians focused on acquiring meat, possibly skins, and canines as hand-tool retouchers of blades (Kitagawa, Krönneck, Conard, & Münzel, 2012).

Prior to the arrival of the Aurignacians to Central Europe ~40 ka using the Danube corridor (Conard & Bolus, 2008, p. 894; Conard, 2011; Higham et al., 2012), it is unlikely that Neanderthals who favored thrusting spears for close-range hunting (Schmitt, Churchill, & Hylander, 2003) engaged in intense carcass competition with cave lions. Cave lions were formidable predators and their prey preferences varied among individuals as inferred from isotopic signatures of bone collagen that differed from cave hyenas, suggesting some competitive exclusion of prey species (Bocherens et al., 2011; Camarós, Münzel, Cueto, Rivals, & Conard, 2016). In the aforementioned context of African-lion timidity to humans on foot, cave lions might have been much less intimidated by human presence, and thus posed a great danger to unwary hunters. Habituation to human activity is known to embolden some large-bodied felids, such as pumas (*Puma concolor*) exposed initially to humans during the very late Pleistocene of North America (Coss, Fitzhugh, Schmid-Holmes, Kenyon, & Etling, 2009). The ancestors of cave lions diverged from African lions prior to 600 ka (cf. Argant & Brugal, 2017; Burger et al., 2004), precluding their experiencing the increased dangerousness of carcass competition with archaic and modern humans in Africa.

Perhaps due to the visually provocative qualities of cave lions, the Aurignacians in the Swabian Jura created multiple ivory figurines of them as mobiliary art discarded in domestic spaces (Mendoza Straffon, 2014). A small figurine from Vogelherd cave in the Lone Valley shows a cave lion in a stalking posture with incised lines on its shoulders and outstretched neck (Fig. 2). These repetitive lines might characterize the piloerection of thick, wavy cave-lion hair to illustrate its highly aroused state of attention directed at prey. In support of this premise of thick hair, a small reddish bundle of wavy cave-lion hair with thick underfur was recovered from frozen Pleistocene sediment in Russia (Chernova et al., 2016; Kirillova et al., 2015). Another less realistic Vogelherd figurine of a stalking cave lion shows a series of crosshatched lines along its back also suggestive of piloerected hair (see Fig. 16-4 in Hussain & Floss, 2015, p. 109). It must be noted in this context, that piloerection of angry African lions is depicted as bristled hair in more contemporary San rock-paintings in South Africa (Hollmann, 2002).

There are several worthwhile speculations about the cultural function of these figurines based on other cultures. Since these figurines would likely attract attention because of their ecological significance to group members, one could envision an apotropaic function in which these figurines were carried about for protection from cave lions, other people, or imaginary agents in the believed spirit world (see Hussain & Floss, 2015). Such an apotropaic function would be analogous to the shiny amulets worn in the Middle East and South Asia to ward off the malignant “evil eye” (see Coss, 1981; Woodburne, 1981). Other plausible functions include using them as props for animated storytelling about cave-lion behavior (Piprani, 2011; Porr, 2010) and other forms of cultural transmission perhaps assisted by



**Fig. 2** Top: Young female lion stalking zebras in the Ngorongoro Crater, Tanzania. Photograph by Richard Coss, 2013. Bottom: Aurignacian ivory figurine of a cave lion from Vogelherd cave, Swabian Jura. Dimensions: Length 68 mm, height 24 mm, breadth 14.5 mm, dated at circa 32 ka. Museum der Universität Tübingen (Photograph by Don Hitchcock, 2015). Note the stalking posture with outstretched neck and incised lines on the neck and shoulder blades that could represent piloerection of thick hair. The engraved pits likely portray a coat pattern of rosettes

rituals conducted under altered states of consciousness (Lewis-Williams & Clottes, 1998).

Mammoth ivory is a medium-hard material that makes detailed carving and engraving difficult with the prismatic blade technology common in Aurignacian sites. Achrati (2012) proposes that mammoth ivory was softened prior to carving by possibly soaking it in water, urine, or digestive rumen fluids from the stomach contents of herbivorous game. With this ivory softening technique in mind, an example of a finely detailed cave-lion head from Vogelherd (Fig. 3) shows the prominent cheetah-like cheek stripe that caught the attention of Aurignacian artists and cross-hatching that, again, might represent thickly matted hair. Bristling of hair is not depicted explicitly in the charcoal drawings of the 75 cave lions appearing in Chauvet cave in Vallon-Pont-d'Arc, Ardèche, France that, according to Clottes and Azéma (2005), represent more than 60% of the lions portrayed in European Upper





**Fig. 3** Ivory carving of a cave-lion head from Vogelherd cave that was originally part of a complete figurine. The cheek stripe is prominently engraved and the crosshatched pattern could represent thick hair with a wavy down. Dimensions: Length 25 mm, height 18 mm, breadth 6 mm. Copyright: Landesmuseum Württemberg, Hendrik Zwietausch

Paleolithic art. There are marked differences in the quality of these cave-lion drawings (Packer & Clottes, 2000) that could reflect individual differences in autobiographical mental imagery (Bergmann, Genç, Kohler, Singer, & Pearson, 2016; Cui, Jeter, Yang, Montague, & Eagleman, 2007; Greenberg & Knowlton, 2014) and the ability to translate these images into well-delineated drawings (De Pisapia, Bacci, Parrott, & Melcher, 2016; Ellamil, Dobson, Beeman, & Christoff, 2012).

Many of the cave-lion drawings in Chauvet cave are depicted with their heads extended as if inspecting potential prey that are drawn alongside them. The prominent cheek stripe is frequently delineated in these charcoal drawings (Fig. 4) which, considering a possible cultural link between Aurignacians occupying Chauvet cave and those in the Swabian Jura spanning 35–30 ka (Igarashi & Floss, 2019), strongly supports the argument that cheek stripes were a prominent facial feature of cave lions. The facial pattern of short bars above the eyes that merge with the cheek stripes via the inner eyelids (Fig. 4) is indubitably ancient in felids, as inferred from its variable presence in cat-like viverrids and prionodontids whose stem ancestor diverged from felids ~30 Ma based on a mitochondrial phylogeny (see Paijmans et al., 2017, p. 3332). If indeed present on Late Miocene felid predators, such as *Megantereon*, natural selection on hominin assessment of predatory threats might have added these salient facial stripes to the already provocative facing eyes to facilitate detection of partially occluded felids waiting to ambush from cover.

**Fig. 4** Top: Asiatic lion (*Panthera leo persica*) from the Gir forest Sanctuary, India. Photograph by Hiren Khambhayata. Bottom: Two charcoal drawings of cave lions in the Gallery of Lions, Chauvet Cave, from the 2011 film *Cave of Forgotten Dreams* (Werner Herzog, director). Note the whitish lower eyelid and short bar above the left eye of this Asiatic lion that extends into the cheek stripe and the similarity of this facial pattern with the cave-lion drawings



## 7 Conclusion

The saliency of cave lion facial markings and stalking body postures is suggested by their depiction in the charcoal drawings of cave lions in Chauvet cave and the small ivory figurines from Vogelherd cave made by Aurignacian hunter-gatherers in the early Upper Paleolithic of Europe. The prominence of these cave-lion features in artistic renditions might reflect their provocative qualities that enhanced mental-image vividness and the anatomical accuracy of these renditions. The evolved ability to recognize face-like schemata is present in human neonates and likely provides the neurological scaffolding for the generalization of human-face perception to other species, including felid predators. During hominin evolution, natural selection acting on successful assessment of felid-predator dangerousness might have capitalized on the adaptive utility of this face-generalization process. On the whole, the renditions of cave lions in Chauvet cave illustrate their prominent cheek stripes,

eye-lid coloration, ear positions, and in some cases, their stalking postures shown by their lowered profiles with extended heads, elevated shoulder blades, and upright ears. Other anatomical details on some of the small cave-lion figurines from the Swabian Jura in southwestern Germany include engraved pitting of the ivory suggestive of a coat pattern of rosettes similar to that of young African lions. Serrated lines and crisscrossing on the backs of these stalking figurines could well connote the piloerection of thick hair of highly aroused lions. Together, these artistic renditions of cave lions recreate the formidable appearance of an extinct adversary of Upper Paleolithic humans with a prominent, but unknowable, social significance.

## References

- Achrati, A. (2012). How the ice in the ice age led to the rise of sculptures. *L'art pléistocène dans le monde*, Tarascon-Sur-Ariège, septembre 2010 – Symposium: Datation et taphonomie de l'art pléistocène. [https://blogs.univ-tlse2.fr/palethnologie/wp-content/files/2013/fr-FR/version-longue/articles/DAT2\\_Achrati.pdf](https://blogs.univ-tlse2.fr/palethnologie/wp-content/files/2013/fr-FR/version-longue/articles/DAT2_Achrati.pdf)
- Allen, W. L., Cuthill, I. C., Scott-Samuel, N. E., & Baddeley, R. (2011). Why the leopard got its spots: Relating pattern development to ecology in felids. *Proceedings of the Royal Society B*, 278, 1373–1380. <https://doi.org/10.1098/rspb.2010.1734>
- Amedi, A., Malach, R., & Pascual-Leone, A. (2005). Negative BOLD differentiates visual imagery and perception. *Neuron*, 4(5), 859–872. <https://doi.org/10.1016/j.neuron.2005.10.032>
- Argant, A., & Brugal, J. P. (2017). The cave lion *Panthera (Leo) spelaea* and its evolution: *Panthera spelaea intermedia* nov. subspecies. *Acta Zoologica Cracoviensia*, 60(2), 59–104. [https://doi.org/10.3409/azc.60\\_2.59](https://doi.org/10.3409/azc.60_2.59)
- Arribas, A., & Palmqvist, P. (1999). On the ecological connection between sabre-tooths and hominids: Faunal dispersal events in the lower Pleistocene and a review of the evidence for the first human arrival in Europe. *Journal of Archaeological Science*, 26, 571–585. <https://doi.org/10.1006/jasc.1998.0346>
- Aubert, M., Brumm, A., Ramli, M., Sutikna, T., Saptomo, E. W., Hakim, B., ... Dosseto, A. (2014). Pleistocene cave art from Sulawesi, Indonesia. *Nature*, 514, 223–227. <https://www.nature.com/articles/nature13422>
- Aubert, M., Brumm, A., & Huntley, J. (2018). Early dates for 'Neanderthal cave art' may be wrong. *Journal of Human Evolution*, 125, 215–217. <https://doi.org/10.1016/j.jhevol.2018.08.004>
- Auger, S. D., Mullally, S. L., & Maguire, E. A. (2012). Retrosplenial cortex codes for permanent landmarks. *PLoS One*, 7, e43620. <https://doi.org/10.1371/journal.pone.0043620>
- Bar, M. (2009). The proactive brain: Memory for predictions. *Philosophical Transactions of the Royal Society B*, 364, 1235–1243. <https://doi.org/10.1098/rstb.2008.0310>
- Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., ... Hämäläinen, M. S. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the United States of America*, 103(2), 449–454. <https://doi.org/10.1073/pnas.0507062103>
- Barry, J. C. (1987). Large carnivores (*Canidae*, *Hyaenidae*, *Felidae*) from Laetoli. In M. D. Leakey & J. M. Harris (Eds.), *Laetoli: A Pliocene site in northern Tanzania* (pp. 235–258). Oxford, England: Clarendon.
- Bartlett, J. L., Sumner, B., Ellis, R. G., & Kram, R. (2014). Activity and functions of the human gluteal muscles in walking, running, sprinting, and climbing. *American Journal of Physical Anthropology*, 153, 124–131. <https://doi.org/10.1002/ajpa.22419>

- Bauer, H., & de Iongh, H. H. (2005). Lion (*Panthera leo*) home ranges and livestock conflicts in Waza National Park, Cameroon. *African Journal of Ecology*, 43, 208–214. <https://doi.org/10.1111/j.1365-2028.2005.00570.x>
- Berdica, E., Gerdes, A. B. M., Pittig, A., & Alpers, G. W. (2014). Inhibition of return in fear of spiders: Discrepant eye movement and reaction time data. *Journal of Ophthalmology*, 2014, Article ID: 183924. <https://doi.org/10.1155/2014/183924>
- Bergmann, J., Genç, E., Kohler, A., Singer, W., & Pearson, J. (2016). Neural anatomy of primary visual cortex limits visual working memory. *Cerebral Cortex*, 26(1), 43–50. <https://doi.org/10.1093/cercor/bhu168>
- Bertels, J., Bayard, C., Floccia, C., & Destrebecqz, A. (2018). Rapid detection of snakes modulates spatial orienting in infancy. *International Journal of Behavioral Development*, 42(4), 381–387. <https://doi.org/10.1177/0165025417693955>
- Black, J. E., & Greenough, W. T. (1986). Induction of pattern in neural structure by experience: Implications for cognitive development. In B. Rogoff, M. E. Lamb, & A. L. Brown (Eds.), *Advances in developmental psychology* (Vol. 4, pp. 1–50). New York, NY: Lawrence Erlbaum Associates.
- Blanchette, I. (2006). Snakes, spiders, guns, and syringes: How specific are evolutionary constraints on the detection of threatening stimuli? *The Quarterly Journal of Experimental Psychology*, 59(8), 1484–1504. <https://doi.org/10.1080/02724980543000204>
- Blumstein, D. T. (2006). The multipredator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology*, 112(3), 209–217. <https://doi.org/10.1111/j.1439-0310.2006.01209.x>
- Bocherens, H., Drucker, D. G., Bonjean, D., Bridault, A., Conard, N. J., Cupillard, C., ... Ziegler, R. (2011). Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in North-Western Europe: Prey choice, competition and implications for extinction. *Quaternary International*, 245, 249–261. <https://doi.org/10.1016/j.quaint.2011.02.023>
- Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, 117(3–4), 220–242. <https://www.jstor.org/stable/4534940>
- Brain, C. K. (1970). New finds at the Swartkrans australopithecine site. *Nature*, 225, 1112–1119. <https://www.nature.com/articles/2251112a0>
- Brain, C. K. (1981). *The hunters or the hunted? An introduction to African cave taphonomy*. Chicago, IL: University of Chicago Press.
- Brunet, M., Guy, F., Pilbeam, D., Lieberman, D. E., Likius, A., Mackaye, H. T., ... Vignaud, P. (2005). New material of the earliest hominid from the upper Miocene of Chad. *Nature*, 434, 752–755. <https://www.nature.com/articles/nature03392>
- Bunn, H. T., & Gurtov, A. N. (2014). Prey mortality profiles indicate that early Pleistocene *homo* at Olduvai was an ambush predator. *Quaternary International*, 322–323, 44–53. <https://doi.org/10.1016/j.quaint.2013.11.002>
- Burger, J., Rosendahl, W., Loreille, O., Hemmer, H., Eriksson, T., Götherström, A., ... Alt, K. W. (2004). Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Molecular Phylogenetics and Evolution*, 30, 841–849. <https://doi.org/10.1016/j.ympev.2003.07.020>
- Busse, C. (1980). Leopard and lion predation upon chacma baboons living in the Moremi wildlife reserve. *Botswana Notes and Records*, 12, 15–21. <https://www.jstor.org/stable/40980790>
- Bywater, M., Andrade, J., & Turpin, G. (2004). Determinants of the vividness of visual imagery: The effects of delayed recall, stimulus affect and individual differences. *Memory*, 12(4), 479–488. <https://doi.org/10.1080/09658210444000160>
- Camarós, E., Münzel, S. C., Cueto, M., Rivals, F., & Conard, N. J. (2016). The evolution of Paleolithic hominin-carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *Journal of Archaeological Science: Reports*, 6, 798–809. <https://doi.org/10.1016/j.jasrep.2015.11.010>
- Chang, L., & Tsao, D. Y. (2017). The code for facial identity in the primate brain. *Cell*, 169(6), 1013–1028. <https://doi.org/10.1016/j.cell.2017.05.011>
- Chernova, O. F., Kirillova, I. V., Shapiro, B., Shidlovskiy, F. K., Soares, A. E. R., Vevchenko, V. A., & Bertuch, F. (2016). Morphological and genetic identification and isotopic study of the hair of

- a cave lion (*Panthera spelaea* Goldfuss, 1810) from the Malyi Anyui River (Chukotka, Russia). *Quaternary Science Reviews*, 142, 61–73. <https://doi.org/10.1016/j.quascirev.2016.04.018>
- Christiansen, P. (2013). Phylogeny of the sabertoothed felids (Carnivora: Felidae: Machairodontinae). *Cladistics*, 29(5), 543–559. <https://doi.org/10.1111/cla.12008>
- Clottes, J., & Azéma, M. (2005). Les images de félins de la Grotte Chauvet. *Bulletin de la Société Préhistorique Française*, 102(1), 173–182. <https://doi.org/10.3406/bspf.2005.13349>
- Conard, N. J. (2009). A female figurine from the basal Aurignacian of Hohle Fels cave in southwestern Germany. *Nature*, 459, 248–252. <https://doi.org/10.1038/nature07995>
- Conard, N. J. (2011). The demise of the Neanderthal cultural niche and the beginning of the upper Paleolithic in southwestern Germany. In N. J. Conard & J. Richter (Eds.), *Neanderthal lifeways, subsistence and technology* (pp. 223–240). New York, NY: Springer. [https://doi.org/10.1007/978-94-007-0415-2\\_19](https://doi.org/10.1007/978-94-007-0415-2_19)
- Conard, N. J., & Bolus, M. (2008). Radiocarbon dating the late middle Paleolithic and the Aurignacian of the Swabian Jura. *Journal of Human Evolution*, 55(5), 886–897. <https://doi.org/10.1016/j.jhevol.2008.08.006>
- Corbett, J. E. (1947). *The man-eating leopard of Rudraprayag*. New York, NY: Oxford University Press.
- Coss, R. G. (1968). The ethological command in art. *Leonardo*, 1(3), 273–287. <https://doi.org/10.2307/1571871>
- Coss, R. G. (1981). Reflections on the evil eye. In A. Dundes (Ed.), *The evil eye* (pp. 181–191). New York, NY: Garland Publishing.
- Coss, R. G. (1991a). Context and animal behavior III: The relationship between early development and evolutionary persistence of ground squirrel antisnake behavior. *Ecological Psychology*, 3(4), 277–315. [https://doi.org/10.1207/s15326969eco0304\\_1](https://doi.org/10.1207/s15326969eco0304_1)
- Coss, R. G. (1991b). Evolutionary persistence of memory-like processes. *Concepts in Neuroscience*, 2(2), 129–168.
- Coss, R. G. (1999). Effects of relaxed natural selection on the evolution of behavior. In S. A. Foster & J. A. Endler (Eds.), *Geographic variation in behavior: Perspectives on evolutionary mechanisms* (pp. 180–208). Oxford, England: Oxford University Press.
- Coss, R. G. (2003). The role of evolved perceptual biases in art and design. In E. Voland & K. Grammer (Eds.), *Evolutionary aesthetics* (pp. 69–130). Heidelberg, Germany: Springer.
- Coss, R. G. (2017). Drawings of representational images by Upper Paleolithic humans and their absence in Neanderthals reflect historical differences in hunting wary game. *Evolutionary Studies in Imaginative Culture*, 1(2), 15–38. <https://doi.org/10.26613/esic/1.2.46>
- Coss, R. G., & Biardi, J. E. (1997). Individual variation in the antisnake behavior of California ground squirrels (*Spermophilus beecheyi*). *Journal of Mammalogy*, 79(2), 294–310. <https://doi.org/10.2307/1382883>
- Coss, R. G., Fitzhugh, E. L., Schmid-Holmes, S., Kenyon, M. W., & Etling, K. (2009). The effects of human age, group composition, and behavior on the likelihood of being injured by attacking pumas. *Anthrozoös*, 22(1), 77–87. <https://doi.org/10.2752/175303708X390491>
- Coss, R. G., & Goldthwaite, R. O. (1995). The persistence of old designs for perception. In N. S. Thompson (Ed.), *Perspectives in ethology, 11: Behavioral design* (pp. 83–148). New York, NY: Plenum.
- Coss, R. G., & Moore, M. (2002). Precocious knowledge of trees as antipredator refuge in preschool children: An examination of aesthetics, attributive judgments and relic sexual dimorphism. *Ecological Psychology*, 14(4), 181–222. [https://doi.org/10.1207/S15326969ECO1404\\_1](https://doi.org/10.1207/S15326969ECO1404_1)
- Coss, R. G., & Penkunas, M. J. (2016). Sex difference in choice of concealed or exposed refuge sites by preschool children viewing a model leopard in a playground simulation of antipredator behavior. *International Journal of Psychological Research*, 9(2), 8–19. <https://doi.org/10.21500/20112084.2325>
- Coss, R. G., & Ramakrishnan, U. (2000). Perceptual aspects of leopard recognition by wild bonnet macaques (*Macaca radiata*). *Behaviour*, 137, 315–335. <https://www.jstor.org/stable/4535708>

- Coss, R. G., Ramakrishnan, U., & Schank, J. (2005). Recognition of partially concealed leopards by wild bonnet macaques (*Macaca radiata*): The role of the spotted coat. *Behavioural Processes*, 68(2), 145–163. <https://doi.org/10.1016/j.beproc.2004.12.004>
- Coss, R. G., Ruff, S., & Simms, T. (2003). All that glistens: II. The effects of reflective surface finishes on the mouthing activity of infants and toddlers. *Ecological Psychology*, 15(3), 197–213. [https://doi.org/10.1207/S15326969ECO1503\\_1](https://doi.org/10.1207/S15326969ECO1503_1)
- Cott, H. B. (1941). *Adaptive coloration in mammals*. New York, NY: Oxford University Press.
- Cowlishaw, G. (1994). Vulnerability to predation in baboon populations. *Behaviour*, 131(3–4), 293–304. <https://www.jstor.org/stable/4535243>
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: Individual variability can be measured objectively. *Vision Research*, 47(4), 474–478. <https://doi.org/10.1016/j.visres.2006.11.013>
- Davis, J. E., Parr, L., & Gouzoules, H. (2006). Response to naturalistic fear stimuli in captive Old World monkeys. *Annals of the New York Academy of Sciences*, 1000(1), 91–93. <https://doi.org/10.1196/annals.1280.019>
- De Bonis, L., Peigné, S., Mackaye, H. T., Likius, A., Vignaud, P., & Brunet, M. (2010). New sabre-toothed cats in the late Miocene of Toros Menalla (Chad). *Comptes Rendus Palevol*, 9(5), 221–227. <https://doi.org/10.1016/j.crpv.2010.07.018>
- De Pisapia, N., Bacci, F., Parrott, D., & Melcher, D. (2016). Brain networks for visual creativity: A functional connectivity study of planning a visual artwork. *Scientific Reports*, 6, 39185. <https://doi.org/10.1038/srep39185>
- De Ruiter, D., & Berger, L. R. (2000). Leopards as taphonomic agents in dolomitic caves—Implications for bone accumulations in the hominid-bearing deposits of South Africa. *Journal of Archaeological Science*, 27(8), 665–684. <https://doi.org/10.1006/jasc.1999.0470>
- Drapeau, M. S. M., Bobe, R., Wynn, J. G., Campisano, C. J., Dumouchel, L., & Geraads, D. (2014). The Omo Mursi formation: A window into the east African Pliocene. *Journal of Human Evolution*, 75, 64–79. <https://doi.org/10.1016/j.jhevol.2014.07.001>
- Ellamil, M., Dobson, C., Beeman, M., & Christoff, K. (2012). Evaluative and generative modes of thought during the creative process. *NeuroImage*, 59(2), 1783–1794. <https://doi.org/10.1016/j.neuroimage.2011.08.008>
- Eppinger, M., Baar, C., Linz, B., Raddatz, G., Lanz, C., Keller, H., ... Schuster, S. C. (2006). Who ate whom? Adaptive *Helicobacter* genomic changes that accompanied a host jump from early humans to large felines. *PLoS Genetics*, 2(7), 1097–1110. <https://doi.org/10.1371/journal.pgen.0020120>
- Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). The mind's eye—precuneus activation in memory-related imagery. *NeuroImage*, 2(3), 195–200. <https://doi.org/10.1006/nimg.1995.1025>
- Folk, C. L., & Remington, R. (2006). Top-down modulation of preattentive processing: Testing the recovery account of contingent capture. *Visual Cognition*, 14(4–8), 445–465. <https://doi.org/10.1080/13506280500193545>
- Fox, E., Griggs, L., & Mouchlianitis, E. (2007). The detection of fear-relevant stimuli: Are guns noticed as quickly as snakes? *Emotion*, 7(4), 691–696. <https://doi.org/10.1037/1528-3542.7.4.691>
- Freiwald, W. A., & Tsao, D. Y. (2010). Functional compartmentalization and viewpoint generalization within the macaque face-processing system. *Science*, 330(6005), 845–851. <https://doi.org/10.1126/science.1194908>
- Fujita, I., & Fujita, T. (1996). Intrinsic connections in the macaque inferior temporal cortex. *Journal of Comparative Neurology*, 368(4), 467–486. [https://doi.org/10.1002/\(SICI\)1096-9861\(19960513\)368:4<467::AID-CNE1>3.0.CO;2-2](https://doi.org/10.1002/(SICI)1096-9861(19960513)368:4<467::AID-CNE1>3.0.CO;2-2)
- Fulford, J., Milton, F., Salas, D., Smith, A., Simler, A., Winlove, C., & Zeman, A. (2018). The neural correlates of visual imagery vividness—an fMRI study and literature review. *Cortex*, 105, 26–40. <https://doi.org/10.1016/j.cortex.2017.09.014>
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, 3(2), 191–197. [https://www.nature.com/articles/nn0200\\_191](https://www.nature.com/articles/nn0200_191)

- Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform ‘face area’ increases with expertise in recognizing novel objects. *Nature Neuroscience*, 2(6), 568–573. [https://www.nature.com/articles/nn0699\\_568](https://www.nature.com/articles/nn0699_568)
- Gommery, D., Pickford, M., & Senut, B. (2007). A case of carnivore-inflicted damage to a fossil femur from Swartkrans, comparable to that of a hominid femur representing *Orrorin tugenensis*, BAR 1003/00 (Kenya). *Annals of the Transvaal Museum*, 44(1), 215–218. <https://hdl.handle.net/10520/EJC83650>
- Goren, C. C., Sarty, M., & Wu, P. Y. K. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, 56(4), 544–549. <https://pediatrics.aappublications.org/content/56/4/544.short>
- Gottlieb, G. (1973). Introduction to behavioral embryology. *Studies on the Development of Behavior and the Nervous System*, 1, 3–45. <https://doi.org/10.1016/B978-0-12-609301-8.50007-6>
- Greenberg, D. L., & Knowlton, B. J. (2014). The role of visual imagery in autobiographical memory. *Memory & Cognition*, 42(6), 922–934. <https://doi.org/10.3758/s13421-014-0402-5>
- Hanazawa, A., & Komatsu, H. (2001). Influence of the direction of elemental luminance gradients on the responses of V4 cells to textured surfaces. *The Journal of Neuroscience*, 21(12), 4490–4497. <https://doi.org/10.1523/JNEUROSCI.21-12-04490.2001>
- Haile-Selassie, Y., Latimer, B. M., Alene, M., Deino, A. L., Gibert, L., Melillo, S. M., ... Lovejoy, C. O. (2010). An early *Australopithecus afarensis* postcranium from Woranso-mille, Ethiopia. *Proceedings of the National Academy of Sciences of the United States of America*, 107(27), 12121–12126. <https://doi.org/10.1073/pnas.1004527107>
- Haile-Selassie, Y., Melillo, S. M., Vazzana, A., Benazzi, S., & Ryan, T. M. (2019). A 3.8-million-year-old hominin cranium from Woranso-mille, Ethiopia. *Nature*, 573(7773), 214–219. <https://doi.org/10.1038/s41586-019-1513-8>
- Hemmer, H. (1976). Fossil history of living felidae. In R. L. Eaton (Ed.), *The World's cats* (pp. 1–14). Seattle, WA: Carnivore Research Institute, Burke Museum.
- Higham, T., Basell, L., Jocobi, R., Wook, R., Ramsey, C. B., & Conard, N. J. (2012). Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radio-carbon chronology of Geißenklösterle. *Journal of Human Evolution*, 62(6), 664–676. <https://doi.org/10.1016/j.jhevol.2012.03.003>
- Hoffmann, D. L., Standish, C. D., García-Diez, M., Pettitt, P. B., Milton, J. A., Zilhão, J., ... Pike, A. W. G. (2018). U-Th dating of carbonate crusts reveals Neandertal origin of Iberian cave art. *Science*, 359(6378), 912–915. <https://doi.org/10.1126/science.aap7778>
- Hoffmann, D. L., Standish, C. D., Pike, A. W. G., García-Diez, M., Pettitt, P. B., Angelucci, D. E., ... Zilhão, J. (2018). Dates for Neanderthal art and symbolic behavior are reliable. *Nature Ecology & Evolution*, 2, 1044–1045. <https://www.nature.com/articles/s41559-018-0598-z>
- Hollmann, J. (2002). Natural models, ethology and San rock-paintings: Pilo-erection and depictions of bristles in southeastern South Africa. *South African Journal of Science*, 98(11–12), 563–567. <https://hdl.handle.net/10520/EJC97421>
- Hussain, S. T., & Floss, H. (2015). Sharing the world with mammoths, cave lions and other beings: Linking animal-human interactions and the Aurignacian “belief world.” *Quartär*, 62, 85–120. [https://doi.org/10.7485/QU62\\_4](https://doi.org/10.7485/QU62_4)
- Huttenlocher, P. R., & Dabholkar, A. S. (1997). Regional differences in synaptogenesis in human cerebral cortex. *The Journal of Comparative Neurology*, 387(2), 167–178. [https://doi.org/10.1002/\(SICI\)1096-9861\(19971020\)387:2<167::AID-CNE1>3.0.CO;2-Z](https://doi.org/10.1002/(SICI)1096-9861(19971020)387:2<167::AID-CNE1>3.0.CO;2-Z)
- Igarashi, J., & Floss, H. (2019). Signs associated with figurative representations Aurignacian. Examples from Grotte Chauvet and the Swabian Jura. *Quaternary International*, 503(Part B), 200–209. <https://doi.org/10.1016/j.quaint.2017.12.048>
- Isbell, L. A., Bidner, L. R., Van Cleave, E. K., Matsumoto-Oda, A., & Crofoot, M. C. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, 118, 1–13. <https://doi.org/10.1016/j.jhevol.2018.02.003>

- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, 28(3), 979–990. [https://doi.org/10.1016/S0896-6273\(00\)00168-9](https://doi.org/10.1016/S0896-6273(00)00168-9)
- Janssen, P., Vogels, R., Liu, Y., & Orban, G. A. (2001). Macaque inferior temporal neurons are selective for three-dimensional boundaries and surfaces. *The Journal of Neuroscience*, 21(23), 9519–8429. <https://doi.org/10.1523/JNEUROSCI.21-23-09419.2001>
- Jarós, F. (2012). *The ecological and ethological significance of felid coat patterns (Felidae)* (Doctoral dissertation). Charles University, Prague, Czech Republic.
- Jirari, C. G. (1970). *Form perception, innate form preferences and visually mediated head-turning in the human neonate* (Doctoral dissertation). University of Chicago.
- Johnson, C. R., & McBrearty, S. (2010). 500,000 year old blades from the Kapthurin formation, Kenya. *Journal of Human Evolution*, 58(2), 193–200. <https://doi.org/10.1016/j.jhevol.2009.10.001>
- Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, 6, 766–774. <https://doi.org/10.1038/nrn1766>
- Johnson, M. H., Senju, A., & Tomalski, P. (2015). The two-process theory of face processing: Modifications based on two decades of data from infants and adults. *Neuroscience & Biobehavioral Reviews*, 50, 169–179. <https://doi.org/10.1016/j.neubiorev.2014.10.009>
- Jolly, P. (2002). Therianthropes in san rock art. *South African Archaeological Bulletin*, 57(176), 85–103. <http://hdl.handle.net/11427/26837>
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America*, 107(25), 11163–11170. <https://doi.org/10.1073/pnas.1005062107>
- Kirilova, I. V., Tiunov, A. V., Levchenko, V. A., Chernova, O. F., Yudin, V. G., Bertuch, F., & Shidlovskiy, F. K. (2015). On the discovery of a cave lion from the Malyi Anyui River (Chukotka, Russia). *Quaternary Science Reviews*, 117(1), 135–151. <https://doi.org/10.1016/j.quascirev.2015.03.029>
- Kitagawa, K., Krönneck, P., Conard, N. J., & Münzel, S. C. (2012). Exploring cave use and exploitation among cave bears, carnivores and hominins in the Swabian Jura, Germany. *Journal of Taphonomy*, 10(3–4), 439–461. [http://www.journaltaphonomy.com/JT-articles/2012/issue3-4/16\\_Kitagawa%20et%20al\\_TRIS.pdf](http://www.journaltaphonomy.com/JT-articles/2012/issue3-4/16_Kitagawa%20et%20al_TRIS.pdf)
- Kravitz, D. J., Saleem, K. S., Baker, C. L., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework for the processing of object quality. *Trends in Cognitive Science*, 17(1), 26–49. <https://doi.org/10.1016/j.tics.2012.10.011>
- Kveraga, K., Ghuman, A. S., Kassam, K. S., Aminoff, E. A., Hämäläinen, M. S., Chaumon, M., & Bar, M. (2011). Early onset of neural synchronization in the contextual associations network. *Proceedings of the National Academy of Sciences of the United States of America*, 108(8), 3389–3394. <https://doi.org/10.1073/pnas.1013760108>
- Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T., ... Foster, S. A. (2009). Relaxed selection in the wild. *Trends in Ecology and Evolution*, 24, 487–496. <https://doi.org/10.1016/j.tree.2009.03.010>
- Landova, E., Bakhshaliyeva, N., Janovcová, M., Peléšková, S., Suleymanova, M., Polák, J., ... Frynta, D. (2018). Association between fear and beauty evaluation of snakes: Cross-cultural findings. *Frontiers in Psychology*, 9, 333. <https://doi.org/10.3389/fpsyg.2018.00333>
- Langergraber, K. E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., ... Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 109(39), 15716–15721. <https://doi.org/10.1073/pnas.1211740109>
- Lee-Thorp, J. J., Thackeray, F., & van der Merwe, N. (2000). The hunters and the hunted revisited. *Journal of Human Evolution*, 39(6), 565–576. <https://doi.org/10.1006/jhevol.2000.0436>
- Lehmann, G. U. C., Strauß, J., & Lakes-Harlan, R. (2007). Listening when there is no sexual signalling? Maintenance of hearing in the asexual bushcricket *Poecilimon intermedius*. *Journal of Comparative Physiology A*, 193(5), 537–545. <https://doi.org/10.1007/s00359-007-0209-y>



- Leihitu, I., & Permana, R. C. E. (2019). A reflection of painting tradition and culture of the Austronesian based on the rock art in Misool, Raja Ampat, West Papua. *Journal of Southeast Asian Studies*, 24(1), 220–242. <https://doi.org/10.22452/jati.vol24no1.10>
- Lewis, M. E. (1997). Carnivoran paleoguilds of Africa: Implications for hominid food procurement strategies. *Journal of Human Evolution*, 32(2–3), 257–288. <https://doi.org/10.1006/jhev.1996.0103>
- Lewis-Williams, D. J., & Clottes, J. (1998). The mind in the cave—the cave in the mind: Altered consciousness in the upper Paleolithic. *Anthropology of Consciousness*, 9(1), 13–21. <https://doi.org/10.1525/ac.1998.9.1.13>
- LoBue, V., Matthews, K., Harvey, T., & Stark, S. L. (2014). What accounts for the rapid detection of threat? Evidence for an advantage in perceptual and behavioral responding from eye movements. *Emotions*, 13(4), 816–823. <https://doi.org/10.1037/a0035869>
- Marquet, J.-C., Lorblanchet, M., Oberlin, C., Thamo-Bozso, E., & Aubry, T. (2016). Nouvelle datation du “Masque” de la Roche-Cotard (Langeais, Indre-et-Loire, France). *Paleo, Revue d'Archéologie Préhistorique*, 2016, 253–263. <http://journals.openedition.org/paleo/3144>
- Mendoza Traffon, L. (2014). Art in the making. *The evolutionary origins of visual art as a communication signal* (Doctoral dissertation). Leiden University, Netherlands. <https://openaccess.leidenuniv.nl/handle/1887/28698>
- Minami, I., Tamura, H., Fujita, I., & Tanaka, K. (1995). Size and position invariance of neuronal responses in monkey inferotemporal cortex. *Journal of Neurophysiology*, 73(1), 218–226. <https://doi.org/10.1152/jn.1995.73.1.218>
- Moczek, A. P., Sultan, S., Foster, S., Ledón-Rettig, C., Dworkin, I., Nijhout, H. F., ... Pfennig, D. W. (2011). The role of developmental plasticity in evolutionary innovation. *Proceedings of the Royal Society B*, 278, 2705–2713. <https://doi.org/10.1098/rspb.2011.0971>
- Moeller, S., Freiwald, W. A., & Tsao, D. Y. (2008). Patches with links: A unified system for processing faces in the macaque temporal lobe. *Science*, 320(5881), 1355–1359. <https://doi.org/10.1126/science.1157436>
- Morales, J., & Pickford, M. (2018). A new barbouroufelid mandible (Carnivora, Mammalia) from the early Miocene of Grillental-6, Sperrgebiet, Namibia. *Communications of the Geological Society of Namibia*, 18, 113–123. [http://www.mme.gov.na/files/publications/4ab\\_Morales%20and%20Pickford%202018\\_Carnivore%20mandible%20from%20the%20Sperrgebiet.pdf](http://www.mme.gov.na/files/publications/4ab_Morales%20and%20Pickford%202018_Carnivore%20mandible%20from%20the%20Sperrgebiet.pdf)
- Mottram, J. C. (1915). Some observations on pattern-blending with reference to oblitative and concealment of outline. *Proceedings of the Zoological Society of London*, 85(4), 679–692. <https://doi.org/10.1111/j.1469-7998.1915.00679.x>
- Mottram, J. C. (1916). An experimental determination of the factors which cause patterns to appear conspicuous in nature. *Proceedings of the Zoological Society of London*, 86(2), 383–419. <https://doi.org/10.1111/j.1096-3642.1916.tb02020.x>
- Mullally, S. L., & Maguire, E. A. (2011). A new role for the parahippocampal cortex in representing space. *The Journal of Neuroscience*, 31(20), 7441–7449. <https://doi.org/10.1523/JNEUROSCI.0267-11.2011>
- Nasr, S., Liu, N., Devaney, K. J., Yue, X., Rajimehr, R., Ungerleider, L. G., & Tootell, R. B. H. (2011). Scene-selective cortical regions in human and nonhuman primates. *The Journal of Neuroscience*, 31(39), 13771–13785. <https://doi.org/10.1523/JNEUROSCI.2792-11.2011>
- Nguyen, M. N., Matsumoto, J., Hori, E., Maior, R. S., Tomaz, C., Tran, A. H., ... Nishijo, H. (2014). Neuronal responses to face-like and facial stimuli in the monkey superior colliculus. *Frontiers in Behavioral Neuroscience*, 8, Article 85. <https://doi.org/10.3389/fnbeh.2014.00085>
- Nothdurft, H.-C. (2007). Saliency and target selection in visual search. *Visual Cognition*, 14(4–8), 514–542. <https://doi.org/10.1080/13506280500194162>
- O'Connell, J. F., Hawkes, K., & Jones, N. B. (1988). Hadza scavenging: Implications for Plio/Pleistocene hominid subsistence. *Current Anthropology*, 29(2), 356–363. <https://www.jstor.org/stable/2743414>
- Ortolani, A. (1999). Spots, stripes, tail tips and dark eyes: Predicting the function of carnivore colour patterns using the comparative method. *Biological Journal of the Linnean Society*, 67(4), 433–476. <https://doi.org/10.1111/j.1095-8312.1999.tb01942.x>

- Packer, C., & Clottes, J. (2000). When lions ruled France. *Natural History*, 109(11), 52–57.
- Packer, C., Swanson, A., Ikanda, D., & Kushnir, H. (2011). Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLoS One*, 7, e22285. <https://doi.org/10.1371/journal.pone.0022285>
- Packer, C., Shivakumar, S., Athreye, V., Craft, M. E., Dhanwatey, H., Dhanwatey, P., ... Fountain-Jones, N. M. (2019). Species-specific spatiotemporal patterns of leopard, lion and tiger attacks on humans. *Journal of Applied Ecology*, 56(3), 585. <https://doi.org/10.1111/1365-2664.13311>
- Paijmans, J. L. A., Barnett, R., Gilbert, M. T. P., Zepeda-Mendoza, M. L., Reumer, J. W. F., de Vos, J., ... Hofreiter, M. (2017). Evolutionary history of saber-toothed cats based on ancient mitogenomics. *Current Biology*, 27(21), 3330–3336. <https://doi.org/10.1016/j.cub.2017.09.033>
- Panichello, M. F., Cheung, O. S., & Bar, M. (2013). Predictive feedback and conscious visual experience. *Frontiers in Psychology*, 3, Article 620. <https://doi.org/10.3389/fpsyg.2012.00620>
- Patterson, J. H. (1907). *The man-eaters of Tsavo*. London, England: Macmillan. <http://www.public-library.uk/pdfs/9/433.pdf>
- Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental imagery: Functional mechanisms and clinical applications. *Trends in Cognitive Sciences*, 19(10), 590–602. <https://doi.org/10.1016/j.tics.2015.08.003>
- Peigné, S., de Bonis, L., Likius, A., Mackaye, H. T., Vignaud, P., & Brunet, M. (2005). New machairodontine (Carnivora, Felidae) from the late Miocene hominid locality of Toros-Menalla, Chad. *Comptes Rendus Palevol*, 4, 243–253.
- Peltola, M. J., Leppänen, J. M., Palokangas, T., & Hietanen, J. K. (2008). Fearful faces modulate looking duration and attention disengagement in 7-month-old infants. *Developmental Science*, 11(1), 60–68. <https://doi.org/10.1111/j.1467-7687.2007.00659.x>
- Penkunas, M. J., & Coss, R. G. (2013a). Rapid detection of visually provocative animals by pre-school children and adults. *Journal of Experimental Child Psychology*, 114, 527–536. <https://doi.org/10.1016/j.jecp.2012.10.001>
- Penkunas, M. J., & Coss, R. G. (2013b). A comparison of rural and urban Indian children's visual detection of threatening and nonthreatening animals. *Developmental Science*, 16(3), 463–475. <https://doi.org/10.1111/desc.12043>
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, 47(3), 329–342. <https://doi.org/10.1007/BF00239352>
- Pickford, M., & Senut, B. (2001). The geological and faunal context of late Miocene hominid remains from Lukeino, Kenya. *Comptes Rendus de l'Académie des Sciences: Serie IIA. Sciences de la Terre et des Planetes*, 332(2), 145–152. [https://doi.org/10.1016/S1251-8050\(01\)01528-2](https://doi.org/10.1016/S1251-8050(01)01528-2)
- Pickford, M., Senut, B., Gommery, D., & Treil, J. (2002). Bipedalism in *Orrorin tugenensis* revealed by its femora. *Comptes Rendus Palevol*, 1(4), 191–203. [https://doi.org/10.1016/S1631-0683\(02\)00028-3](https://doi.org/10.1016/S1631-0683(02)00028-3)
- Piprani, J. (2011). Material culture, behavior, and identity: The human body as experiential nexus. *Time and Mind: The Journal of Archaeological Consciousness and Culture*, 4(3), 325–336. <https://doi.org/10.2752/175169711X13046099195591>
- Porr, M. (2010). Paleolithic art as cultural memory: A case study of the Aurignacian art of southwestern Germany. *Cambridge Archaeological Journal*, 20(1), 87–108. <https://doi.org/10.1017/S0959774310000065>
- Raichlen, D. A., Gordon, A. D., Harcourt-Smith, W. E. H., Foster, A. D., & Haas, W. R., Jr. (2010). Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLoS One*, 5(3), e9769. <https://doi.org/10.1371/journal.pone.0009769>
- Rafal, R. D., Koller, K., Bultitude, J. H., Mullins, P., Ward, R., Mitchell, A. S., & Bell, A. H. (2015). Connectivity between the superior colliculus and the amygdala in humans and macaque monkeys: Virtual dissection with probabilistic DTI tractography. *Journal of Neurophysiology*, 114(3), 1947–1962. <https://doi.org/10.1152/jn.01016.2014>

- Ramakrishnan, U., Coss, R. G., & Pelkey, N. W. (1999). Tiger decline caused by the reduction of large ungulate prey: Evidence from a study of leopard diets in southern India. *Biological Conservation*, 89(2), 113–120. [https://doi.org/10.1016/S0006-3207\(98\)00159-1](https://doi.org/10.1016/S0006-3207(98)00159-1)
- Ramakrishnan, U., & Coss, R. G. (2000). Recognition of heterospecific alarm vocalizations by bonnet macaques (*Macaca radiata*). *Journal of Comparative Psychology*, 114(1), 3–12. <https://doi.org/10.1037/0735-7036.114.1.3>
- Reid, V. M., Dunn, K., Young, R. J., Amu, J., Donovan, T., & Reissland, N. (2017). The human fetus preferentially engages with face-like visual stimuli. *Current Biology*, 27(12), 1825–1828. <https://doi.org/10.1016/j.cub.2017.05.044>
- Richmond, B. G., Begun, D. R., & Strait, D. S. (2001). Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Yearbook of Physical Anthropology*, 44(116), 70–105. <https://doi.org/10.1002/ajpa.10019>
- Richmond, B. G., & Jungers, W. L. (2008). *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science*, 319, 1662–1665. <https://www.jstor.org/stable/20053635>
- Rodríguez-Vidal, J., d'Errico, F., Pacheco, F. G., Blasco, R., Rosell, J., Jennings, R. P., ... Finlayson, C. (2014). A rock engraving made by Neanderthals in Gibraltar. *Proceedings of the National Academy of Sciences of the United States of America*, 111(37), 13301–13306. <https://doi.org/10.1073/pnas.1411529111>
- Roe, A. W., Chelazzi, L., Connor, C. E., Conway, B. R., Fujita, I., Gallant, J. L., ... Vanduffel, W. (2012). Toward a unified theory of visual area V4. *Neuron*, 74(1), 12–29. <https://doi.org/10.1016/j.neuron.2012.03.011>
- Rousselet, G. A., Fabre-Thorpe, M., & Thorpe, S. J. (2002). Parallel processing in high-level categorization of natural images. *Nature Neuroscience*, 5(7), 629–630. <https://doi.org/10.1038/nm866>
- Sala, B. (1990). *Panthera leo fossilis* (v. Reich., 1906) (Felidae) de Isernia la Pineta (Pléistocène Moyen Inférieur d'Italie). *Geobios*, 23(2), 189–194. [https://doi.org/10.1016/S0016-6995\(06\)80051-3](https://doi.org/10.1016/S0016-6995(06)80051-3)
- Schel, A. M., & Zuberbühler, K. (2009). Responses to leopards are independent of experience in guereza colobus monkeys. *Behaviour*, 146(12), 1709–1737. <https://www.jstor.org/stable/40599640>
- Schmitt, D., Churchill, S. E., & Hylander, W. L. (2003). Experimental evidence concerning spear use in Neandertals and early modern humans. *Journal of Archaeological Science*, 30(1), 103–114. <https://doi.org/10.1006/jasc.2001.0814>
- Sewards, T. V., & Sowards, M. A. (2002). Innate visual object recognition in vertebrates: Some proposed pathways and mechanisms. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 132(4), 861–891. [https://doi.org/10.1016/S1095-6433\(02\)00119-8](https://doi.org/10.1016/S1095-6433(02)00119-8)
- Shabbir, M., Zon, A. M. Y., & Thuppil, V. (2018). Repetition is the feature behind attentional bias for recognizing threatening patterns. *Evolutionary Psychology*, 2018, 1–12. <https://doi.org/10.1177/1474704918754782>
- Shea, J. J., & Sisk, M. L. (2010). Complex projectile technology and *Homo sapiens* dispersal into western Eurasia. *PaleoAnthropology*, 2010, 100–122. <https://doi.org/10.4207/PA.2010.ART36>
- Simons, D. J. (2000). Attentional capture and inattention blindness. *Trends in Cognitive Sciences*, 4(4), 147–155. [https://doi.org/10.1016/S1364-6613\(00\)01455-8](https://doi.org/10.1016/S1364-6613(00)01455-8)
- Sommer, M. A., & Wurtz, R. H. (2004). What the brain stem tells the frontal cortex. I. Oculomotor signals sent from superior colliculus to frontal eye field via mediodorsal thalamus. *The Journal of Neurophysiology*, 91(3), 1381–1402. <https://doi.org/10.1152/jn.00738.2003>
- Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature Letters*, 444(6), 374–377. <https://doi.org/10.1038/nature05279>
- Sütterlin, C. (2003). From sign and schema to iconic representation. Evolutionary aesthetics of pictorial art. In E. Voland & K. Grammar (Eds.), *Evolutionary aesthetics* (pp. 131–170). Heidelberg, Germany: Springer.
- Tamietto, M., & de Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience*, 11, 697–709. <https://doi.org/10.1038/nrn2889>

- Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, 19, 109–139. <https://doi.org/10.1146/annurev.ne.19.030196.000545>
- Tanaka, K. (2003). Columns for complex visual object features in the inferotemporal cortex: Clustering of cells with similar but slightly different stimulus selectivities. *Cerebral Cortex*, 13(1), 90–99. <https://doi.org/10.1093/cercor/13.1.90>
- Tanaka, K., Saito, H.-A., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology*, 66(1), 170–189. <https://doi.org/10.1152/jn.1991.66.1.170>
- Thomas, E. M. (1990, October 15). *The old way*. The New Yorker. Retrieved from <https://www.newyorker.com/magazine/1990/10/15/the-old-way>
- Thomas, E. M. (2003). The lion/bushman relationship in Nyae Nyae in the 1950s: A relationship crafted in the old way. *Anthropologica*, 45(1), 73–78. <https://www.jstor.org/stable/25606114>
- Treves, A., & Palmqvist, P. (2007). Reconstructing hominin interactions with mammalian carnivores (6.0–1.8 ma). In S. L. Gursky & K. A. I. Nekaris (Eds.), *Primate anti-predator strategies* (pp. 355–381). Boston, MA: Springer. [https://doi.org/10.1007/978-0-387-34810-0\\_17](https://doi.org/10.1007/978-0-387-34810-0_17)
- Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), 19514–19519. <https://doi.org/10.1073/pnas.0809662105>
- Turner, A., & Antón, M. (1998). Climate and evolution: Implications of some extinction patterns in African and European Machairodontine cats of the Plio-Pleistocene. *Estudios Geológicos*, 54(5–6), 209–230. <https://doi.org/10.3989/egeol.98545-6220>
- Uphyrkina, O., Johnson, W. E., Quigley, H., Miquelle, D., Marker, L., Bush, M., & O'Brien, S. J. (2001). Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. *Molecular Ecology*, 10(11), 2617–2633. <https://doi.org/10.1046/j.0962-1083.2001.01350.x>
- Vogelsang, R., Richter, J., Jacobs, Z., Eichhorn, B., Linseele, V., & Robert, R. G. (2010). New excavations of Middle Stone Age deposits at Apollo 11 rockshelter, Namibia: Stratigraphy, archaeology, chronology and past environments. *Journal of African Archaeology*, 8(2), 185–218. <https://www.jstor.org/stable/43135517>
- Ward, C., Leakey, M., & Walker, A. (1999). The new hominid species *Australopithecus anamensis*. *Evolutionary Anthropology*, 7(6), 197–205. [https://doi.org/10.1002/\(SICI\)1520-6505\(1999\)7:6<197::AID-EVAN4>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1520-6505(1999)7:6<197::AID-EVAN4>3.0.CO;2-T)
- Werdelin, L., & Lewis, M. E. (2005). Plio-Pleistocene Carnivora of eastern Africa: Species richness and turnover patterns. *Zoological Journal of the Linnean Society*, 144(2), 121–144. <https://doi.org/10.1111/j.1096-3642.2005.00165.x>
- Werdelin, L., & Olsson, L. (1997). How the leopard got its spots: A phylogenetic view of the evolution of felid coat patterns. *Biological Journal of the Linnean Society*, 62(3), 383–400. <https://doi.org/10.1111/j.1095-8312.1997.tb01632.x>
- Wilkins, J., & Chazan, M. (2012). Blade production ~500 thousand years ago at Kathu Pan 1, South Africa: Support for a multiple origins hypothesis for early Middle Pleistocene blade technologies. *Journal of Archaeological Science*, 39(6), 1883–1900. <https://doi.org/10.1016/j.jas.2012.01.031>
- Wilkins, J., Schoville, B. J., Brown, K. S., & Chazan, M. (2012). Evidence for early hafted hunting technology. *Science*, 338(6109), 942–946. <https://doi.org/10.1126/science.1227608>
- Willems, E. P., & van Schaik, C. P. (2017). The social organization of *Homo ergaster*: Inferences from anti-predator responses in extant primates. *Journal of Human Evolution*, 109, 11–21. <https://doi.org/10.1016/j.jhevol.2017.05.003>
- Winlove, C. I. P., Milton, F., Ranson, J., Fulford, J., MacKisack, M., Macpherson, F., & Zeman, A. (2018). The neural correlates of visual imagery: A co-ordinate-based meta-analysis. *Cortex*, 105, 4–25. <https://doi.org/10.1016/j.cortex.2017.12.014>
- Woodburne, A. S. (1981). The evil eye in south Indian folklore. In A. Dundes (Ed.), *The evil eye* (pp. 55–65). New York, NY: Garland Publishing.

- Yahner, R. H. (1980). Barking in a primitive ungulate, *Muntiacus reevesi*: Function and adaptiveness. *The American Naturalist*, *116*(2), 157–177. <http://links.jstor.org/sici?sici=00030147%28198008%29116%3A2%3C157%3ABIAPUM%3E2.0.CO%3B2-8>
- Yorzinski, J. L., & Coss, R. G. (2019). Animals in upright postures attract attention in humans. *Evolutionary Psychological Science*, *6*, 30. <https://doi.org/10.1007/s40806-019-00209-w>
- Yorzinski, J. L., Penkunas, M. J., Platt, M. L., & Coss, R. G. (2014). Dangerous animals capture and maintain attention in humans. *Evolutionary Psychology*, *12*(3), 534–548. <https://doi.org/10.1177/147470491401200304>
- Yorzinski, J. L., Tovar, M. E., & Coss, R. G. (2018). Forward-facing predators attract attention in humans (*Homo sapiens*). *Journal of Comparative Psychology*, *132*(4), 410–418. <https://doi.org/10.1037/com0000126>
- Yoshioka, T., & Dow, B. M. (1996). Color, orientation and cytochrome oxidase reactivity in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research*, *76*(1–2), 71–88. [https://doi.org/10.1016/0166-4328\(95\)00184-0](https://doi.org/10.1016/0166-4328(95)00184-0)
- Yoshioka, T., Dow, B. M., & Vautin, R. G. (1996). Neuronal mechanisms of color categorization in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research*, *76*(1–2), 51–70. [https://doi.org/10.1016/0166-4328\(95\)00183-2](https://doi.org/10.1016/0166-4328(95)00183-2)
- Zollikofer, C. P. E., Ponce de León, M. S., Lieberman, D. E., Guy, F., Pilbeam, D., Likius, A., ... Brunet, M. (2005). Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature*, *434*, 755–759. <https://www.nature.com/articles/nature03397>
- Zuberbühler, K., & Jenny, D. (2002). Leopard predation and primate evolution. *Journal of Human Evolution*, *43*(6), 873–886. <https://doi.org/10.1006/jhev.2002.0605>