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Titel der Diplomarbeit

To see and not be seen.
Camouflage and Deceptive Markings.

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The hardest thing to see is what is in front of your eyes.

Johann Wolfgang von Goethe (1749 – 1832)

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Introduction

The present work will give a theoretical framework of a field of research that has not yet been focused to a great extent, and even less by psychologists.

At the beginning, different forms of camouflage, with diverse and sometimes extraordinary strategies, in the animal kingdom are presented. Of special interest is the question of how prey is perceived by predators and reverse, and how the senses of one´s predator or prey can be influenced to remain undetected or unrecognized (Ruxton, Sherratt & Speed, 2004; Stevens & Merilaita, 2011). The advantage of being concealed from enemies seems easy to understand, but for connecting this primary biological theme with psychology, it is necessary to explore the capacities and limitations of predators or conspecifics sensations. Psychological methods open a new insight of how predators see their prey and conspecifics, and while testing the interactions of sensory systems, a contribution for the understanding of perceptual systems in humans and other species is installed.

Therefore different ways of how to investigate an animal’s visual system will be presented and discussed. Such methods include producing pastry prey or painting parts of animals bodies, especially those of insects, to observe a predators reaction, especially that of birds. Also, the investigation of cuttlefish plays a major role, and conclusions can be drawn from their rapid adaptive behavior to different backgrounds.

Since we can´t investigate well animals sensory systems, as a next step some principles of how camouflage related perception is functioning in humans is given. Essential for the intent of understanding how camouflage mechanisms may function are among others mechanisms of target-background segmentation, object recognition and edge detection, which will be presented. Nevertheless, the emphasis on the broad viewer differences between species is stated, and an animal that doesn´t appear cryptic to us can be cryptic to its predators. As a consequence, studies with human subjects can only try to connect the underlying mechanism that appears in all different forms of camouflage behavior.

Finally, the influence of camouflage used in the animal kingdom and its practical applications for human adaptions is given, showing it´s extent in military, but also in other parts of human society, such as arts and popular culture.

Part I. Different types of visual camouflage

1. Overview

There are a great number of different definitions that have been used to describe the various types of camouflage. This means that same classifications have been applied differently by various researchers, differing in a small to large extent, but nearly all are comprehensible from the author’s point of view.

Ruxton, Sherratt and Speed (2004) discriminate between mechanism of avoiding detection, avoiding attack and deceiving predators. Others authors like Hanlon & Messenger (1988) define camouflage types primarily based on appearance which is common practice in studies with cephalopods (see chapter 3.2). This may be crucial because differences in visual perception across animal groups result in similar pattern types having entirely distinct functions in different animals and circumstances (Stevens & Merilaita, 2011).

Stevens and Merilaita (2009a; 2011) therefore concentrate on the function of the camouflage types, trying to describe what the adaptation may produce, although admitting that they don´t know enough about the perceptual mechanisms involved. Concerning visual camouflage, they use the term camouflage to describe all forms of concealment, including strategies for preventing detection (crypsis) and those for preventing recognition (e.g. masquerade, motion dazzle, motion camouflage). Crypsis in this case refers to “all traits that reduce an animal’s risk of becoming detected when it is potentially perceivable to an observer“ (Stevens & Merilaita, 2009a, p. 425), including background matching, disruptive coloration, self-shadow concealment and obliterative shading. For an overview of different forms of camouflage in accord to Stevens & Merilaita (2009a, p.424) see table 1.

Background matching:		The appearance match the color, lightness and pattern of one or several background types
Disruptive coloration:		A set of markings that creates the appearance of false edges and boundaries, and hinders the detection or recognition of an object´s or part of an object´s, true outline and shape
countershading	Self-shadow concealment:	directional light, that create shadows, is cancelled out by countershading
	Obliterative shading:	countershading leads to the obliteration of three-dimensional form

Masquerade:	Resembling an uninteresting object (a leaf, a stick) to prevent recognition
Distractive markings:	direct the attention of the receiver from traits that would reveal the animal (like the outline)
Motion dazzle:	markings that complicate estimations of speed and trajectory
Motion camouflage:	Movement that decrease the probability of movement detection

Table 1: Overview of the most common forms of camouflage.

Like Ruxton, Sherratt and Speed (2004) emphasize, it´s important to remember that traits which influence the perception of one animal by its predators or prey is likely to be driven by more than one mechanism. Also, potential prey species possess many different ways to save themselves from predators, and antipredator adaptions seem not to be independent traits but rather form a continuum. Instead of concentrating on semantics and classifications, Ruxton et al. (2004) highlight the search of general underlying principles to predator-prey aspects of sensory ecology. Further they note that most adaptations would be understandable without great details, nevertheless a few classification will be given:

1.1. Background matching

Merilaita and Stevens (2011) describe that to lower the detection risk by its predators or prey, an animal using background matching possesses body colors or patterns that are similar to those in the surrounding environment. Local features which should be matched include color, lightness, edges, lines and texture, to hinder figure ground segregation (see Fig. 1 and 2). When the animals' appearance deviates from the background, prey or predators can be detected and easier recognized. In general, animals can adapt to match their environment, select backgrounds that match their appearance or adapt their appearance to changes in their surroundings. It is to consider that backgrounds are multivariate and the background that must be matched always depends on the viewer. Ruxton et al. (2004, p. 11) further describe background as a function of the physical habitat and illumination, the sensory physiology of the viewer, and the positions in the physical habitat of both the viewer and the viewed organism.

The most famous example of background matching lies in the industrial melanism of the peppered moth (*Biston betularia)* (Kettlewell, 1955, 1961).

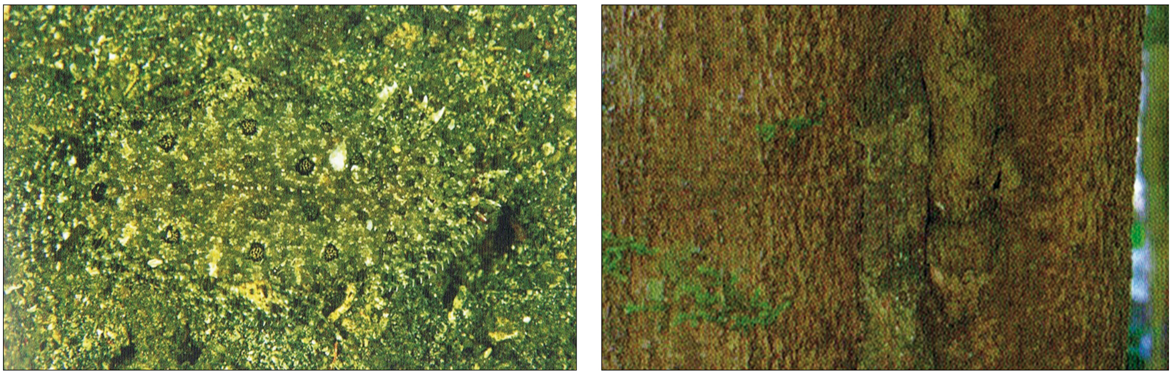

Figure 1: Examples of background matching animals.
Left: panther flounder *(Bothus pantherinus)*, with the ability to change color to its background, matching the seabed (Blechman, 2004, p. 43; by Alexander Mustard). Right: A color changing leaf tailed gecko *(Uroplatus imbriatus)* matching its backdrop (Blechman, 2004, p. 197; by Parks D.R.).

Figure 2: Mottle coloration for background matching.
(A) Owlet moth (*Leuconycta lepidula*; common in N. America). (B) Flowery cod (*Epinephelus fuscoguttatus*; Great Barrier Reef). (C) Toad (northern New Hampshire, USA). (D) Owl (All images derived from Chiao, Chubb, Buresch, Barbosa, et al. (2010, p. 195).

1.2. Disruptive coloration

Stevens and Merilaita (2009b, p. 484) define that, "Disruptive coloration is a set of markings that creates the appearance of false edges and boundaries and hinders the detection or recognition of an object´s, or part of an object´s, true outline and shape" (for examples of disruptive coloration see Fig. 3 and 4). This means that the use of high-contrast markings can break up the appearance of an animal which prevents the detection of the objects body shape (Stevens & Merilaita, 2009a). A special case seems to be coincident disruptive coloration, which animals use to conceal special body parts like legs and wings (Cuthill & Székely, 2009, 2011). Various experiments have tested the efficacy of disruptive coloration, using artificial prey in field and/or human studies of detecting computer targets (Barbosa et al., 2007; Cuthill et al., 2005; Cuthill & Székely, 2009; Hanlon et al., 2009; Mäthger et al., 2007; Schaefer & Stobbe, 2006; Stevens & Cuthill, 2006; Stevens, Cuthill, Parraga, & Troscianko, 2006).

Figure 3: Examples of disruptive colorated animals.
Left: Snake in natural environment (derived from www.duskyswondersite.com). Right: Ornate Cowfish, *Aracana ornata* (image copyright Phillip Colla / Oceanlight.com).

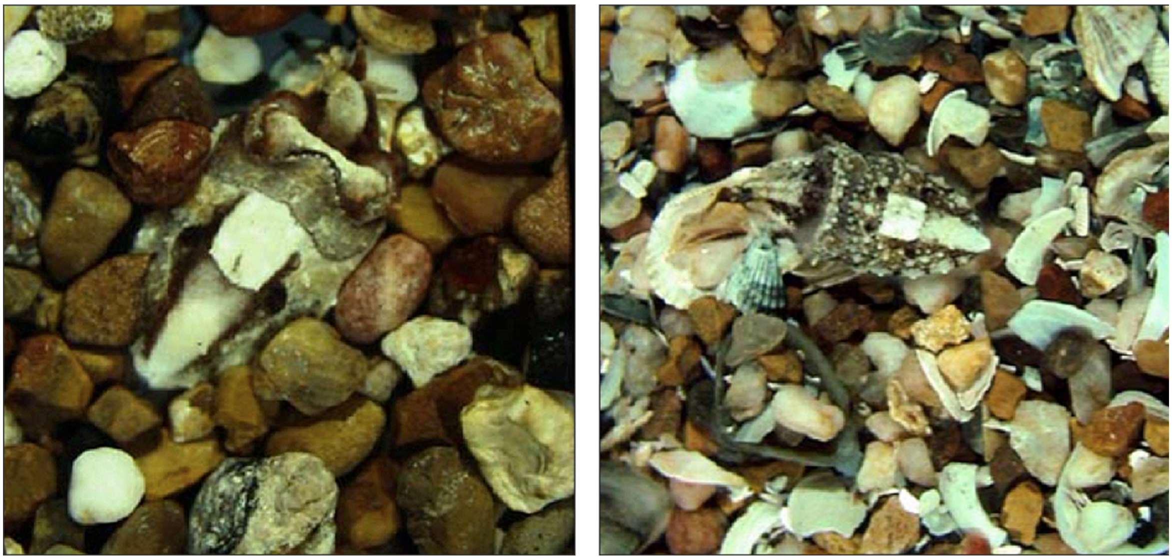

Figure 4: Cuttlefish showing disruptive behavior on natural ground.
Sepia officinalis and its typical pattern on stony environment (Maethger, Barbosa, Miner & Hanlon, 2006, p. 1750).

1.3. Countershading

Countershaded animals possess a “darker pigmentation on those surfaces exposed to the most lighting“ (Rowland, 2009). For camouflage, the two most important functions are Self-shadow concealment (SSC) through compensating the animal´s own shadow, and countershading by changing the three-dimensional appearance (see Fig. 5).

Similar to disruptive coloration, countershading has rarely been studied with real prey, but using artificial prey with predator birds in field (Rowland, Cuthill, Harvey, Speed, & Ruxton, 2008; Rowland et al., 2007; Speed, Kelly, Davidson, & Ruxton, 2005). Also studies of machine vision and detection of concealed three-dimensional objects contribute to the understanding of countershading (Tankus & Yeshurun, 2009).

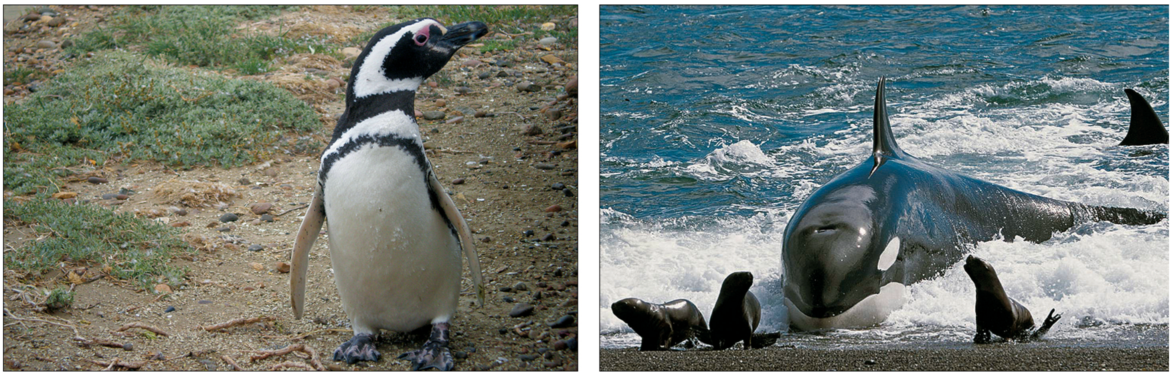

Figure 5: Examples of countershaded animals.
Left: Mangellanic pinguin, *Spheniscus magellanicus* (taken by the author in Monte Leon, Patagonia). Right: Orca (by Alberto Patrian).

1.4. Masquerade

A lot of animals mimic objects of no interest to the potential predator, like leaves, sticks, rocks, thorns or even bird droppings (Ruxton, Sherratt, et al., 2004). A fascinating example is the leafy sea dragon (*Phyllopteryx eques*) that possess many outgrowths simulating sea weed (see Fig. 6). Often the distinction that distinguish masquerade from crypsis is not that clear, thinking of differences between resembling the background and looking like an uninteresting object. Some authors separate these parts clearly, defining masquerade as acting against recognition and therefore not being part of crypsis (Stevens & Merilaita, 2009a; Skelhorn, Rowland, Speed, & Ruxton, 2010).

Figure 6. Examples of mimicing animals.
Left: This stone or toad grasshopper of the family *Pamphagidae* mimics a stone (Blechman, 2004; p. 45). Middle: A stick-insect resembling its resting place (www.duskyswondersite.com/animals/animal-camouflage). Right: A leafy sea-dragon, blending in with the seaweed (by George Grall).

1.5. Other forms of camouflage

Apart from the main forms of camouflage there exist various other types of camouflage in the animal kingdom. Motion camouflage and motion dazzle are two strategies that avoid or hinder correct detection during movement and will be commented more detailed subsequently. Further kinds of camouflage that appear underwater are transparency, silvering and bioluminescence (see chapter 3 “Underwater Camouflage“). Other forms that deceive predators are distractive markings, Müllerian and Batesian mimicry.

2. Empirical evidences for the main forms of camouflage

Most empirical evidences have been given so far for the three main forms of camouflage preventing detection: background matching, disruptive behavior and countershading.

2.1 Background matching

Background matching has been used as an example in early evolutionary writings, promoting the idea of adaptation (Merilaita & Stevens, 2011). Nearly all organisms will be seen against different backgrounds, at least the change in light conditions varies the background which an animal attempts to match. Therefore an important point of interest is how animals cope with the visual variation in background (Merilaita & Stevens, 2011; Ruxton et al., 2004). Probably the first attempt to solve this problem was done by Abbott H. Thayer (1918) by suggesting that animals should use the average of the samples of the background, which are seen through the eye of the object the animal is hiding from.

An observer probably detects deviation between the animal surface and its surroundings when the animal does not match its background closely enough (Merilaita & Stevens, 2011). Distinguishing an object from the background is reached by comparison of local features in subsequent visual processing (e.g. Mather, 2009; as cited in Merilaita & Stevens, 2011; see Part 2). Many animals appear similar to their backgrounds, and also many animals are able to change coloration to backgrounds through immediate (e.g. cephalopods) or slow response (e.g. lepidopteran larvae and spiders). Observation alone does not prove the adaptive utility of background matching, but numerous predation experiments show that predation risk is decreased by prey similarity with the background. Some of them will be given now.

2.1.1 Adaptions of background matching

Using an analytical model for studying crypsis in two heterogeneous microhabitats, Merilaita, Tuomi and Jormalainen (1999) showed that the optimal coloration of prey is either full adaption to only one of the different backgrounds or a compromise between the requirements. Similar results can also be found in another model developed by Houston, Stevens and Cuthill (2007). Another study tried to answer the question if an animal should specialize its matching to one particular background, or if it should seek a compromise of crypsis against various backgrounds, without matching exactly any of them (Merilaita, Lyytinen, & Mappes, 2001). Using two background types and three types of artificial paper prey shown in Fig. 7 (matching the small background pattern, larger pattern, and intermediate-size pattern), it has shown that in a situation where both backgrounds were encountered with equal frequency, the intermediately pattern prey would be best protected of getting eaten by great tits (*Parus major*). On the small patterned background, small patterned prey were most cryptic, on the large patterned background, the small patterned prey was least cryptic (Merilaita et al., 2001). Merilaita and Stevens (2011) summarized their experiments that at least under certain conditions a coloration compromise seems to be the best chose.

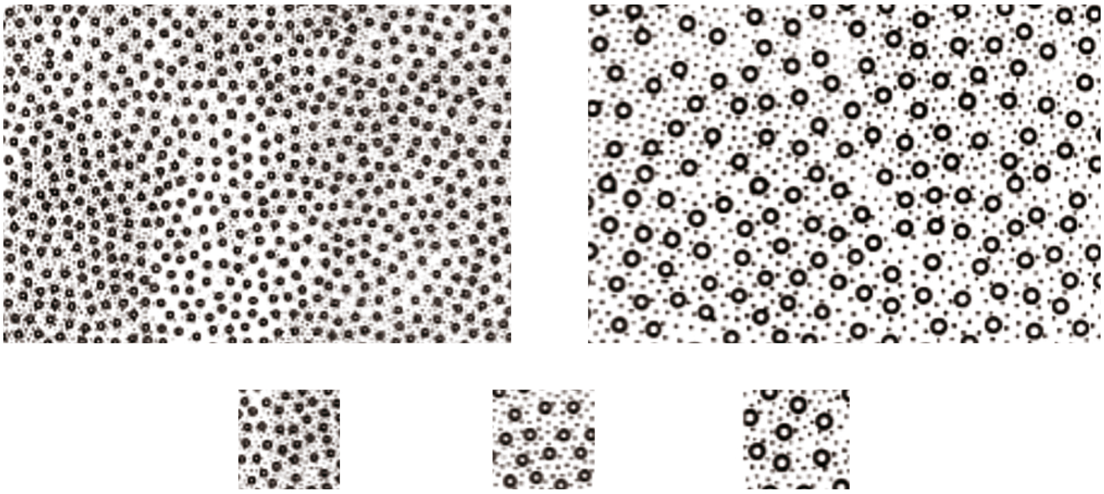

Figure 7: Crypsis in visually heterogeneous habitats.
The two large images above show the small and large background patterns, and the three small squares below show the small, compromised and large prey patterns. Used in the experiment of Merilaita et al., (2001, p. 1926).

In this context it seems also noteworthy that cuttlefish use both uniform and mottle patterns for obtaining background matching (see chapter 4).

Bond and Kamil (2006) conducted an experiment on the evolution of prey coloration on heterogeneous backgrounds. Using blue jays (*Cyanocitta cristata*) searching for digital moths on different scaled patches, they concluded that polymorphism in camouflaged prey would depend on a complex interaction between habitat structure and the predator cognition. Further, other methods of measurement have been designed, using for example web-based experiments to investigate the evolution of background matching (Sherratt, Pollitt, & Wilkinson, 2007). In this study, visitors of an experimental web site were rewarded for finding artificial prey viewed against uniform and heterogeneous backgrounds. Experiments using humans as observers always have to be interpreted carefully, having in mind the different visual systems. However when human vision and observing animal ´s vision don´t differ a lot, it seems that a compromise to background patterning or geometry is favored over a color compromise (Merilaita & Stevens, 2011; Sherratt et al., 2007).

To address the interaction between cryptic visual appearance and motion, Ioannou and Krause (2009) investigated the suggestion that background matching doesn't reduce the risk of detection when animals are in motion. In a controlled experiment they showed that chironomid larvae need both to match the background and keep still to avoid being attacked by a fish, the three-spined sticklebacks (*Gasterosteus aculeatus*).

In future, more empirical work is needed to connect camouflage with predator perception. Studies on optimizing the prey appearance with different surroundings are also required like experiments concerning habitat-use patterns by prey and how visual systems of their predators work (Merilaita & Stevens, 2011).

2.1.2 Background matching and coloration

Additional studies have given emphasis especially on the coloration in animals. For example Thery (2007) tested the effects of background matching in the color-changing female crab spider (*Misumena vatia*) and their adaptive camouflage on reflected light as seen by their prey (to compare also with color-changing animals and aggressive mimicry). Bursell and Dyck (2003) conducted a study about bird plumage, and it´s possible detection by a predator. However their investigation demonstrates the quantification of background colors for wild birds as seen only by humans on the ground. Caro (2009) considers in his work of coloration in animals, that background matching may explain pelage in white mammals, thinking of the polar bear or animals that turn white only in winter like the artic fox and some weasels.

2.1.3 Measuring background matching

One challenging task concerning experiments of this type is measuring the level of background matching to identify the degree of similarity between animal and it´s background. Merilaita and Stevens (2011) noted that the methods for measuring visual similarity between an animal and its surroundings lie mostly in quantifying the degree of color and luminance match. Instead of comparing different species, it appears to be useful to study color-changing species like cephalopods. Shohet, O´Baddeley, Anderson, and Osorio (2007), for example, conducted a quantitative study to identify aspects to reach good pattern matching in cuttlefish. Other pattern analysis focuses on spatial frequency (Godfrey, Lythgoe, & Rumball, 1987) or work with granularity analysis (Hanlon et al., 2009; Barbosa, Mäthger, et al., 2008).

2.1.4 live backgrounds

Abbott & Dukas (2011) changed the general opinion that animals are the active players matching them against a passive background, highlighting that in many cases backgrounds are alive. Examples for this are parts of plants or larger animals surrounding camouflaged individuals. Predators can hide on living backgrounds for capturing prey (like crab spiders that attack insect pollinators) but there are also herbivores feeding on plants and hiding themselves from predators. In that case, background organisms may actually be active players, co-evolving with the animals and being affected by the outcome of the predator-prey interaction (Abbott & Dukas, 2011). Such background evolution involves for example variation in leaf colors. To further investigate that aspect, Abbott (2010) previously had developed a game-theoretical model involving hiders, seekers and live backgrounds to predict the optimal strategy of the live backgrounds.

2.1.5 Background matching and relations to other kinds of camouflage

- Disruptive coloration: Ruxton et al. (2004) points out that background matching and disruptive coloration are separate mechanisms, although acknowledges that one cannot generally expect the disruptive mechanism to operate completely isolated from background matching.
- Countershading: One has to have in mind that countershading can be part of background matching, depending on the direction form where it is observed (Ruxton et al. 04; see chapter 2.3).
- Masquerade: Background matching is considered very different from masquerade, because it is limited to body coloration and detection and not recognition (Merilaita & Stevens, 2011; Stevens & Merilaita, 2009a). However this is still unsolved and there may be some overlap in masquerade examples like insects mimicking twigs of leaves, and seahorses mimicking seaweed.

2.2 Disruptive Coloration

Like already stated, disruptive coloration is used to make the detection of edges and boundaries more difficult (Ruxton, Sherratt, et al., 2004; Stevens & Cuthill, 2006; Stevens, Cuthill, Windsor, & Walker, 2006). This can be achieved by contrasting colors in places where no real boundaries are, or by breaking up real boundaries so that there is not a constant coloration along the edges (Ruxton, Sherratt, et al., 2004). Cott (1940; as cited in Ruxton et al.; p. 26) described the first technique as “constructive relief“ and the latter one as “differential blending“. Both of these mechanisms reduce the detection rate by producing the impression of an object quite different in shape than it´s actually is.

In the investigation of disruptive coloration mostly artificial moth-like targets are exposed to bird predators, with for example a dead mealworm as the edible body (Cuthill et al., 2005) or like already described anterior, pastry bodies.

2.2.1 Separating disruptive coloration from background matching

Many animals use coloration that is neither obviously a form of background matching nor disruptive coloration and there may be patterns that function through background matching but also disruptively (Ruxton, Sherratt, et al., 2004). One example are some freshwater fishes with light and dark stripes which match the background of rocky substrates as well as breaking up the fish into smaller units (Armbruster & Page, 1996). Some animals that can show a clear disruptive pattern, such as cephalopods, but most studies on animal camouflage that deal with disruptive coloration, include at the same time ideas about background matching. Schaefer and Stobbe (2006) show that disruptive coloration on the outline of an animal (see Fig. 8 for the used material) works independent of the background and that also background matching and disruptive coloration on the body interior provide cryptic functions, but that these are background-specific.

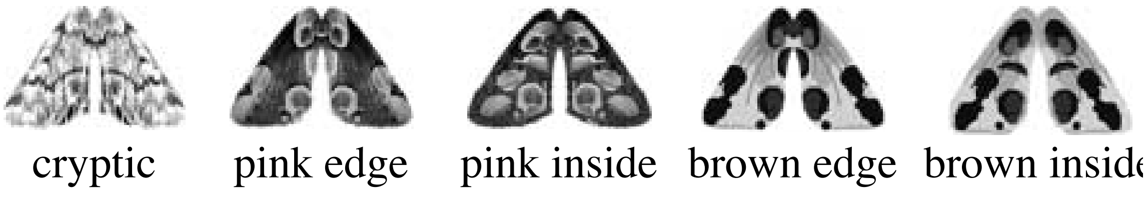

Figure 8: Artificial moths with disruptive coloration.
Material used by Schaefer and Stobbe for testing the survival probabilities on either birch trunk or moss (2006, p. 2430).

2.2.2 Coincident disruptive coloration

Abbott Thayer (1909) and Hugh Cott (1940) noticed that disruptive coloration is also used to prevent detection and recognition of specific body parts, like the eyes or limbs, terming the successful disguise of body part features as “coincident disruptive coloration“ (as cited in Cuthill & Székely, 2011; Ruxton, Sherratt, et al., 2004). This seems easy comprehensible, having in mind that eyes are more fragile compared to other body parts and are often attacked by predators (Ruxton, Sherratt, et al., 2004). But not all eye-stripes seem to fulfill Cott´s theory and rather are examples of reduced conspicuousness of the eye and not disruption of eye shape (Cuthill & Székely, 2011).

Cuthill and Székely (2009) presented a study concerning the theory of coincident disruptive coloration using field experiments with artificial moth-like targets placed on trees and wild birds as their predators. The paper-wings and eatable pastry-bodies of these moths possessed two-tone disruptive patterns that were variously coincident or not. Coincidence, as the authors describe, supposes no phase disjunction when the body parts meet, causing different sections of the body to blend perceptually. Cuthill and Székely also created conditions where the cylindrical body matches the wings, or not, without having coincident patterns. In doing so they wanted to separate the benefits of disguising a body part color-matched to the rest of the body from the benefits of breaking up the shape of the body part. Additionally Cuthill and Székely replicated in the same study the field experiment in the laboratory with humans searching for analogous targets on a computer screen, because an anterior study (Fraser, Callahan, Klassen, & Sherratt, 2007) revealed that it seems that there are common features in human and animal perception of camouflage. In this visional search task moth images were presented against pictures of oak bark, converted to greyscale, using a design developed originally by Fraser et al. (2007). In both experiments, the complementary field and laboratory studies, they come to the conclusion that coincident disruptive coloration is effective to conceal an otherwise noticeable body form, supporting Cott´s principle of coincident disruptive coloration (Cuthill & Székely, 2009, 2011).

2.3 Countershading

Countershading is a widespread pattern of coloration, appearing in various groups of terrestrial and aquatic animals (Rowland, 2009, 2011). Many and quite different groups of animals possess countershading, such as birds, various lepidopteran larvae, squirrels, penguins and sharks. Also, countershading has been well explored in cephalopods and upside-down swimming freshwater fish (Chapman, Kaufman, & Chapman, 1994; Ferguson & Messenger, 1991). The transition of the pattern from dark to light can be very sharp, like in penguins, or more gradual, like in squirrels (Ruxton, Speed, et al., 2004).

Countershading is often explained as an adaptive trait that increase crypsis and decrease predation risk from visual predators (Rowland, 2009; Ruxton, Speed et al., 2004), although according to Kamilar and Bradley (2011), few quantitative studies have tested this assumption. Countershading in general reduce the conspicuousness of the dorsum and shadow of an animal under various lighting situations (Braude, Ciszek, Berg, & Shefferly, 2001). Thayer (1896) and Cott (1940) named this originally “obliterative shading“, although nowadays “countershading“ is used (as cited in Rowland, 2011; Ruxton, Speed, et al., 2004). Poulton (1902) discussed the widespread occurrence of countershading (“the wide underside“) in prey defense. Countershading as a definition is often used to refer both the appearance of the coloration and to the mechanisms by which prey may be protected (Rowland, 2009); although most researchers agree that the term refers to the phenotype and not the function (Rowland, 2009; Rowland, 2011; Ruxton, Speed, et al., 2004; Stevens & Merilaita, 2011).

2.3.1 Concealment mechanisms of countershading

Increasing crypsis by a countershaded color pattern may operate in two different ways. First, the most common used explanation for the protective mechanism of countershading is self-shadow concealment (SSC; Kiltie, 1988; as cited in Rowland et al., 2008). SSC compensates directional light that falls on a bodyside and produces a shadow on the opposite side (Rowland et al., 2008; Merilaita & Stevens 2011). A clear explanation give Kamilar and Bradley (2011): An animal without a countershaded body would have a lighter dorsal part when lightened from the sun from above and also produce a self-cast shadow. Therefore in countershaded animals, the dark dorsal surface becomes lighter from the sun, and the lightly colored ventral surface becomes darker from the produced shadow. Due to this, SSC can also change the three-dimensional appearance of the individual. Detection cues of a three-dimensional shape are impeded by obscuring lightness differences caused by directional light (Merilaita & Stevens, 2011). This results in reducing the capacity of a visual predator to detect and to recognize bodies as three-dimensional when viewed from the side (Behrens, 2009; Ruxton et al., 2004).

The second mechanism by which countershading shows a cryptic function concerns background matching. A dark dorsal coloration pattern may appear less conspicuous to objects from above, because it matches the dark color of the ground. Alternatively, an animal with a lighter underside may match the bright sky from the perspective of a terrestrial individual below (Kamilar & Bradley, 2011; Rowland, 2009; Ruxton, Sherratt, et al., 2004). Therefore self-shadow concealment depends also on the viewer's position and makes animals less conspicuous to their predators or prey (Gotmark, 1987).

Rowland (2009) notes that there is a general lack in empirical testing of the mechanisms by which countershading reduce predator attacks. She lists four main mechanisms which may aid concealment: (1) self-shadow concealment which results in improved background matching (2) SSC which flattens the form when viewed from the side (and hinders shape perception); (3) background matching when viewed from above or below; and (4) body outline obliteration when viewed from above (important in the context of edge properties). Ruxton, Speed et al. (2004) had similar suggestions, pointing out that countershading could be interpreted as background matching against the countershading of the fish´s flank when the animals are viewed from the side; and as background matching when viewed from above or below. In contrast to Rowland (2009), Ruxton, Speed, et al., however note that self-shadow concealment works only when the animal is viewed from the side.

2.3.2 Tests of concealment

a) Pastry larvaes:

Some authors conducted direct empirical studies testing the detection rate of countershaded artificial pastry prey. For example Edmunds & Dewhirst (1994) followed the early ideas of other colleagues (de Ruiter, 1956; Turner, 1961) to show the survival value of countershaded prey, but with four different types of bait. In this and the following experiments countershaded caterpillars are made by connecting small half-cylinders of dark and light shaded green-colored pastry along the long axis, to create a two-tone ‘caterpillar’. In their study they found that uniformly light prey and reverse-shaded prey were taken the most by wild birds, which is consistent with the hypothesis that countershading enhances protection by obliterating ventral shadowing. Speed et al. (2005) used similar study designs, presenting also dark, light, countershaded and reverse shaded pastry prey and birds in the field as predators. They found that the efficacy of countershaded baits vary with species of predator, discovering that blackbirds were taking countershaded prey least often, but blue tits and robins showed no special preference. Apart from this stunning result, they also received data sets in which countershading provided no crypsis enhancement compared to plain dark prey. Speed et al. supposed that this may be due to varying effectiveness of countershading crypis in visual conditions different than those used in the experiment.

Rowland (2007) later extended the study design and presented the prey to free living birds on lawns and to individual blackbirds on color-matching green boards. In both experiments countershaded prey was superior to uniform colored prey in reducing predator attacks, and therefore matched the predictions of enhanced crypsis. Concerning a key criticism of the theory of SSC through countershading, Rowland et al. (2008) planned a following study under a range of illuminations and diurnal changes. They presented artificial prey resembling lepidopteran larvae on the upper and lower surfaces of branches of beech trees with the sun varying across the day (see Fig. 9). This incorporated many different viewing angles of free living predators under natural lighting conditions. Dealing with quantitative measure of background matching for countershaded animals they analyzed pastry and background reflectance spectra for assessing the match of the pastry prey color according to bird vision. This design is especially important because it tries to address the color perception of the animal which is viewing the object, independently of human perception (Rowland et al., 2008).

Figure 9: Artificial pastry prey pinned on the upper surface of a tree branch.
From left to right: Dark, countershaded, light, and reverse-shaded prey (Rowland et al., 2008, p. 2541).

When presented on the upper surface of tree branches countershaded prey showed a higher survival rate compared to uniformly colored prey, like in the study of Rowland et al. (2007). This result maintained also when the prey was fixed on the underside of a branch, simulating the resting position of tree-living caterpillars. A reversal of the orientation of countershaded coloration, with a dark surface closest to illumination therefore also enhances protection from predation (which is used by some reversed countershaded animals). Rowland et al. (2008) conclude that these findings provide evidence that a dark surface closest to illumination provides a camouflage benefit and a significant survival advantage against avian predators.

b) Properties of countershading related to habitat, activity and movement:

The degree of contrast seems to be related with the habitat and activity of animals (Rowland, 2011). Kiltie (1989) demonstrated on grey squirrels (*Sciurus carolinensis*) that countershading may work, but only if squirrels are horizontally but not vertically orientated. For that Kiltie took photographs of squirrels when illuminated from above and placed horizontally or vertically, and later measured the effect of dorsoventral contrast on shadow obliteration.

Another indirect evidence comes from Braude et al. (2001), who investigated naked mole-rats (*Heterocephalus glaber*). In these animals countershading (purple-grey dorsal but pale pink ventral skin) appears in young individuals from 2-3 weeks of age. Newborn mole-rats, most queens, breeding animals and animals older than 7 years don´t show this coloration pattern and are uniform pink. The authors suggest that countershading may provide camouflage when young naked mole-rats are above ground attempting to disperse, and animals that are unlikely to leave the burrow like older workers and reproductives may lose this coloration pattern. Braude et al. also give alternative hypotheses for pigmentation (protection from UV light; thermoregulation; protection from abrasion) which will be mentioned later (see “other functions of countershading“).

Others investigations concerning countershading include animals like even-toed ungulates (Stoner, Caro, & Graham, 2003), and for example a paper of Gotmark (1987) showing that gulls are less efficient at catching fish when painted black on their underside.

Kamilar (2009) used a comparative approach to explain countershading in primates, taking photographs of museum skins to quantify the luminance values of the ventral and dorsal surfaces. The results showed that interspecific variation in countershading (Bradley & Mundy, 2008; Caro, 2005) is related to group size, positional behavior and body size. He found that the degree of countershading diminishes as body mass increase, explaining that this could be because large animals show lower levels of predation risk than small ones. Also, species in large groups seem to show increased conspicuousness, but this has no effect on countershading intensity. Further, Kamilar and Bradley (2011) showed that primates of any size that mainly position themselves vertically show weak or absent countershading, independent of their body mass and group size. Concluding to the authors an advantage of crypsis seems only gained when being horizontal, like Kiltie (1988, 1989, 1992) proposed earlier in squirrels. In general, for anti-predator benefits gained from countershading the relationship between the direction of the light source and the animals’ body is important (Kamilar & Bradley, 2011).

Concerning countershading in nocturnal animals, Kamilar (2009) showed that nocturnal and diurnal primates show similar grades of countershading, which refutes the UV-protection hypothesis as an alternative function of countershading. This suggests that nocturnal species also gain an antipredator benefit, which could partly be due to the relationship between body mass and countershading, because all nocturnal primates have small bodies, but is also associated with increased activity levels under bright moonlight.

c) Conclusion of concealment experiments:

The results of several studies under a variety of different conditions, like natural and artificial environments, or under changing light, provide evidence that countershaded color pattern reduces detection and predation through SSC. The actual countershading mechanisms by which attacks are decreased still miss investigation and it is unknown if the functions that deceive the human visual system also function like this in animals (Rowland, 2011; Rowland et al., 2008).

2.3.3 Special forms of countershading

a) Reverse countershading:

In most animals the dorsal parts are dark and the ventral side light. In some caterpillars (such as the privet hawk moth) and fish (such as catfish of the Mochokidae family) the normal resting position is inverted, facing the underside upward and the back downward. The mechanism of these is called reverse countershading (Ruxton et al., 2004; Rowland, 2011). The prediction from the theory of SSC for this is that they should have a light dorsa and dark ventral, such that the orientation of countershaded coloration is reversed, but the reduction of shadow kept maintained (Rowland et al., 2008). This is consistent with the founding that prey showing lighter dorsal surfaces indeed often rest or orient themselves upside-down (Chapman et al., 1994) and also provide evidence that a reduction in pigmentation on the side of an animal furthest form the light source provides a camouflage benefit (Rowland et al., 2008).

b) Counterillumination:

Another important mechanism related to countershading is counterillumination, appearing mainly in water habitants. Ruxton, Sherratt et al. (2004) mention that some animals use bioluminescence to produce light that matches the down welling ambient light to be protected from detection from below. Further they supposes that the primary mechanism for counterillumination seems background matching and not self-shadow concealment, because in the sea individuals can be attacked from any direction, not only from the side.

2.3.4 Critics of the concealment theory through countershading

Like noted earlier in this chapter, countershading may be influenced by a variety of variables like the direction and brightness of the sun (Rowland, 2011). Ruxton, Sherratt et al. (2004) state that SSC works best in water, because light in water is equally distributed. In contrast, self-shadow concealment in terrestrial animals seems determined by the direction of the light source, which varies with time, season and clouds (Kilite, 1988; as cited in Rowland, 2011). A key criticism of the theory of SSC through countershading for predation protection consists of the argument that diurnal changes of the sun light may render SSC ineffective, because not all illumination comes directly from overhead (Ruxton et al., 2004). Rowland et al. (2008) have already discussed this critic, showing that shadow concealment also works for countershaded prey in woodlands where lighting is often diffuse and non-directional. They demonstrated that diurnal variation of the sun doesn´t result in a failure of countershading compensation for the varied shadows, leaving prey in total for 66 hours (Rowland, 2009).

2.3.5 Other functions of countershading

Alternative explanations for countershading apart from concealment are protection from UV, thermoregulation and protection from abrasion. They are explained more detailed for example by Braude et al. (2001) and Rowland et al. (2008). Summarizing, many evidences in different groups of animals raise doubts about these explanations, considering them present day as rather unlikely (Rowland, 2011; Braude et al., 2001; Kamilar, 2009; Kamilar & Bradley, 2011), so that more data would be needed. One exception from this is countershading in penguins that may aid thermoregulation, with the animals turning their backs to the sun when cold, and their white undersides to the light when hot (Chester, 2001; quoted by Rowland, 2011, p. 67). This would also be an answer to the critic raised by Ruxton, Sherratt et al. (2004), who suggested that penguins white underparts would only function under specific circumstances, because penguins approach their prey from all directions.

3. Underwater Camouflage

All categories of camouflage known on land, including mimicry, disruption, simple matching and motion camouflage appear also in the sea, although there are great differences in camouflage and visual systems between animals on land and in the water (Marshall & Johnsen, 2011). Typical strategies in underwater habitats are silvery camouflage, transparency and bioluminescent countershading, which will be mentioned briefly. Like in all animals, the visual systems of potential observers must be explored to understand camouflage strategies used in the sea. Concerning underwater perception it seems of special interest how other fish and sea animals perceive colors. Overall, the most fascinating animals for studying camouflage and visual systems in animals seem to be cephalopods, which are described more detailed in a following part. Also, various organisms in the water attempt to appear very un-fish-like, to name examples like the stonefish or the leafy seadragon (see “masquerade“).

Concerning the different depths and water habitants’ one should also always be aware of the varying properties underwater. For example, the mid-water environment differs from coral reefs in many ways, there are no objects to hide behind and also the water is far clearer (Marshall & Johnsen, 2011). Some of the many adaptions developed by animals to possess better sight also in deep depths, are for example eyes or retinal areas pointing upwards or downwards with increased resolution (Land, 2000; Locket, 2000). Before illustrating types of underwater camouflage, some properties of visual perception underwater have to be mentioned, such as light and color perception:

Light underwater:

Reflection, refraction and other physical processes like absorption and scattering have an influence on light when it passes between objects and the medium surrounding it (Marshall & Johnsen, 2011; Ruxton, Sherratt, et al., 2004). Marshall and Johnsen (2011) noted that different visual systems of sea-animals can be due to physical differences of the light field in water and on land, because “underwater light is dimmer and more varied in spectral and spatial distribution“ (p. 91). This and the differences in path-length of travelling light results in a relatively dark side-welling and upwelling light field (Marshall & Johnsen, 2011).

Color perception underwater

Color of an object depends on both its reflectance and on the light illuminating. Therefore even pure water appears blue, because it preferentially absorbs red and orange light (Lythgoe, 1976; Marshall & Johnsen, 2011).

The ability to resolve details in water is far worse than on land, this fact seems especially relevant for patterned animals, meaning that stripes and color-spots become easily blurred (Marshall & Johnson, 2011). Studies (Marshall, 2000; Marshall, Jennings, McFarland, Loew, & Losey, 2003) working on how aquatic animals appear to each other show that most of the colorful patterns are used for camouflage function and to a far lesser extent for advertisement of mates and sexual selection. The evidence that some animals are color-blind (Marshall & Messenger, 1996) makes consider that animals like the cuttlefish use intensity rather than wavelength information.

3.1 Special forms of camouflage underwater

1) Transparency

Transparent organisms are challenging to detect, which makes transparency likely to be effective in mid-depths of open water regions (Ruxton, Sherratt, et al., 2004). Due to lesser refractive index difference between bodies in the water and the surrounding water there are fewer reflections from the body surface, so that transparency is easier to achieve in water than air and therefore more common in aquatic than terrestrial individuals (Marshall & Johnsen, 2011; Ruxton, Sherratt, et al., 2004). Another thing that can influence the cryptic function of transparency is polarization of light in water, and therefore animals that are sensitive to the polarization of light, may use this to detect transparent prey more easily. Among them are several fish, crustaceans and cephalopods. Additionally, also UV radiation can be an important factor in prey-predator relation, revealing for example transparent zooplankton to organisms with UV vision (Johnsen & Widder, 2001).

2) Silvery

Some fishes use silvery platelets around it´s body which reflect the surrounding water, making the animal inconspicuous. Due to this produced vertical mirrored surface, the object is hard to detect as it seems like a sub-sample of the background (Stevens & Merilaita, 2009; 2011). This mechanism is effective except at certain viewing angels where surface illumination may be reflected (Marshall, 2011, p. 205).

3) Bioluminescence

Ventral bioluminescence is often used to match spectral distribution of light at different depths and can be seen as a special case of countershading (Ruxton, Sherratt, et. al., 2004). Many deep-sea species (such as the lanternfish) use photophores for illumination of ventral surfaces to be protected from predators from below (Claes, Aksnes, & Mallefet, 2010; Claes & Mallefet, 2010; Johnsen, Widder, & Mobley, 2004). The appearance of counterillumination seems to be more affected by the viewers' visual acuity than by the water clarity, breaking the camouflage even at large distances (Johnsen et al., 2004).

4. Cephalopods

The fascinating cephalopods seem especially suited for observing sensorial systems of camouflaging animals and will therefore be presented more detailed. Most animals have a slowly changing camouflage pattern, but coleoid cephalopods (such as squid, octopus and cuttlefish) possess a different defense strategy against their predators. They are unique in the animal kingdom because of their exceptional ability to quickly alter their body patterns. This occurs on a wide variety of different backgrounds such as colorful coral reefs, sand, stones, or seagrass, therefore achieving dynamic camouflage (Hanlon et al., 2011). The skin of cuttlefish is neurophysiologically controlled and can vary in color, brightness and texture, allowing rapid changeable coloration and producing a large number of different body patterns (Barbosa, Litman, & Hanlon, 2008; Barbosa, Mäthger, et al., 2007; Hanlon, 2007; Hanlon et al., 2011; Hanlon & Messenger, 1988).

4.1 Body patterns

In the investigation of cuttlefishes other classifications than that described in the first chapter had been established. Instead of differentiating for example background matching or countershading based on their cryptic function (Stevens & Merilaita, 2011), Roger Hanlon and his colleagues define camouflage types based primarily on appearance. Therefore the different types of camouflage patterns used by cephalopods can be synthesized into three major categories: uniform, mottle and disruptive patterns, as shown in Fig. 10 (Hanlon, 2007; Hanlon et al., 2009; Hanlon et al., 2011; Hanlon & Messenger, 1988):

Uniform body patterns are characterized by minimal variation in contrast, in which the whole body of the cuttlefish presents a single design.

A subset of uniform can be classificated as Stipple patterns, described by a uniform distribution of small roundish dark spots, presenting an early transition phase to mottle patterns.

Mottle patterns consist of small-scale light and dark components and some repetition of parts of the pattern covering the body, which correspond roughly to objects in the visual background. There is low-to-moderate contrast between the light and dark patches of the body pattern.

Disruptive body patterns consist of irregular large-scale light and dark patches of varying shape, orientation, scales and contrasts.

In the common European cuttlefish (*Sepia officinalis*), disruptive patterning is most commonly characterized by variable expression of eleven chromatic components, namely five light (such as the white square (WS), white head bar and white mantle bar) and six dark (Chiao, Kelman, & Hanlon, 2005; Kelman, Baddeley, Shohet, & Osorio, 2007; Mäthger et al., 2007) Among these disruptive components, the most important white square of a cuttlefish is expressed when there are other light objects of similar size in the visual background, thereby achieving crypis (Barbosa et al., 2007).

To approach the established general classification of camouflage types, it has shown that uniform and mottle patterns are used for background matching, whereas the disruptive body pattern act through background matching as well as disruption (Buresch et al., 2011; Hanlon et al., 2009).

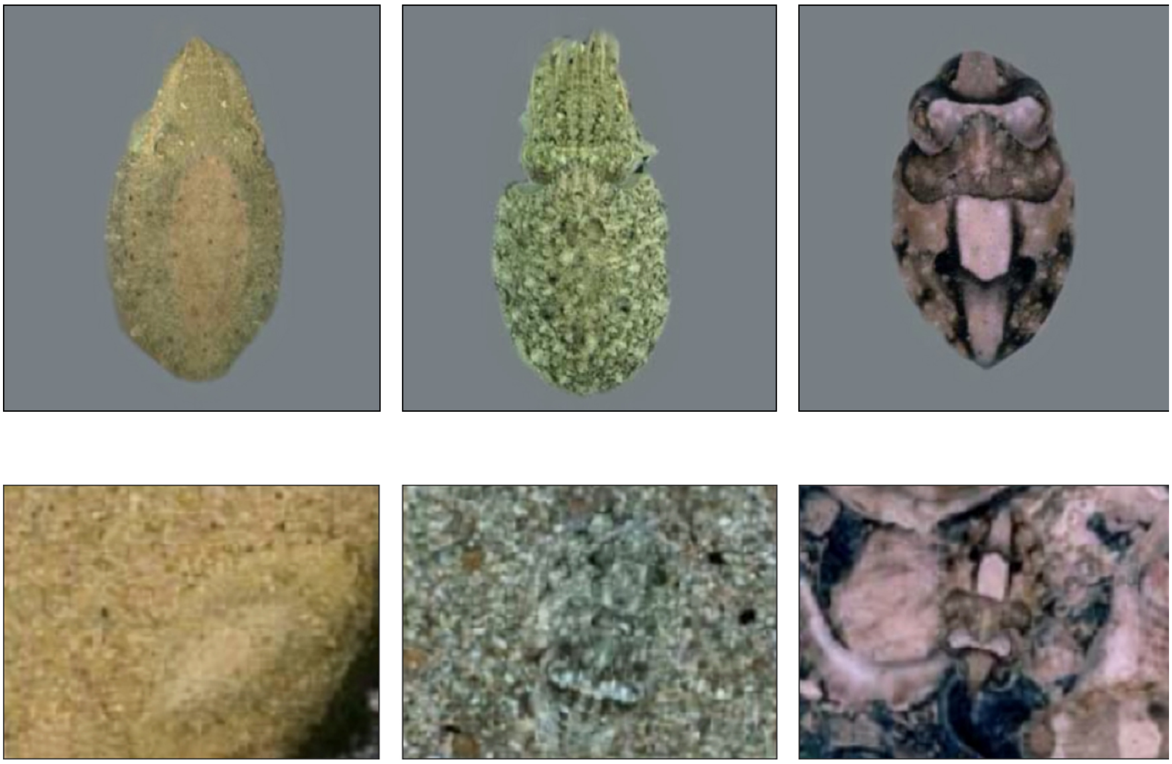

Figure 10: Body pattern forms of cuttlefish.
From left to right: Cuttlefish *Sepia officinalis* showing uniform, mottle and disruptive pattern (Hanlon et al, 2009, p. 430).

Quantitative methods

This classification of uniform, mottle and disruptive patterns based on descriptive methods using different grading schemes of patterning, is also proven statistically by quantitative properties (Hanlon et al., 2011). Various researchers (Barbosa et al., 2008; Chiao, Chubb, Buresch, Siemann, & Hanlon, 2009; Chiao et al., 2010) used fast Fourier transform to analyze different spatial frequency bands (or granularity bands) of cuttlefish images, which measure the size of the light and dark patches as well as their contrast on the body. The resulting shapes of granularity spectra distinguish between uniform, mottle and disruptive patterns.

Further, principal components analysis (PCA) of body pattern responses to artificial backgrounds have also been performed (Zylinski & Osorio, 2011). A majority of the variance between body patterns can be described by two or three principal components (Kelman et al., 2007; Zylinski, Osorio, & Shohet, 2009b). Zylinski and Osorio (2011) however comment that the low number of Pcs could be an artifact of the visual parameters used in the artificial backgrounds (mostly checkerboards) and an impoverished representation of what the animal is capable of.

“Behavioral components“

Although most cephalopod research consists of describing and eliciting the different color patterns, Hanlon and Messenger originally identified in 1988 four types of components that cuttlefish use to control their appearance. These are a) chromatic (coloration pattern), b) skin texture (rough or smooth), c) postural and d) locomotor components (see also (Crook, Baddeley, & Osorio, 2002; Kelman, Osorio, & Baddeley, 2008)).

4.2 Pattern eliciting experiments

Generally

European cuttlefish *(Sepia officinalis)* seem to be particularly suited for testing the visual cues that control the adaption of body patterning. They are especially well adapted to laboratory environments and their camouflage response can be observed through presenting a wide range of different backgrounds, using natural as well as artificial materials. In recent years, the static body patterns of cuttlefish have been studied in detail and there´s a long list of experiments offering substances (like checkerboard images, rocks, shells or three-dimensional objects) in all different sizes and forms that are known for evoking the three camouflage body pattern types (Allen, Mäthger, Barbosa, et al., 2010; Barbosa et al., 2008; Buresch et al., 2011; Chiao, Chubb, & Hanlon, 2007; Mäthger, Barbosa, Miner, & Hanlon, 2006; Mäthger, Chiao, Barbosa, & Hanlon, 2008).

Which factors influence the type of pattern?

Previous studies have shown that many factors are essential for eliciting body pattern types, like area, contrast, edges, texture perception, depth and motion. Factors that mainly influence the type of produced pattern are spatial frequency, contrast and whether or not it contains any bright elements of roughly the size as the cuttlefish White square (Hanlon et al., 2011). The White square has already been subject of a lot of studies, concerning the sizes of objects in the background (different types of gravel as also varying sizes of checkerboard components). For early examples of used checkerboards see Fig. 11. For example it has shown that mottle body patterns can be elicited on black and white checkerboards with a check size of 4-12% of the animals White square or by light and dark gravel which have roughly the size of the WS (Barbosa et al., 2008; Barbosa et al., 2007; Chiao et al., 2010; Shohet, Baddeley, Anderson, & Osorio, 2007). Disruptive body patterns on the other side are evoked with checks approximately 40-120% of the cuttlefish´s White square area or equivalent sized rocks, shells or gravel (Barbosa et al., 2008; Barbosa et al., 2007; Buresch et al., 2011; Chiao et al., 2009; Chiao et al., 2007; Chiao et al., 2005; Kelman et al., 2007; Mäthger et al., 2007). In these studies it has also shown that on very fine-grained background (fine-grained sand or uniformly colored artificial backgrounds), cuttlefish show a strong tendency to produce uniform body patterns.

Additionally, if the contrast of checkerboard backgrounds is manipulated, cuttlefish show low-contrast uniform/stipple patterns on low-contrast checkerboards (Barbosa et al., 2008; Zylinski et al., 2009b). This shows that irrespective of check size, the contrast of the animals´ body pattern increase by raising substrate contrast.

Another important factor that influences the choice of body patterns is the presence of light elements in the background. Even a single white object in an almost entirely homogeneous background produces a disruptive pattern, regardless of shape (Chiao & Hanlon, 2001a) or size and age of the cuttlefish (Barbosa et al., 2007).

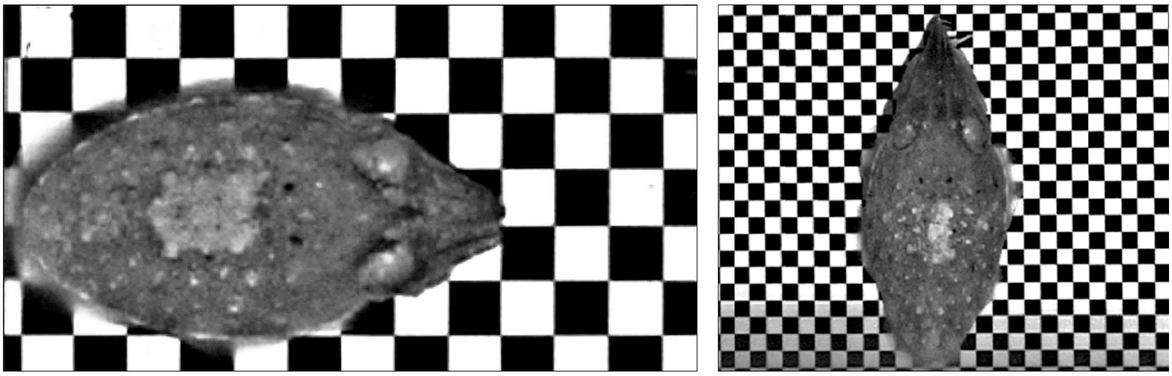

Figure 11: Cuttlefish on squared testing material.
Cuttlefish on squared substrate with a checker size of 13,0mm (left) and 6,5mm (right) (Chiao & Hanlon, 2001a, p. 2122-2123).

Background preference and movement

Observations and laboratory tests assume that cuttlefish do not have a preference for a particular substrate type on which to express a specific body pattern, this supports the animals’ adaption to quickly cope with different habitats because of their predation pressure (Allen, Mäthger, Barbosa, et al., 2010). Interestingly

Buresch et al. (2011) tested if cuttlefish prefer to resemble a 3D object or if they prefer to camouflage to the substrate. In doing so, they discovered that a high contrast would produce a preference to masquerade like the 3D object, emphasizing the role of contrast.

Zylinski et al. (2009a) showed that the body pattern used during movement is context dependent and may be distinct from patterns used when stationary. S. officinalis uses the same pattern during motion when it moves over a background which elicits uniform or mottle patterns, but when moving on substrates that evoke disruptive body patterns cuttlefish reduce their high-contrast elements such as the white square and the white head bar. This could be due to limitations of processing visual information during movement or a tactic to reduce conspicuous components of high contrast during movement (Zylinski & Osorio, 2011).

Some octopus also carry around halves of coconut shells (for using them as a shelter when needed), showing “stilt walking” during movement. This object manipulation is however rather an example of tool-using behavior (Finn, Tregenza, & Norman, 2009).

4.3 Properties of cephalopods

a) changeable skin papillae

In general cuttlefish are able to change their appearance rapidly, in less than one second (e.g. Hanlon, 2007). Their three-dimensional skin is under fine motor control, serving a variety of behavioral functions. Apart from the pigmented chromotaphore organs their skin consists also of iridophores and leucophores, which act as structural reflectors (Hanlon et al., 2011). Concerning the physical texture of camouflage the changeable skin papillae are especially fascinating, ranging from being smooth to spiky and therefore changing their textural appearance (see Fig. 12). Allen et al. (2009) described nine distinct sets of papillae and demonstrated that the skin papillae is regulated by visual input only, without needing tactile information, although Kelman et al. (2008) suggested that substrate three-dimensionality is important for body patterning in cuttlefish testing this by using two and three-dimensional substrates.

Figure 12: Changeable skin structure of cuttlefish.
Sepia officinalis (indicated by the arrow), masquerading as a clump of seaweed (Buresch et al., 2011).

b) Posture

Shohet et al. (2006) found that *S. pharaonis* prefer to orient their body-axis perpendicular to stripes and assume that they maybe use visual patterns like sand ripples to determine water flow. Concerning arm postures of cuttlefish, it has been tested that *S. officinalis* position their arms according to the orientation of stripes which were oriented at 0°, 45° and 90° in relation to the animals´ long axis (Barbosa, Allen, Mäthger, & Hanlon, 2012). This shows that at least some cuttlefish also use visual cues to determine arm postures for camouflage. In general, body patterning has been studied well, whereas body postures and their implementation on different backgrounds have seldom been tested experimentally.

c) Colorblindness

Cuttlefish have been shown to be colorblind (Marshall & Messenger, 1996; Mäthger et al., 2006; Mäthger, Roberts, & Hanlon, 2010), which seems extraordinary, considering that this does not affect their camouflage ability. Regardless of their colorblindness, their color match to natural visual backgrounds appears to be perfect, as many of the cuttlefish predators have two, three or even four visual pigments.

Their colorblindness has been tested in various ways, showing that cuttlefish only respond to differences in intensity, but not in wavelength (Marshall & Messenger, 1996). For example, Mäthger et al. (2006) created different checkerboards substrates (black-white paired with green shades; blue-yellow checkerboards) with various gradings and intensities. Cuttlefish showed non-disruptive coloration on the checkerboards whose color intensities were matched to the Sepia visual system, suggesting that the perceive the substrates as uniform backgrounds.

To measure quantitatively the color match between animal and background, Chiao et al. (2011) used hyperspectral imaging (HSI) discovering that camouflaged cuttlefish show good color match as well as pattern match in the eyes of fish predators.

A recent study discovered also a possible mechanism of light sensing by the skin of cuttlefish, founding the opsin transcripts presented in the eye also in the fin and ventral mantel skin (Mäthger et al., 2010). Future research is needed to investigate the possibility of color sensing in the skin.

d) Night vision

It has also been shown that giant Australian cuttlefish (*S. apama*) use their excellent night vision to perform adaptive camouflage even in dim light to deceive their prey or predators. In these experiments animals also responded to changes in the substrates in the nighttime with appropriate changing camouflage patterns (Allen, Mäthger, Buresch, et al., 2010; Hanlon et al., 2007).

e) Communication

Mäthger, Shashar and Hanlon (2009) have postulated that cephalopods may communicate intraspecifically through polarized reflective patterns, which are produced by their skin. Most of their predators cannot perceive polarized light, resulting that cuttelfish could send signals to conspecifics, while remaining well camouflaged (Mäthger & Hanlon, 2006).

4.4 Cephalopods and their predators:

Visual camouflage is the primary defense of cuttlefish against their predators, who are nearly all of the major carnivores in the ocean (marine mammals, diving birds, teleost fishes). Many of them have di,- tri,- or even tetrachromatic vision, that explains the cuttlefish need of perfect color matches to backgrounds (Chiao et al., 2011). Researchers should concentrate on the color vision of the species that is changing color, and of their signal receivers (Cheney, Skogh, Hart, & Marshall, 2009; Chittka, 2001; Stuart-Fox, Moussalli, & Whiting, 2008; Thery & Casas, 2002; Thery, Debut, Gomez, & Casas, 2005).

Therefore the investigation around cuttlefish camouflage should start with studies about how predators perceive them to further understand how the avoidance of detection and recognition works. Buresch et al. (2011) noted that predators can view cuttlefish from different points of view, like swimming predators perceive them vertically down against the substrate while benthic predators view them horizontally against vertical 3D objects on the substrate. Since visual predation also occur in the night it has shown that *Sepia apama* use their excellent night vision for adaptive camouflage in dim light (Allen, Mäthger, Buresch, et al., 2010; Hanlon et al., 2007), like mentioned above.

Live predator-prey experiments in nature are necessary for understanding camouflage systems fully, but predator-prey testing with cephalopods has yet to be realized, in contrary to already existing experiments with insects). New research is working with high-definition video material, hoping to film foraging cuttlefish or octopus while predicting which camouflage pattern it will show on different backgrounds (Hanlon et al., 2011).

4.5 Sex-specific behavior

Males of the giant cuttlefish *(Sepia apama*) have evolved mating strategies to fool guarding attempts of larger males by switching between the appearance of a female (for not getting attacked) and that of a male (Norman, Finn, & Tregenza, 1999). Often the successfully mate with the female, when the larger male is distracted by another intruder. A recent study from Brown, Garwood and Williamson (2012) revealed that also the male mourning cuttlefish (*Sepia plangon*) can display at the same time two different body patterns. To deceive rival males they display a male pattern to receptive females on one side of the body, and at the same time they show female patterns to a rival male on the other side, hindering the other male in disrupting courtship.

5. Decorating behavior

5.1. Decorator crabs

Decorator crabs in the brachyuran superfamily *Majoidea (majoids)* are a diverse group of crabs famous for attaching materials form the environment on their body (Hultgren & Stachowicz, 2009, 2011). This special form of camouflage depends both on crab morphology and behavior. With morphological component the adaptation of the hooked setae (that facilitates decoration) is meant, and behavioral aspects concern the distinct preferences of crabs of how much to decorate and with which material.

Concerning the adaptive value of decoration, decoration can function as an anti-predator behavior by use of pre-detection defense or post-detection defense. This takes place by reducing the probability of detection or by reducing the probability of recognition or eating when detected, as with other forms of camouflage. An example for the last one would be the use of decoration that makes the crab chemically noxious or smelling like something other than a crab (Stachowicz & Hay, 2000). This also suggests a role for decoration as non-visual crypsis. Other functions of decoration may be food storage, intraspecific signaling or prey capture, although these are not considered as primary function (Cruz-Rivera, 2001; Hultgren & Stachowicz, 2011). The experimental tractability of decorator crabs and their willingness to redecorate readily in the laboratory seem to make them a preferred object of investigation, just as cuttlefish.

5.2. Web decorations

Diverse functions have been connected to the visual appearance of webs, spiders and web decorations, including prey attraction, predator deterrence and camouflage (Thery, Insausti, Defrize, & Casas, 2011).

Spider camouflage includes web color and decorations, body color and movement. The design of webs can facilitate prey capture by making them difficult to detect, although particular silk may also attract prey. Web decorations are structures spanned in webs mostly made of silk but also with a combination of silk and organic items. The silk decorations were originally thought to stabilize the web, therefore they were originally called stabilimenta. Nowadays other functions like camouflage and prey attraction are investigated, revealing for example that when prey attraction function is supported, the anti-predator function is not (Thery & Casas, 2009).

Various experiments concentrate on the functions of web decorations from a predator´s point of view (birds and hymenopterans) by calculating color contrasts of the decorations against the spider´s body.

For example while using spectrophoto-metric analysis it has found that silk decorations were highly conspicuous to both honey bees and birds over short and long distances (Bruce, Heiling, & Herberstein, 2005). Rao et al (2009) could show that the function of decorations may be to confuse the attack of predators. They revealed that with the visual system of birds as well as through the eyes of Hymenoptera, web decorations are perceived more conspicuous than the bodies of the orb-web spider (*Argiope radon*) resting on it (as cited in Thery & Casas, 2009). Additionally a connection between blue and UV light of prey sensitivities and attracting insects has been proven (Blamires, Hochuli, & Thompson, 2008; as cited in Thery & Casas, 2009).

Tan and Li (2009) suggested that detritus decorations (of *Cyclosa mulmeinensis*) have different success rates, depending on their predators and on the decoration type. Gan, Liu, Zhang and Li (10) however showed that orb-web spiders (*Cyclosa octotuberculata*) were camouflaged for both hymenopteran and bird predators over short and long distances. Tseng and Tso (2009) showed that webs (of *Cyclosa mulmeinensis)* with more decorations are attacked more frequently by wasps, mainly because they serve as distractors for predators. In natural settings such conspicuous web decorations would enhance the survival rate.

Recent studies consider the visual systems of prey and predators and light environments, although there is still a lack of comprehensive understanding of, for example, color vision in the same spiders. Visual modeling shows that most often the prey attraction and predator confusion hypothesis is supported and not the hypothesis of spider camouflage by decorations (Thery et al., 2011).

6. Deflection and startling of predators

Animals possess many coloration tactics to minimize the risk of predation, these include, apart from camouflage, also startling signals like “eyespots“ and defensive markings like warning coloration (Stevens, 2007).

6.1 False eyes / eye spots/ false head markings

Various species possess “eyespots”, namely paired circular rings of contrasting colors that prevent being attacked by startling or intimidating their predators (Merilaita et al., 2011; Stevens, Hardman, & Stubbins, 2008). These “false eyes” are round or oval with round or slit pupils and have been mostly studied in insects, especially in lepidopteran species and caterpillars (Janzen, Hallwachs, & Burns, 2010; see Fig. 13). However they are also found on many other animals such as birds, on the fins of various fish (Stevens, 2005) and also on squid (Mäthger & Denton, 2001). It is well known that spots are effective antipredator signals, although it is not clear how they work. Most popular and scientific explanations of wing or fin spots suggest that they mimic eyes, because humans tend to see a similarity between many eyespots and eyes (Merilaita et al., 2011). The color patterns don´t match closely a specific eye model, but even a glimpse of them seems to give the illusion of eyes. Depending on the observation angle of the spots and nearby body parts, the pattern may even resemble different faces (Janzen, Hallwachs, & Burns, 2010).

Figure 13: Eye-like color patterns on tropical caterpillars.
Effective antipredator signals on lepidoptera. From left to right: *Iliana Hesperiidae*, *Rifargia phanerostigma*, *Euselasia cheles*, *Tromba xanthura* (Janzen et al. 2010).

However this eye mimicking seems to be difficult to prove or falsify. Stevens, Stubbins and Hardmann (2008) showed that high contrast and conspicuousness are more important factors than eye mimicry. They show in experiments with eyespots on camouflaged and conspicuous artificial prey with wild birds, that the protective value is strongly influenced by the characteristics of the target which shows them. Wing spots on conspicuous prey avoid attacks, but on otherwise camouflaged targets increase the attack rate. Stevens, Stubbins and Hardmann (2008) conclude that the context of protective signals is determining the success, showing also the interaction of different anti-predator strategies.

In general, two main hypotheses explain the antipredator mechanisms of eyespots. The first asserts that eyespots mimic the presence (of the eyes) of the predators own enemies, meaning that false eyes trigger fear or flee reaction in for example insect-eating birds because they mimic the eyes and faces of their predators as snakes, lizards or other birds in a natural surrounding (Janzen et al., 2010; Merilaita et al., 2011; Stevens, 2005; Stevens, Hardman, et al., 2008). The second suggests that simply the conspicuousness of an eyespot pattern is intimidating other animals and reduces the risk of predation. Possibly due to a sensory bias this promotes avoidance behavior which is independently of the eye mimicry level (Merilaita et al., 2011; Stevens, Hardman, et al., 2008). Also it has been supposed that eyespots function as deflection of predator attacks to other parts of the body, which is not necessarily conflicting to the above mentioned explanations (Stevens, 2005).

Some experiments have been conducted to test if wing spots intimidate predators because of eye mimicry or because of conspicuousness. Stevens, Hardmann and Stubbins (2008) tested the influence of the number, size, shape and displacement of eyespots, creating paper prey with an edible dead mealworm pinned on trees. The noncontrol targets had different stimuli with a black center and a white surrounding, that varied in the characteristics depending on experiments (see Fig. 14). All trials testing spot number and size, spot shape, and spot component displacement support the conspicuous signal hypotheses of explaining avoidance behavior in predators and don´t favor eye mimicry.

As a consequence, Stevens, Hardman et al. (2008) recommend using the terms “wing spot” or “fin spot” instead of eyespot.

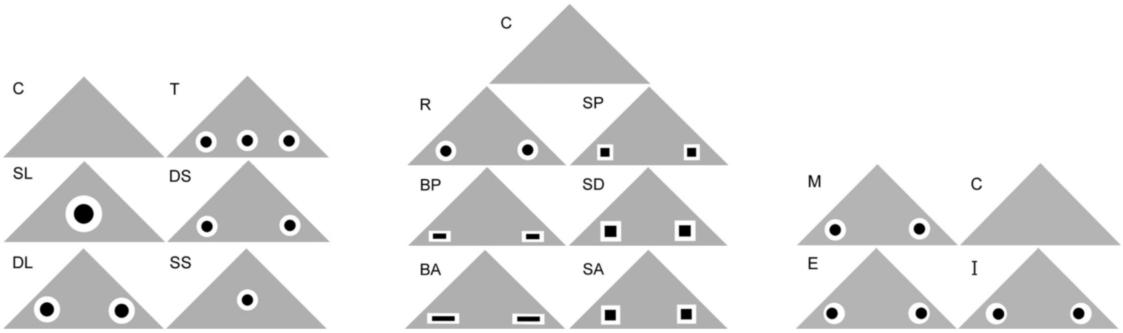

Figure 14: Paper prey for testing the effects of wing spots.
Left: Spots varying in size and number, middle: varying forms (spots, squares, bars), right: spots with the central black component in the middle, displaced outward and displayed inward Materials used by Stevens, Hardmann and Stubbins (2008, p. 527-528).

More recent intents concentrate on innate reactions and naïve predators. Janzen, Hallwachs and Burns (2010) focused on false eyespots of tropical lepidopteran species and pupae and the reaction of their predator birds. The aim of their study was to reveal if the avian reaction to false eyes is innate or rather learned. Janzen and co-workers postulate that the eye-like color patterns displayed by hundreds of tropical caterpillar species constitute an evolutionary generated mimicry complex. Further the authors suppose that their insect-eating predators are innately programmed to flee when they see an eye of another species or something that resembles an eye. This is been argued by the great amount of "false-eyed" caterpillars and pupae that an insect-eating bird may meet per day (tens to hundreds), and the small probability that a bird would learn about each species individually. The comparison with other mimicking species or with the eyes of their own potential predators seem to be very unlikely, because the risk of getting eating while learning to avoid predators would be far too high (Janzen et al., 2010).

Merilaita and colleagues (2011) studied the effect of the number of eyespots (none, two or four) on the peacock butterfly (*Inachis io)* and how it influences intimidation (see Fig. 15). Naïve insectivorous birds (pied flycatcher, *Ficedula hypoleuca*) were presented with different prey items, consisting of mealworms between the wings of dead butterflies.

The authors’ assumptions consisted in a maximum response with a pair of eyespots when eye mimicry is important, and even a stronger effect evoked by more than two eyespots when conspicuousness is important.

Eyespots increased hesitation before attacks, indicating that the response difference was innate, because the birds had been reared in captivity and were naïve to their natural prey and enemies. However, Merilaita and co-workers results on real butterfly color patterns don´t show differences in the deterring effect between prey with two or four eyespots, which contradicts the conspicuousness hypothesis and challenges it´s general explanation for intimidation caused by eyespots. It is suggested that eye mimicry or some still unknown reason explains the intimidating effect on the wings of the peacock butterfly (Merilaita et al, 2011).

Various interpretations of mimicry may need to be altered when the avoidance of “wing spots” is innate.

Figure 15: Peacock butterfly for testing the effect of varying number of eyespots.
Picture of a Peacock butterfly and edible mealworm-body with four eyespots, and after covering the other spots with two or none (Merilaita, et al., 2011, p. 1328).

The peacock is a special case that has to be mentioned when talking about eyespots. Although having a lot of typical spots on his beautiful feathers, these are not for distracting predators but rather develop their effect working on female peacocks through different mechanisms (Lunau, 2011).

6.2 Tails

Areas of color on the tail as shown for example in lizards, tadpoles and weasels may have the function of distracting predators away from vulnerable parts of the body (Caro, 2011; Stevens, 2005). The color of tails probably has several functions because a tail can be displayed or hidden and it might enforce aposematism, signaling to conspecifics, distraction of predators and prey, and also dazzle effects during movement (Caro, 2009).

7. Coloration and color patterns

7.1 In General

The classical experiment to understand functions of animal coloration patterns is to manipulate the color pattern and to examine the responses of the receiver. Examples for this includes studies those paint the body or bodyparts of an animal exposing it later to predators. Also the manipulation of the visual background and observation of the animal´s color response, like in attempts with cuttlefish, reveals information of visual processes and of how particular color patterns are activated (Stuart-Fox & Moussalli, 2009).

An animal´s capacity for color change can be limited by physiological constraints and its visual abilities (Stuart-Fox & Moussalli, 2011). Cephalopods colorblindness for example limits their ability for chromatic background matching (Hanlon, 2007). Like noted earlier, coloration and all traits related with camouflage may appear conspicuous to, for example, conspecifics while remaining concealed from other species or predators that have different visual capabilities (Stuart-Fox & Moussalli, 2011).

Stuart-Fox and Moussalli (2009) claim that color patterns have three primary functions, namely camouflage, communication and thermoregulation. Apart from this, also the earlier explained warning and startling signals play a role, consisting generally of color patches on tails or in form of eyespots.

Further, conspicuous coloration can be a protection from predators, if it signals unpalatability as in aposematism (Ruxton, Sherratt, et al. 2004). Conspicuous coloration can also prevent recognition of prey by dazzle or distractive markings (Dimitrova, Stobbe, Schaefer, & Merilaita, 2009) or disruptive camouflage (Stevens & Merilaita, 2009).

Color patches may be used as intraspecific signals. Also, colorful facial structures of males and red sexual swellings of females are used in sexual selection and can be explained evolutionary (Caro, 2005). Color traits can attract mates or intimidate rivals by signaling superiority, the first working as intersexual selection, and the latter as intrasexual selection (Bradley & Mundy, 2008).

Recent evidence also suggests that colorful feathers of parrots resist bacterial degradation, claiming another function of pigments apart from color generators (Burtt, Schroeder, Smith, Sroka, & McGraw, 2011).

7.2 Warning displays

Aposematism:

Aposematic animals signal their unprofitability to potential predators and often consist of blocks of color with sharp borders that are easy to discriminate, or of repeated color patterns (Caro, 2011). Colors that are often used are red, yellow and black, probably because of the high contrast against a background and resistance to changes in shadows and illuminations (Stevens & Ruxton, 2012; see Fig. 16).

Animals that often use aposematism to appear unpalatable are insects, so that predators avoid attacking them. Interesting seems a possible relation between conspicuousness levels and the degree of toxicity.

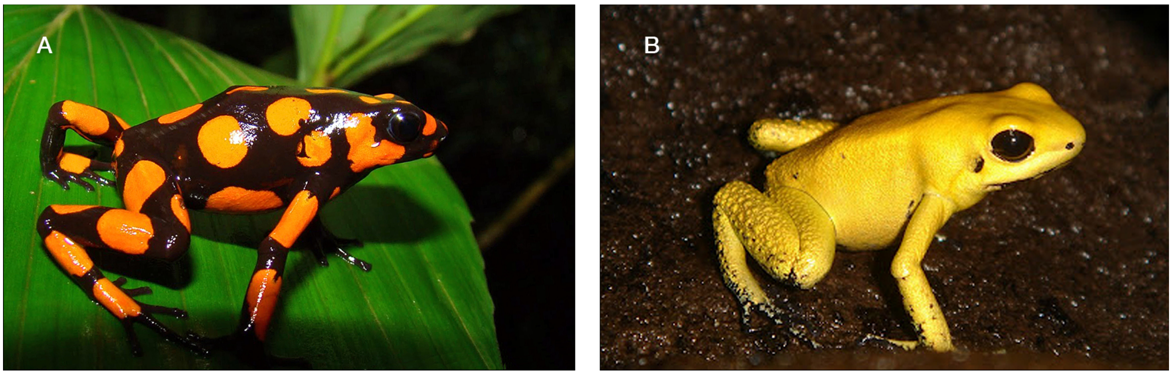

Figure 16: Examples of aposematic colored frogs.
Poison frogs in aposematic coloration (a) *Oophaga histrionica* (photographed by José Alfredo Hernández Díaz), (b) *Phyllobates terribilis* (photographed by Rene Greschner).

7.3 Distractive color patterns

Different forms of protective markings like camouflage and warning coloration can be explored from predator perception and may frequently utilize similar perceptual areas (Stevens, 2007).

Allen, Cuthill, Scott-Samuel and Baddeley (2011) underline that for explaining the diversity of animal color patterns both the development and their adaptive value needs to be understood. In comparative phylogenetic approaches the function of carnivore color patterns has been predicted. The adaptive functions of tail markings for example seem to be evolved for communication reasons, whereas cat coat patterns (spotted, vertically or horizontally striped) for camouflage reasons (Ortolani, 1999) and coat coloring of giraffes both for camouflage and thermoregulatory functions (Mitchell, & Skinner, 2003). Further, the analysis of felid coat patterns show that over short time scales camouflage adapts to ecology (Allen et al., 2011).

Painting body parts of spiders

Tso, Liao, Huang and Yang (2006) altered the chromatic properties of orchid spiders *Leucage magnifica* by adding brightly colored paint to conspicuous body parts for their alteration. Other tactics rather reduce conspicuousness by painting parts similar to those of inconspicuous patterns or masking spiders behind a leaf (Bush, Yu, & Herberstein, 2008; Chuang, Yang & Tso, 2007). All these treatments work and decreased prey capture, suggesting that not only the conspicuousness (visibility) but also chromatic properties like the reflectance spectra are determinant for the attractiveness of spiders to their prey (Chuang et al., 2007). Such studies illustrate the importance of using physiological models of color vision or using animal-eye-specific imaging system (Chiao, Chubb, Buresch, Siemann, & Hanlon, 2009; Thery et al., 2011).

7.4 The cryptic functions of coloration and color change in animals

Not only animals that use aposematic or intraspecific coloration are conspicuous colored, also camouflaged organisms are using contrasting colors (Cuthill & Székely, 2009; Stevens & Merilaita, 2009). Disruptive coloration often consists of high contrast markings that might draw the attention from the observer (Dimitrova et al., 2009) and also background matching animals use colors in surroundings that have dark shadows or snow (Caro, 2009; 2011). Coloration can be conspicuous nearby but cryptic at a distance (Marshall, 2000). Many hypotheses for coloration in mammals and pelage coloration include like already noted, body temperature functions, thermoregulation or protection against ultraviolet radiation.

According to Caro (2005), the best explanation for overall coloration in mammals appears to be camouflage. This explains also the evolution of variable background matching, namely fur that change seasonally or with age (Caro, 2005).

7.4.1 Color-changing animals: Predator specific camouflage

Stuart-Fox and Moussalli (2011) focused on color-changing animals with special interest on features of the environment that influence camouflage strategies, on visual processing mechanisms utilized by the animal, its predator and prey, and on color responses to different predators.

In general, there are two types of color change which differ in their functions and speed: morphological and physiological color change (Stuart-Fox & Moussalli, 2011). Firstly, morphological color change usually needs days or months for changing the density and quality of pigment-containing cells in the dermis. Secondly, physiological color change is much more rapid, due to movement like dispersion or concentration of pigment within cromatophores (Stuart-Fox & Moussalli, 2011). Movement of pigment-containing cells is under neural and/or endocrine control (Nery & de Lauro Castrucci, 1997), but the exception of this are cephalopods, in which color change is rapidly but works by muscle contraction of specialized chromatophore organs (Messenger, 2001).

Anyhow, physiological color change enables animals to show more than one camouflage strategy, not only to various backgrounds but also to multiple predators which differ in their visual capabilities and methods of prey detection (Stuart-Fox & Moussalli, 2009). For example the cuttlefish (*Sepia officinalis*) shows “deimatic display”, which is a high-contrast eyespot signal only towards visual predators (Langridge, Broom, & Osorio, 2007). Also, the dwarf chameleon *Bradypodion taeniabronchum* shows better background color matching in response to birds than snakes, using a model of animal color perception (Stuart-Fox, Moussalli, & Whiting, 2008). This flexible antipredator tactic has been shown as well in *Bradypodion transvaalense* that use the same body postures but change their achromatical contrast depending on different types of predators (Stuart-Fox, Whiting, & Moussalli, 2006). Another interesting result concerning rapid color change shows that selection for conspicuous social signals seems to drive the evolution of color change in the system of the southern African dwarf chameleon (Stuart-Fox & Moussalli, 2008).

In support of the social-signaling hypothesis, a comparative study of agamid lizards show that *Pseudotrapelus sinaitus* change color rapidly and that this is not related to any thermoregulationary function (Norfolk, Melotte, Gilbert, Zalat, & Reader, 2010). Their behavioral response of color change seems to be a form of social communication.

Some species also change their protective coloration between life stages. Examples for this are the plumage of many birds and also particular animals like the striated shieldbug, *Graphosoma lineatum*, which change their brownish-black color to red-black after diapause (Gamberale-Stille, Johansen, & Tullberg, 2010).

Also color changing decisions of western rainbowfish, *Melanotaenia australis*, have been examined by maintaining them in two different visual backgrounds (Rodgers, Kelley, & Morrell, 2010). Their results show that antipredator tactics in fish are mediated by the interaction of behavioral decisions (like shoaling) and morphological color pattern changes.

The color-changing crab spider *Misumena vatia* use active camouflage where the females are able to change from white to yellow and back (see Fig. 17), dependent on the color of background or prey (Thery, 2007; Thery, Insausti, Defrize, & Casas, 2011). This form of crypsis can be both defensive (hiding from predators) and aggressive (hiding from prey).

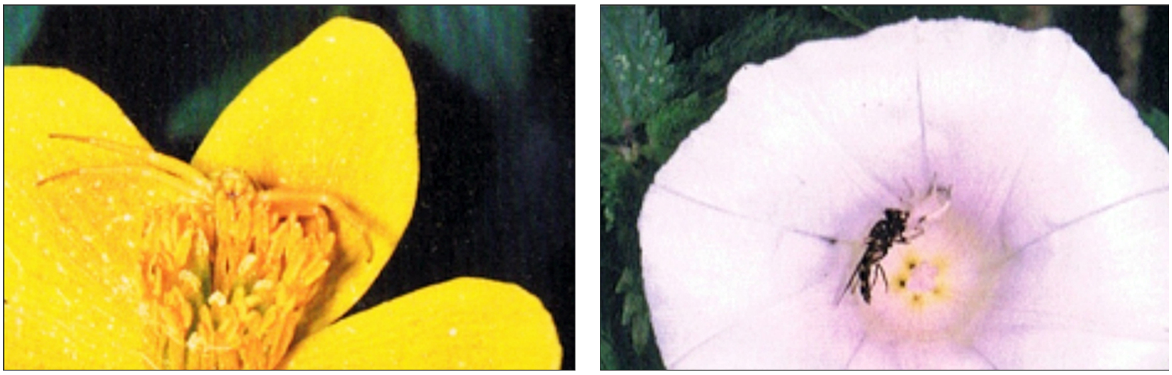

Figure 17: Examples of the color-changing crab spider.
The yellow colored female crab spider (Misumena vatia) lurking behind the stamen of a yellow flower (left), and a white colored spiderling with its prey on a white flower (right). (from Lunau, 2011, p. 40).

Like described in other chapters, the background-matching ability as seen by their prey has been explored by measuring chromatic and achromatic contrast (Chittka, 2001; Thery, 2007; Thery et al., 2005).

Important is to consider that the degree of camouflage is also limited by the speed of color change in relation to the motion of a camouflaged body (Stuart-Fox & Moussalli, 2011).

7.5 The function of black and white coloration

Like already a few times mentioned, the problem of all categorization is that human vision is trichromatic whereas most mammals possess dichromatic vision, so we might view black-and-white coloration differently (Stevens, 2007; Stevens, Párraga, Cuthill, Partridge, & Troscianko, 2007).

Terrestrial mammals

Caro (2009; 2011) synthesized contrasting coloration in 5000 terrestrial mammal species, emphasizing on black and white pelage. In this survey various patterns where analyzed like for example spines (e.g. hedgehog), horizontal bands of white fur (e.g. skunk), black-and-white face masks (e.g. red panda), contrasting necks and chests (e.g. black shouldered possum), bodies with blocks of black-and-white fur (e.g. pied tamarin), dark bodies with white spots or blotches (e.g. quolls), trunks with black transverse stripes (e.g. zebra), contrasting feet, legs and rumps (e.g. swamp wallaby), black-and-white tails (e.g. ring-tailed lemur) or entirely white mammals (e.g. polar bear).

Caro´s conclusions are that the best explanations for black and white pelage in terrestrial mammals are aposematism and conspecific signaling, and not crypsis through background matching or disruptive coloration. An exception is white pelage (albinism aside) that seems to be explained by background matching. The individual variation is great, white mammals like the polar bear show all year round white pelage, other animals like the artic fox turn white only in winter. Apart from being cryptic in some environments, white pelage may also be involved in thermoregulation (Caro, 2009; 2011).

The exact functions of black and white mammals however still remains unknown (Caro, 2009; Caro, 2011). The conspicuous stripes of the often discussed zebra for example have various assumptions. Ruxton (2002) names the protection from predators (resemblance of background, disruption), social functions, thermoregulation and protection from tsetse flies. Predator avoidance strategies for example are that stripes should make zebras look bigger (Cott, 1966, as cited in Ruxton, 2002), which moving stripes would dazzle predators, or that stripes blend in with tall grass (Kingdon, 1984, as cited in Ruxton, 2002), and that zebra stripes are hard to detect in the dark (McLeod, 1987, cited by Ruxton, 2002).

Marine mammals

Many marine animals have also striking colors, and in contrast to terrestrial mammals, the black-and-white coloration in marine mammals may indeed be a form of concealing shadow or background matching (compare with countershading) that aims the capture of prey (Caro, 2009, 2011).

8. Symmetry

Various experiments show that symmetrical color patterns increase the risk of detection, questioning why many cryptic animals therefore still show bilateral symmetry in body coloration. The rarity of cryptic prey with asymmetrical color patterns does not necessarily indicate the unimportance of symmetry for natural selection of camouflaged patterns and rather could be a compromise between color and other traits (Merilaita & Lind, 2006). Although symmetry increases the mortality-rate that cryptic coloration tries to prevent, it may enhance the efficacy of antipredator warning color signals (Forsman & Merilaita, 1999, 2003). Experimental evidence comes for example from studies with domestic chicks and paper “butterflies“ with warning colors (Forsman & Merilaita, 1999) showing that asymmetry reduces the efficacy of warning signals.

Merilaita and Lind (2006) studied the effects of symmetry and also the cost of symmetry for crypsis, because the investigation of the costs associated to antipredator coloration is important for the chosen defense strategy (Merilaita & Lind, 2006; Ruxton, Sherratt, et al., 2004). Their predation experiment has been conducted with great tits (*Parus major*) and artificial black-and-white-patterned prey items (see Fig. 18). Results showed that symmetry leads to a detectability cost for cryptic color patterns (longer detection time for asymmetric variants) but this cost of symmetry seems to vary strongly among different patterns. Merilaita and Lind suggests that selection against symmetric pattern may be less crucial as in earlier experiments suggested and emphasize the importance of selecting according to a decreased detectability cost due to symmetry instead of choosing asymmetric coloration per se. This predicts for example that disruptive coloration may result in cryptic, symmetric patterns with symmetric patches further away from the symmetry axis (Merilaita & Lind, 2006).

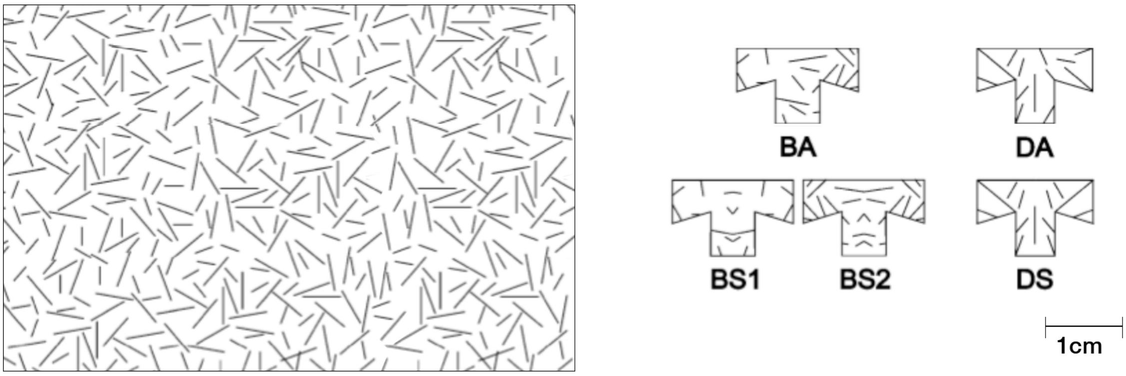

Figure 18: Testing material for symmetrical patterns.
Left: A sample of the background. Right: different prey color patterns used. Above: Two asymmetric patterns, a background matching and a disruptive pattern. Below: three symmetric patterns that were created form the asymmetric ones (Merilaita & Lind, 2006, p. 85).

When testing the survival rate of artificial mothlike targets placed on oak trees with disruptive or non-disruptive color patches and with or without bilateral symmetry, it has shown that symmetry doesn´t compromise the efficiency of disruptive coloration but reduces the effectiveness of both background colorations to a similar degree (Cuthill, Hiby, & Lloyd, 2006).

Langridge (2006) investigated symmetry patterns of cuttlefish (*Sepia officinalis*), which are able to control the amount of symmetry in its coloration. Two behavioral contexts (cryptic and threatened) have been established to see if cuttlefish show cryptic patterns more asymmetrically than “deimatic display“ (Hanlon & Messenger, 1996; as cited in Langridge, 2006), an anti-predator signal. Cryptic patterns were provoked by resting on different substrates and deimatic patterns by introducing a novel stimulus (white plastic square attached to a metal rod) into the water. All situations were filmed. Contrary to the expectations, cryptic body patterns showed a high degree of bilateral symmetry. Even more, in the case of

disruptive patterns, concealment may be actually aided by symmetry. The deimatic display was often expressed asymmetrically, which is also contrary to the predicted use of symmetry in color patterns of predator-prey interactions. The overall symmetry of the body pattern expressed when threatened seems to be less important than the symmetry of the key stimuli, two eye-like shapes. All in all, Langridge (2006) concludes like Merilaita and Lind (2006) that the role of symmetry in both crypsis and visual signaling is not as clear as previously thought.
Later, Troscianko, Benton, Lovell, Tolhurst and Pizlo (2009) stated in contrary to anterior experiments, that symmetric coloration has benefits for camouflage. They explain that symmetry is a spatially global feature that doesn´t ´pop-out´, and while a predator needs time and resources to analyze the symmetry of a cryptic pattern, the prey has time to escape.
Also in the context of symmetry, Landwehr (2009) presented an attempt to investigate the perception of symmetry with methods of psychophysics, explaining a technique to visually camouflage symmetry groups in natural textures.

In general, predators seem to detect prey from a symmetry-revealing angle (Merilaita & Lind, 2006). Tactics to reduce the cost of symmetry can include behavior strategies like folding for example one wing over another or placing the appendages asymmetrically (Cuthill, Stevens, et al., 2006; Cuthill, Hybi, et al., 2006; Lunau, 2011). Also in some species of tropical moths that imitate dead leaves, the front part of the wings differiates from the back part, and leads to the impression of an asymmetrical leaf (see Fig. 19).

Figure. 19: Leaf-mimicking butterfly.
This moth imitates a leaf and hides his symmetrical body by showing a front-back-asymmetry (from Lunau, 2011, p. 29).

9. Imperfect mimicry

“Imperfect mimics“ don´t appear to human eyes like their hypothesized models, but their appearance and behavior are easily distinguishable from the animals which they attempt to mimic (Chittka & Osorio, 2007; Stevens, 2007). Explanations for this include differences between human and predator vision (for example, UV-vision), species matching multiple models at the same time resulting in a compromise by appearing intermediate to all of them (Sherratt, 2002), the unnecessarity of perfect mimicry when highly toxic and also the possibility of high costs of mimicry (Gilbert, 2005; as cited in Stevens, 2007). Further, the generalization processes (such as speed-accuracy decisions and categorization) of predators to similar prey may protect poor mimics sufficiently (Lars Chittka & Osorio, 2007; Johnstone, 2002; Ruxton et al., 2004). Predator decision making between dangerous models and imperfect mimics might result in enough time for edible mimics to escape. Also, categorization of prey types may save mimics that have something in common with noxious prey (Chittka & Osorio, 2007).

Imperfect mimics are for example palatable animals (like hoverflies) that imperfectly mimic well-defended animals (like wasps; see Fig. 20), gaining therefore increased protection (Chittka & Osorio, 2007). Also some spiders mimic the morphology and/or behavior of ants, including modifications of color and form (Thery, Insausti, Defrize, & Casas, 2011).

In the context of categorization “mimicry rings“, the grouping of similar but distinguishable prey species is also of interest (Lunau, 2011). Often animals engage in Müllerian mimicry, where various defended species resemble each other, so that individuals can take advantage of a previous predator experience with an insect of a different species (Ruxton, Chittka, et al. 2004).

Figure 20: Example of imperfect mimics.
From left to right: The wasp *Vespula germanica* is mimicked by the hoverfly *Sericomyia silentis* (from Chittka, Skorupski, & Raine, 2009, p. 404; Tom Ings).

10. Camouflage involving senses other than vision

Ruxton (2011) gives some evidence of applied crypsis in non-visual contexts. The important difference between vision and other senses seems to be that, “with vision, detection and localization generally happen simultaneously, whereas with other senses the processes of detection and localization can be distinct“ (p. 345). Ruxton considers that every cryptic individual always produces an effect and makes an impact on the sensory system of the viewer. If a camouflaged organism would be removed even when it has not been detected, the information flow of the observer would be changed.

Apart from visual camouflage, there exist other forms of concealing oneself. To appear uninteresting for predators, some animals display tonic immobility or death feigning. Some non-visual camouflage forms include the use of sound, olfaction, electricity, hydrodynamic and substrate vibrations.

Sound

Many animals are silent when in risk of predation and avoid making noises, although this is considered as hiding and not camouflaging (Ruxton, 2011). However examples of auditory crypsis are modifications of calls to prevent detection by predators, also distress calls are often used. Further, alarm calls can be produced at high frequency, so that not every species hear them.

Ruxton highlights the difference between visual crypsis and crypsis in the sensory modalities: by detecting an individual visually, also information of its position is obtained. With sound, a listener can detect the existence of objects, but not it´s specific location.

Olfaction

Like in other topics, the literature consists of various confusing definitions and subtypes of chemical mimicry and camouflage. Dettner and Liepert (1994) give an overview, concentrating on species that chemically disguise themselves as others or that simulate uninteresting objects. They describe different strategies used by animals, among others the integration into colonies of insects, penetration into nests of other insects, mutualism between ants and other species, and the luring of prey. More strategies are reproduction, chemical interrelationships between insects and plants and Müllerian mimicry of warning odors. In recent years there has been a huge increase in the understanding of chemical signals associated with locating prey (Akino, Nakamura, & Wakamura, 2004; Carthey, Bytheway, & Banks, 2011; Lindstedt, Huttunen, Kakko, & Mappes, 2011; Raffa, Hobson, LaFontaine, & Aukema, 2007; Silveira, Oliveira, & Trigo, 2010; Strohm et al., 2008; Youngsteadt & Devries, 2005). For example Akino et al. (2004) studied the chemical background matching of caterpillars of the species *Biston robustum*, that visually look like twigs of plants. Impressively only the cuticular chemicals of these caterpillars that resemble these twigs protect them from predatory ants, which even walk over their prey without attacking the caterpillars. A similar experiment, which is of Silveira et al. (2010) show that treehoppers also use chemical crypsis against their predator ants.

An example of this in the world of plants, is the special case of Rafflesia gigantea, that mimics optical and olfactorial a cadaver to attract insects for pollination (see Fig. 21).

Figure 21: Example of olfactory camouflage.
The enormous flower of *Rafflesia gigantea* can gain upto 1,5 metres diameter (photographed by the author at Cameron Highlands, Malaysia).

Electricity

Many fish detect changes in electric fields in water using their electroreceptive sense (e.g. wobbegong sharks). The functional significance of such electrosensory capabilities is interesting in terms of camouflage (Collin & Whitehead, 2004; Theiss, Collin, & Hart, 2011).

Hydrodynamic crypsis

In predator-prey interactions also detection of fluid disturbance and substrate vibrations is of interest (Jiang & Kiorboe, 2011; Noren & Edwards, 2011; Ruxton, 2011).

Part II. Psychology and Camouflage

The field of visual perception and camouflage is as widespread as interesting. The general benefits of camouflage seem clear, but understanding how the observer is deceived and how the adaptation to other viewers takes place is a challenge.

Already H. J. Eysenck wrote a note on Psychology and Camouflage in 1940, concerning the importance of psychologists in the investigation of Camouflage. For a full comprehension of camouflage mechanisms an interdisciplinary collaboration of biologists, perceptual psychologists, neuroscientists and computer scientists is needed (Cuthill & Troscianko, 2009). Therefore in the following a few selected areas which are related with some basics of the visual perception of camouflaged objects will be mentioned, trying to integrate different disciplines.

11. Viewer differences: human – animals

The properties of visual systems vary a lot between humans and animals and also between different species (compare a mole with a cuttlefish, bee or bird). Effective crypsis depends on the visual and cognitive abilities of the perceiver, therefore an animal that doesn´t appear cryptic to us can be cryptic to its predators. Thayer (1918) gives an example of the role of different points of views: Humans probably easy detect skunks because of its white patch and we classify it as conspicuous. Contrary to this, a skunk is naturally colored to conceal themselves from small creatures that are its prey. One explanation for this lies in the interspecific color sensitivities that can explain camouflage in varying visual systems (Thery, Debut, Gomez, & Casas, 2005). This are for instance differing wavelength sensibility between species, or that some deep-water animals use red light for intraspecific signaling unobserved from their predators. An example for the differences between humans and predators are also animals that appear to human eyes as “imperfectly“ camouflaged (Stevens, 2007), as mentioned in chapter 9.

Research on camouflage needs to be done with the eyes of the species concerned (as far as possible with the animal in situ; or at least modeled in situ), and within behavioral context of the potential interactions for which camouflage may have evolved (Marshall & Johnson, 2011).

The use of human subjects to value the markings of animals is often inappropriate because of the differences between species in visual perception such as animal communication outside the range of human sensitivity (Stevens, 2007). Nevertheless, more is known about human vision than about that of most other creatures. In the 1950s it was common to think that human and birds have a similar perception (Ruxton, Sherratt, et al., 2004) only much later the cognitive systems of animals perceiving an object have been considered.

From studies with human subjects general principles about animal coloration can be derived when the stimuli is designed especially for the presentation. Further, it is of special interest whether the mechanisms of visual perception in different species are related, because “universal processing rules“ could be explored and the function and evolution of different protective strategies could be understand (Stuart-Fox & Moussalli, 2009; Stevens, 2007).

Therefore despite the differences in visual systems, there exists evidence that some functions work the same in humans and animals. For instance, earlier research on texture perception involving other species suggests that general results derived from humans also apply to other vertebrates (Kiltie, 1992). Also, object recognition in humans may be similar to that in cuttlefish and their predators (e.g. Kelman, Osorio, & Baddeley, 2008). Additionally Troscianko, Benton, Lovell, Tolhurst, and Pizlo (2009) suggest that the visual perception mechanisms of animals may be similar to those of humans, although it is not clear which, if any, animal share these.

12. Visual perception and camouflage breaking

Cuthill & Troscianko (2009) explain that the relevance of camouflage to psychology is more the viewer and not the object. Camouflage breaking consists of revealing mechanisms of target-background segmentation and object recognition which are of great importance in visual perception, and even more under difficult conditions.

For the testing of object recognition by humans exist rather little literature with strong camouflaged objects, but quite a lot on visual search situations with for example complex natural backgrounds and polymorphic targets (e.g. Bond & Kamil, 2006). Apart from testing figure-ground segmentation processes, it is also important to discriminate between the target and similar objects in the same scene (Metzger, 1936).

While applying principles from visual psychology Troscianko et al. (2009; 2011) explain that the main issues of visual systems concern the sensitivity of the system, the light level, the field of view, spectral and motion information and spatial and temporal characteristics. Mechanisms of visual encoding, of grouping and object encoding, and of search are also general principles for understanding visual concealment. Encoding of certain discontinuities (in pattern and motion) is of great importance for encoding complex scenes. Apart from motion, grouping and object-encoding mechanisms, which are strategies that disrupt the encoding of edges, are also necessary considering camouflage and concealment.

Various concepts involved in visual perception which are part of camouflage and camouflage breaking shall now be discussed:

12.1. Illumination and objects

The key property of perception is dependent of the incident light, which is modified by the medium through which it is sent (air or water) and by reflections from surfaces (Ruxton, Sherratt, et. al., 2004; Troscianko et al., 2011). Light influence the perception of material properties, borders and the given spectral information. Object changes are further influenced by light behavior like spatial, temporal and spectral factors. Edges are often described by abrupt changes in intensity (Stevens & Cuthill, 2006) like illumination changes, changes in the orientation or distance from the viewer and changes in the surface reflectance (Marr & Hildreth, 1980). Intensity borders are detectable because they are different from the immediate background and therefore identified. Troscianko et al. (2011) describe two types of intensity edges which are not coincident with the boundaries of bodies, namely “Illumination edge“ and “internal marking“. Illumination edges are known as shadows and with internal marking the texture or internal features is meant. These types of intensity edges cause a problem for edge-detection systems that fail when strong shadows or textures exist, therefore separate detectors for discovering texture and shadows are needed (Troscianko et al., 2011).

Shadows in general are rich in short wavelengths, therefore humans perceive them dark and blue, and animals with UV vision dark and UV-colored (Troscianko et al., 2009). Animals that can sense spectral information, the wavelength composition of light, are able to distinguish shadows (illumination edges) from object edges (Troscianko et al., 2009).

12.2. Edge detection

Finding object counters results difficult, because the edges of images can be caused by illumination and changes in material (Brady & Kersten, 2003).

Troscianko et al. (2009) describe two stages of object identification or figure-ground processing: low-level and higher-level. The detection of locations, polarity and orientation of small edge segments by neurons (V1 “edge detectors“) takes places in the low-level process (Hubel & Wiesel, 1959, 1986; as cited in Troscianko et al., 2009; S. 451). Each “simple cell“ in V1 has a receptive field where light causes excitation or inhibition in different regions. The second (higher-level) stage identifies edges belonging to an object and rejects others that belong to the background, therefore grouping edge information (Lamme 1995; Grossberg et al. 1997; as cited in Troscianko et al., 2009, S. 451).

Most evidence of edge detection comes from investigation of disruptive coloration. Edge-detectors are confused by disruptive coloration, making conclusions about prey shape difficult or even impossible (Endler, 2006). From a prey´s point of view, the animal can match the background color (depending on its predators wavelength perception) and therefore making small edge segments difficult to detect; or the animal can complicate the edge grouping process by deleting some edge information or presenting information about edges that are not present (Stevens & Cuthill, 2006; Troscianko et al., 2009).

Data from non-human predator showed how edge detection in early visual processing works, using for example a computational model of bird vision (Stevens & Cuthill, 2006). False edges provoked by disruptive coloration in this study were detected within the body and not at its outline, showing the effectiveness of disruptive pattern. In general most knowledge of how edge perception could work in animals comes from cuttlefish.

Another point worth noting are illusory contours, appearing in visual illusions like shapes or edges, when in truth, there are no physical image contrast and therefore no borders (Carman & Welch, 1992; von der Heydt, Peterhans, & Baumgartner, 1984). This might fool a predator´s visual system, believing for example that there are coherent objects which do not resemble the outline of prey (Troscianko et al., 2011).

Anderson, O´Vari and Barth (2011) comment on new forms of illusory contours and surfaces that are difficult to explicate with existing probabilistic models asserting the completion phenomena. They reported new forms of visual interpolation while performing experiments with motion displays to assess the elements that influence the vividness of illusory figures.

12.3. Objects and three-dimensional shape

Color, texture and size of animals are details that are identified after the more important shape of an object is recognized (Troscianko et al., 2009).

In animal´s visual system the task of understanding how animals perceive three-dimensional bodies still persists. Troscianko et al. (2009) point out that it would be necessary to know how the visual system of animals completes their two-dimensional retinal information to recognition of a three-dimensional shape for understanding camouflage. Therefore they illustrate our limited knowledge about three dimensional shape perceptions in animals, explaining that research concentrates on human visual systems. Troscianko et al. (2009) further specify that for perceiving three-dimensional shapes, humans must 1) detect the presence of a shape, 2) recognize a familiar shape and 3) reconstruct the shape.

For detection of objects in two-dimensional images the importance would lie in the 1) detection of features not part or the background (visual search), 2) identification of regions in the image representing an object, 3) description of its contours and 4) verification that the two-dimensional shape is produced by an object (Troscianko et al., 2009).

The further recognition of a three-dimensional shape can be based on characteristic parts of the shape, which is the main idea behind Biederman´s (1987) ´Recognition by Components´ theory (as cited in Troscianko et al., 2011). Concerning this matter the question rises if animals learn specific shapes of their prey and predators, or if they are born with that information.

For reconstruction of shape, finding primarily objects in a two-dimensional image is essential. Troscianko and colleagues (2009) refer this figure-ground organization to specifying planar outlines that represent three-dimensional shape contours, determining symmetric pairs of feature in the three-dimensional interpretation and determining two-dimensional forms in the three-dimensional interpretation. Symmetry is an important cue in the study of visual perception and most animals have a plane of symmetry that is not present in their environment (Cuthill, Hiby, & Lloyd, 2006). This symmetry can therefore be used to recover a three-dimensional shape by using a single two-dimensional image (Troscianko et al., 2009; see Fig. 22).

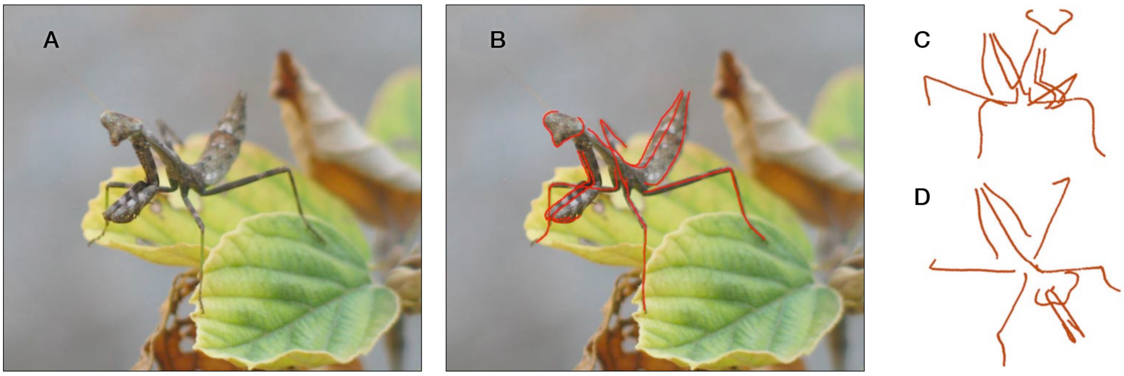

Figure 22: Recovering a 3D shape from a 2D image.
A: 2D picture of a mantis. B: superimosed countors. C-D: recoverd 3D shape of the same mantis (Troscianko et al., 2009; supplemental material).

If any of these steps fail, a three-dimensional object will be camouflaged. This happens for example, when an animal has a similar color like its surrounding, when an animal´s skin has geometric segments unrelated to its three-dimensional shape (like zebra stripes), or when an animal pattern indicates two-dimensional symmetry.

Shape, camouflage and learning

Prior knowledge facilitates the detection of objects that are poorly visible, hidden or camouflaged. Zhang and Srinivasan (1994) showed that this is not unique to higher animals, but that even insects can learn to break camouflage. When trained on a simpler task with figures that are exposed also later in camouflage, bees use prior experience for processing visual images, showing an advantage in discriminating between differently shaped and camouflaged figures.

In general, cognition, learning and memory are involved in a great amount of sended and received signals, and are of special importance when thinking of learning effects and awareness, for example in aposematism, but also for novel objects.

12.4. Shape, shadow and countershading: 3D

Like stated earlier, visual links such as shading, contour, perspective and texture influence the perception of three-dimensional shape and outline of a body (Rowland, et al. 2008).

Rowland (2009) notes that psychophysical evidence for three-dimensional perception by non-humans is rare and sometimes contradictory, leaving us unaware whether countershading balances the illumination effects in this way also in non-human systems.

Ramachandran (1988) studied the perception of shape from shading, using examples of objects illuminated from above to demonstrate its effect on three-dimensional bodies. Relating to this is the already explained concept of countershading applied by various animals: when an animal is illuminated from above, a shadow will be cast on the ventral underside, producing a contrast between upper and lower surfaces (see Fig. 23). Therefore predators can recognize the animal as different from its background (Rowland et al., 2008). To counteract this, some animals are darkest on top to reduce the shading difference, preventing recognition as a three-dimensional object when viewed from the side or by flattening.

This has been already discovered by Poulton in 1886, although he didn´t call it countershading, and has been further promoted by Abbott Thayer using duck decoys to demonstrate this effect (Behrens, 2011; Rowland, 2011). As an artist, Thayer practiced shading or top-down lighting, by which flat surfaces take seems voluminous and discovered that countershading is simply the inverse shading mechanism (see chapter 19).

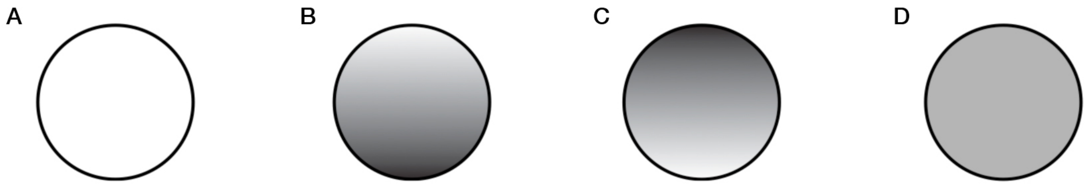

Figure 23: Different stages to demonstrate countershading.
From left to right: a) a flat expanse of paper; b) artistic shading or top-down lightning, by which the surface looks voluminous; c) countershading, where the underside of an animal is lighter than the parts that are more exposed to sunlight; and d) a flat expanse of tone, where countershading cancels out shading (From Behrens, 2009, p. 498).

When viewed from the side, the self-shadow concealment or “flattening” reduces the visual cues of shape. The mechanisms of shape perception in non-humans need to be investigated, and also how the perceptual and cognitive functions of countershaded patterns work in predators (Rowland, 2009). Some of the few studies derived from non-human animals on shading and shape perception are from Hess (1950, 1961) on chicks. The result of Hershberger´s (1970) study, chicks preferring to peck grains with shadows below, assumes that at least some non-humans have similar abilities of depth and shade perception (as cited in Rowland, 2009).

Another function how shadow influence the shape perception relevant to camouflage lies in body outline obliteration when the body is viewed from above. Predators have been shown to detect the edges of prey in studies of disruptive coloration (Cuthill et al., 2005). However, Rowland (2009) gives an example of dorsoventral gradation in color in a countershaded body, obliterating the outline, so that the capacity of predators detecting edges of countershaded animals when viewed from above may be reduced.

Mathematical model of countershading

The research on breaking mathematical operators and countershading is a new promising approach: Tankus and Yeshurun (2011; 2009) illustrated an operator for detection of cylindrical objects that might be used in the visual system of predators (see Fig. 24). Showing that “D_{arg}“ works regardless of image edges, counters and texture, the authors speculate that this operator might be employed in biological vision systems. Tankus and Yeshurun state that its use for detection of curved objects on flat backgrounds appears highly effective, that countershading of prey animals tries to inhibit this detection, and that the neural network implementation seems simple.

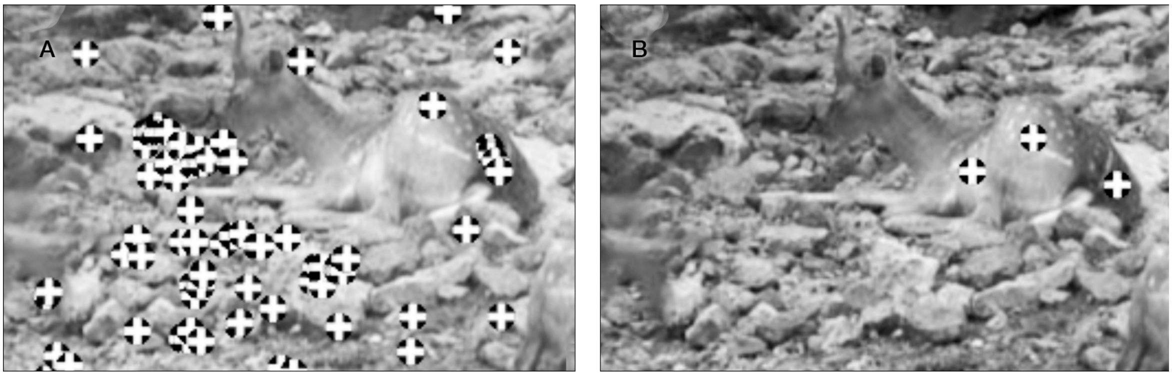

Figure 24. Object detectors for breaking breaking camouflage.
Persian fallow deer on a stony background. Left: When using radial symmetry detection, the tones of the deer blend with the background, and the stones result more important for edge-based methods. Right: Detection by D.arg, breaking the camouflage and detecting the deer (Tankus & Yeshurun, 2009, p. 533).

13. Color perception

The ability to perceive colors is used for specific behaviors and is essential for understanding how camouflage may function. Many animals have color vision and use it for object recognition and classification (Kelber, Vorobyev, & Osorio, 2003; Osorio & Vorobyev, 2005). There is a great diversity in animal coloration, color pattern and defensive markings to reduce the risk of predation. Different forms of camouflage and warning colors may be linked in various ways and can, as already noted, only be seen clearly with the knowledge of each predators visual system (Stevens, 2007). In response to the different color vision systems in predators, animals have evolved various camouflage techniques and flexible predation behavior (Thery & Gomez, 2010).

Because color is context-dependent and not a property of any object, the reflectance spectrum, ambient light spectrum, transmission properties of the medium and the veiling light spectrum all influence in color perception and always depends on the visual system of the observer (Endler, 1990; Ruxton, Sherratt, et al., 2004).

Theories of color vision derived from studies on human perception, stating for example that colors have the achromatic aspect of brightness and the chromatic aspects of hue and saturation (Kelber et al., 2003). Color vision is classified depending of the number of lights required to match any spectral light as dichromatic, trichromatic, tetrachromatic and so forth (Kelber et al., 2003; Osorio & Vorobyev, 2005). Receptors have been named like the spectrum part to which they are most sensitive, for example red, green, blue, and UV. A second manner of naming the receptor is long (L), short (S) and medium (M), according by their wavelength sensitive relative to other receptors in the eye (Kelber et al., 2003). The two main types of photoreceptor cells are rods, that are normally active at low light intensities, and cones, which are normally active at high intensities. For color vision mainly the cone signals are used (Kelber et al., 2003).

Normal humans have trichromatic vision, matching any spectrum by a combination of the three primary spectra. Birds have four types of cones (ultraviolet as additionally to that of humans), while carnivore predators possess only two color-sensitive retinal cones (Caro, 2005).

The different visual spectras suggests that an animal may for example be conspicuous to humans but not to nonprimate animals, or they may be cryptic to humans but conspicuous to birds (Caro, 2005).

Saito et al. (2005) supposed an advantage of dichromats over trichromats for certain visual tasks in primates. This was already demonstrated earlier for humans in breaking camouflage (Morgan, Adam, & Mollon, 1992), and the results show that this applies also for the discrimination of color-camouflaged stimuli in New World monkeys.

In studies of animal coloration it is unrewarding to use methods which rely upon human vision or subjective judgments of conspicuousness. Methods should address the color spectrum of animal pattern elements (patches) and their visual surrounding depending on the perception of the conspecifics, predators or preys (Endler, 1990). Methods of measuring a patch´s color should be conducted under the conditions of normal use of color patterns and works both on terrestrial and aquatic habitats (Endler, 1990).

Despite all this, testing the color perception of animals still results difficult, so that most work have dedicated just on proofing the existence of color vision in general, rather than investigating neural mechanisms (Kelber et al., 2003). Experiments testing animal color vision are for example those of Osorio and colleagues, testing color vision of domestic chicks. They trained chicks to find food in paper bins with a pattern that can only be differed by specific combinations of receptors (see Fig. 25), demonstrating tetrachromatic color vision in chicks (Osorio, Vorobyev, & Jones, 1999).

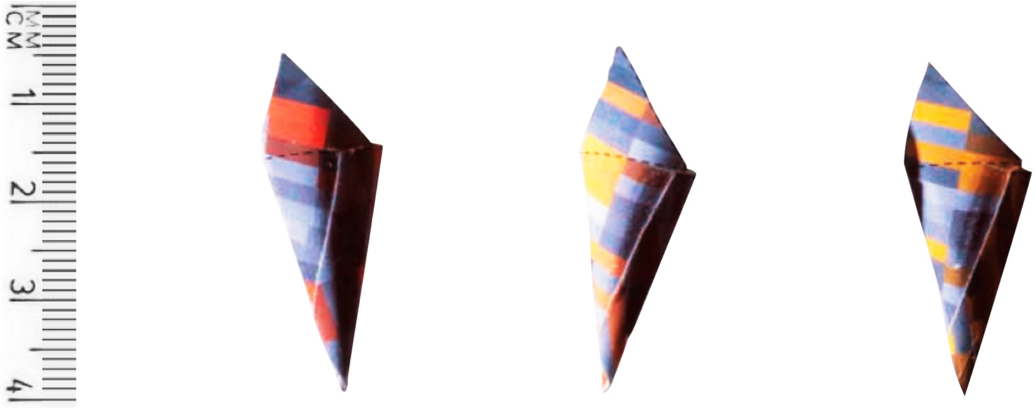

Figure 25: Material for testing the color perception of animals.
Photograph of the experimental stimuli used in Osorio, Vorobyev, and Jones (1999, p. 2956).

Also they show that chicks use chromatic and achromatic information differently, depending on their utility for object recognition in nature (Osorio, Miklósi, & Gonda, 1999). Associations of color are more learned and memorized than achromatic associations, which could significate that the chromatic aspects of warning signals may often be of major importance than the achromatic components (Osorio, Miklósi, et al., 1999). Further, discrimination of large targets seems to use chromatic (color) information, whereas detection of small objects and texture needs achromatic (brightness) contrast (Osorio, Miklósi, et al., 1999; Osorio, Vorobyev, et al., 1999).

In 2005, Osorio and Vorobyev reviewed the photoreceptor sensitivities in terrestrial animals, demonstrating that mammals and honeybees use their long-wavelength receptors for achromatic and color vision, while flies and birds probably use separate receptors for this two purposes.

An attempt to explain camouflage in different visual systems concentrates on specific color sensitivities of both prey and predator. Thery, Debut, Gomez and Casas (2005) identified the involved photoreceptors of hymnopteran prey and bird predator of crab spiders. Doing so they measured chromatic and achromatic contrast of pairs of spider and flowers (where they sit on) and determined the detection ability (short and long-range) in both animal visual systems. The measure of contrast on flowers used brightness contrast and color contrast, using spectroradiometry and physiological models of color vision instead of human vision (Chittka, 2001; Thery & Casas, 2002).

Another method to quantify colors independently of human perception was established for example with an avian predator visual model testing countershading effects of pastry caterpillars (Rowland et al., 2008). Like noted above, birds are tetrachromatic using four single cone types, but also possess an additional type of cone, namely “double cones“ (Rowland et al., 2008). These seem to be involved in achromatic vision and have a broad spectral sensitivity (Osorio, Miklósi, et al., 1999; Osorio & Vorobyev, 2005). Using this model of visual perception and information how it is assumed to function in avian color discrimination (Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998), they analyzed pastry and background reflectance spectra.

Also Stevens and Cuthill (2006) considered the function of avian double cones. Photographs of disruptive patterns were calibrated to bird color vision, transforming each image into different color channel images that were analyzed separately. With a computational vision model of edge detection they presented the effectiveness of disruptive coloration. Birds detect false edges rather within an object, reducing successfully the detection of the outline of an animal´s body (Stevens & Cuthill, 2006).

The blue striped fangblenny (*Plagiotremus rhinorhynchos*) uses aggressive mimicry and changes its coloration to copy other coral fishes. Cheney, Skogh, Hart and Marshall (2009) investigated their visual capacity and found that blue striped fangblennies have rod photoreceptors, single cones and double cones. Theoretical vision models showed that the fangblenny can discriminate between their colors and the colors of similar fish. However their potential signal receivers perceive the coloration of most mimics identical like their models, only fishes with UV-vision could discriminate better between mimics and their associated fish (Cheney et al., 2009).

Such studies illustrate the need of using animal vision models for understanding how different forms camouflage and protective coloration may function.

Marshall and Johnsen (2011) demonstrate that most coral reef fish patterning is mainly for camouflage, no matter how conspicuous it is to our eyes. In various studies Marshall and colleagues (Marshall, 2000; Marshall et al., 2003; Marshall & Vorobyev, 2003) addressed color perception in reef fishes and how coral fish appear to other fish. Their results reveal that yellow and blue colors are most frequently used, and are designed to be conspicuous to a color vision system when near, but well camouflaged at a distance. Many of the larger predators have dichromatic vision, and therefore may struggle to detect blue fish in the blue ocean (Marshall et al., 2003). Apart from matching well the background this colors can also be used for communication, always depending on the context, because reef fishes seem to use a combination of color and behavior to regulate their crypsis and conspicuousness (Marshall & Johnsen, 2011).

Color vision varies not only among different species but even among individuals within a social group, as showed Bradley and Mundy (2008). In some diurnal lemurs and most New World monkeys (except howlers), some females have full trichromatic color vision, but all males and the remaining females are red-green colorblind. This means that some conspecifics, even groupmates perceive each other differently. Some of the theories discussing the evolution and adaptive value of trichromatic vision in primates include that advantages in finding reddish fruit in a green forest or differianting more nutritious young red leaves from green leaves (Bradley & Mundy, 2008).

14. Texture perception

The perception of visual textures and its discrimination is relevant for camouflage, both in terms of camouflaging animals and in military camouflage. Considering for example animal coats as visual textures, the psychophysical research on human vision can reflect ways of uncovering camouflaged prey (Kiltie & Laine, 1992).

The usual way of studying texture perception has been by implying artificial textures made of random dots or repeated shapes. Ninio (2007) demonstrated how to design camouflaging textures both by computer and by hand for use in stereoscopic visual studies, which is important for depth perception and camouflage painted buildings. Like in real life, camouflaging textures incorporate edges at all orientations. Large sheets of manually designed textures were generated from small fragments of photographs (tree trunks, leaves, stones, figurative paintings) or of a manually produced first-generation texture. These patches can be cutted zigzagging and assembled into coherent textures. Ninio further describes that important camouflaging factors are the absence of extended edges and the local heterogeneity of the texture. This allows covering curved surfaces with textures produced that way, which is of mayor interest in terms of military camouflage.

To refrain from designing textures, machine vision programs for natural texture synthesis have improved rapidly in the last years. Combining such computer models with texture representations in the human visual system now opens up new perspectives of animal patterns. Balas (2006) for example found an interaction between texture type and image statistics in human vision, proposing that different representations may be used for various texture families.

In combat situations one needs to identify targets, discriminate a target against a background and also similar targets from one another. This is complicated by camouflage, but visual discrimination of fractal textures can reveal important insights to our perception of camouflaged targets. Billock et al. (2008) used Fourier image statistics to investigate the discrimination of fractal camouflaged targets from other targets or natural backgrounds. Their rather technical methods of studying human abilities to discriminate images differing in their ß-signature uncover data for the discrimination of both static and dynamic fractal images and how this varies as a function of circumstances and experimental methods. While discriminating between friendly and enemy camouflaged targets Billock et al. showed that fractal objects are harder to discover when their statistics are similar to that of natural images. This is true even when friendlies and hostiles are both visible against their surroundings, suggesting that camouflage should be planned like fractal-like natural backgrounds. Some implications of fractal discrimination for camouflage and combat identification concerning the texture mentioned by Billock et al. are using many spatial scales for effective camouflage almost independent of distance and adding filtered noise to sensor images to possible break camouflage schemes.

The design of camouflage material changed from individual manually produced patterns to digitally generated forms in mass production (Blechman, 2004). By taking elements for example from local culture and landscape, new patterns arise, therefore camouflage patterns can also be seen as a snapshot of history.

Recent achievements in aerial warfare and the developing of satellites and observation equipment’s in military strengthened the need for generating patterns that nearly resemble the natural environment (Baušys & Danaiti 2010).

Baušys and Danaiti (2010) proposed a new approach for computer-generated camouflage pattern designs and presented a mathematical background for generating patterns based on the selected background. While collecting the geometry of color spots, color gamma and coloring relationship of camouflage, a function expresses the effectiveness of the intended pattern over a range of backgrounds and conditions. With an analytical method the effectiveness was expressed as a function of various parameters like the distance and time of observation, the brightness contrast of the building with its surrounding and the meteorological visibility range.

In general, small rectangular pixels of color, form a digital camouflage pattern which should mimic the texture and rough boundaries that are found in nature.

At the present time not many computer programs exist for performing experimental stimulations with camouflage patterns calculating their effectiveness. However as technology is evolving constantly, also more special tools for assessing the effectiveness of camouflage patterns will be introduced in the next years (Baušys, Danaiti, 2010, p. 856).

15. Special forms of vision

15.1 Polarization vision

Polarization vision plays an important role in the perception in many animals, like some marine species but also insects. It is especially useful in water of various depths and optical quality where color can´t be used anymore as a reliable cue. Many animals are capable of analyzing the polarization of incoming light as produced by scattering or reflection, possessing photoreceptors that are sensitive to polarization (Cronin et al., 2003; Stecher, Morgan, & Buschbeck, 2010).

Polarization sensitivity has been associated with behavioral tasks like orientation and navigation, but can be used for contrast enhancement, camouflage breaking, prey detection, communication and optical signaling (Cronin et al., 2003; Tuthill & Johnsen, 2006). Various material has been published on polarization vision mainly on plankton (Johnsen, Marshall, & Widder, 2011; Sabbah & Shashar, 2006) or on cephalopods (Grable, Shashar, Gilles, Chiao, & Hanlon, 2002; Mäthger & Hanlon, 2006, 2007; Mäthger, Shashar, & Hanlon, 2009; Shashar, Hagan, Boal, & Hanlon, 2000; Shashar, Rutledge, & Cronin, 1996). Polarization sensitivity in certain species is supposed to serve for raising the contrast of their prey or well-camouflaged targets in water, like transparent zooplankton (Johnsen et al., 2011; Lythgoe & Hemmings, 1967). For example in crayfish it has shown that polarization vision facilitates the detection of moving transparent objects (Tuthill & Johnsen, 2006). Polarization however is also used as a hidden communication channel in cephalopods. This is made possible by the light-reflecting iridophore cells in their complex skin that can be regulated for sending polarized signals to conspecifics that most of cephalopod´s predators can´t detect (Mäthger & Hanlon, 2006; Mäthger et al., 2009).

15.2. Night vision and nocturnal camouflage

Night vision in animals seems to be better than previously imagined. Visual predation occurs day and night, therefore many predators have a good night vision (Allen et al., 2010). Camouflage during daytime is well known and has now also been documented in dim and dark light, highlighting nocturnal visual predation (Warrant, 2007). The best demonstration of camouflage patterns against different backgrounds at night comes from research on cephalopods. The giant Australian cuttlefish *(Sepia apama)* shows adaptable camouflage body patterns fitting to its environment even in the dark, protecting them from nocturnal predators (Allen et al., 2010; Hanlon et al., 2007).

Conspicuous body coloration also gives cues for the function of night vision and can be utilized not just for hiding from predators but also for capturing prey. An interesting result showed Chuang, Yang and Tso (2007) in quantifying how nocturnal lepidopteran insects view a conspicuously colored spider. The coloration of the giant wood spider *(Nephila pilipes)* attracts both diurnal and nocturnal prey in different field manipulations. The presence of those spiders in their nets increased significantly their capturing rates, but decreased them significantly when the colored parts of N. pilipes have been painted black. The same has been shown for nocturnal orb spiders *(Neoscona punctigera)* by altering the color signal of their ventrum spots (Chuang, Yang, & Tso, 2008). This demonstrated that, in the night, some animals present visual markings to attract prey, although most organisms that are active in the night are inconspicuously colored.

If the color pattern of an animal is just researched in few light conditions the conclusions might be biased. Therefore while studying animal camouflage, color patterns and communication we should have a good understanding of the visual systems of all animals involved in an interaction and also under different light conditions (Chuang et al., 2007).

16. Visual search

There are two forms of visual search as stated by Cuthill and Troscianko (2009), searching for targets among distractors (Fig. 26a), or focusing on the segmentation process itself and on the distinction of objects form the background (Fig. 26b).

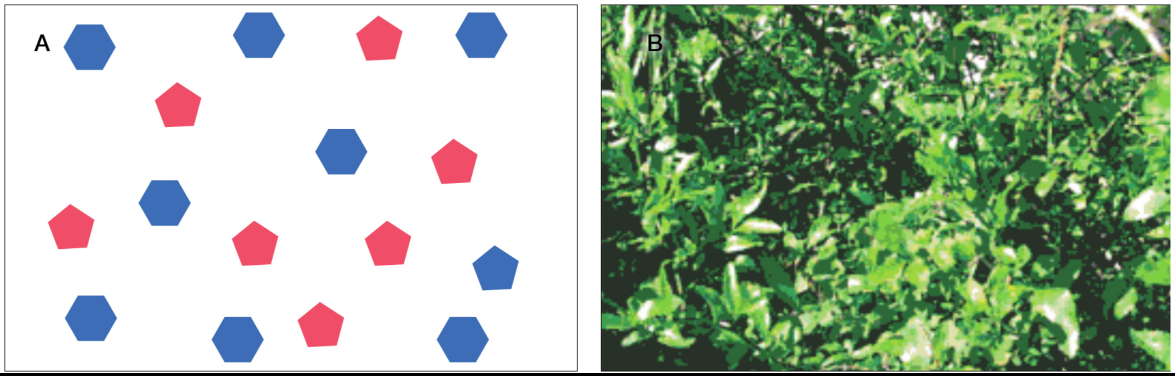

Figure 26: Forms of visual search.
Two different ways to study perceptual processes required for camouflage breaking: a) distinguishing the target (blue pentagon) from similar distractor objects (blue hexagons and red pentagons). b). distinguishing objects of interest (chameleon) from a complex background (Cuthill & Troscianko, 2009, p. 8).

Typical studies that concern visual search attend the detection of a target among other elements, centering upon search efficiency. The effortlessly process of separating objects which differ in their second-order statistics from each other characterizes the “pop-out”-phenomenon. In contrast to this stands the difficult search process for camouflaged bodies in full backgrounds, using computational strategies for segmentation (Billock, Cunningham, & Tsou, 2008).

In most early visual search experiments objects were presented on a blank background in the laboratory. In the real world the surrounding is far more complex, although rather little is known about visual search for targets on natural backgrounds (Blakely, Boot, & Neider, 2010; Green, Willis, & Egan, 2009). More recent studies concern the role of target-background similarity with human subjects, of which some are commented now briefly.

Separating objects from the background seems to be of special interest for camouflage and detecting targets. Wolfe, Olivia, Horowitz, Butcher and Bompas (2002) investigated human visual abilities, detecting that the main effect of complex backgrounds that are similar to the search objects, seem to slow the information in recognition stages.

Various experiments (e.g. Duncan & Humphrey, 1982; 1992; as cited in Troscianko et al., 2011) have shown that search is most difficult when the targets are similar to the distractors and the distractors are heterogeneous. This is of interest for visual camouflage, thinking of background matching and masquerade strategies.

Neider and Zelinsky (2006) conducted a study of searching for camouflaged targets, investigating especially the effects of target-background similarity on visual search. Human observers searched for real-world toy targets among different-sized distractors and varying target-background similarity in four different experiments. The backgrounds were correlated only with the target object and the distractors were dissimilar to the targets and backgrounds (see Fig. 27). Eye movement analysis showed that mostly the distractors were fixated and not the background, even under high target-background similarity. Neider and Zelinsky conclude that target-similar background regions are more or less neglected, but salient patterns segmented from a background are preferred, at least in experiments with human vision. These findings maybe help to a better understanding of visual search in naturalistic contexts under high camouflage conditions. Therefore, in a search situation, one should focus on irregularities in the background that may be a camouflage target and rather ignore patterns that can be easily segmented in a scene (Neider & Zelinsky, 2006). From the other point of view, namely to avoid detection by a searcher, the authors propose to keep a distance from highly outstanding objects that may attract examination.

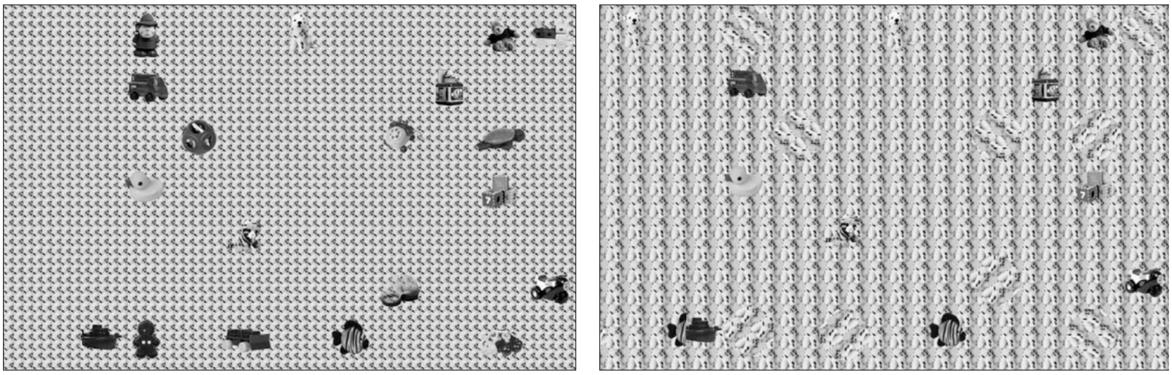

Figure 27: Visual search situation for testing target-background similarity.
Examples of different stimuli used in the experiment of Neider & Zylinsky (2009, p.2221, p. 2230). The target, a Dalmatian dog, is located at the middle top of the images. The search task is more challenging in the right image, where the texture of half of the distractor elements is visually similar to the target.

King, Stanley, and Burrows (1984) used in an early report real-world stimuli, namely photographs of concealed soldiers, investigating possible strategies for target detection.

Works on symmetry reveal that symmetry can be interpreted as an organizational principle of vision. So symmetry is accepted as an important cue in visual search for cryptic objects, but the amount of nun-human studies concerning symmetry is far from satisfactory (Cuthill et al., 2006). An explanation of why symmetry influences the probability of detection lies in the perceptional mechanisms of figure-ground segmentation, because symmetrical regions tend to be perceived as a figure (Merilaita & Lind, 2006). Landwehr (2009) shows this by testing discriminability of selected visually camouflaged symmetry groups in natural textures.

Patterns and texture perception overlaps partly with visual search, because the different backgrounds used in search experiments consist of distinct textures.

To design and evaluate camouflage patterns and automatic target recognition systems, there exists also computational model for the search and discrimination of natural patterns from its surrounding (Copeland 01).

Green et al. (2009) conducted a study with humans searching under diffuse daylight for differently camouflaged moths (images varying in luminance and pattern size) on various backgrounds (paved boards, stucco wall, stone parts, leaves). They report a significant effect on search time depending on background (shortest for paved surface, longest for the stucco wall), arguing that visual search seems to follow segregation of a scene into distinct objects. Some other studies with humans, searching for moths on a computer screen (e.g. Fraser, Callahan, Klassen, & Sherratt, 2007; Webster, Callahan, Godin, & Sherratt, 2009) have been presented similarly.

Training and transfer of visual search in camouflaged environments

An interesting question seems to be if training in the search of camouflaged bodies does have an effect and can be transferred. Boot, Neider and Kramer (2009) examined this by using a paradigm that created a complex background from tiled square parts of the target objects. A good transfer of training was achieved and the human participants found targets in new camouflage sessions almost in the same time like in highly familiar search situations. In contrast to earlier suggestions of the advantages of search strategies focused on the background (e.g. Neider & Zelinsky, 2006), Boot et al. also showed that a “background search”-strategy not necessarily improves performance. Even with the instruction to search background regions participants did not show more oculomotor attention to these areas. A modified paradigm of this experiment revealed the importance of camouflage in structured and unstructured search environments (Blakely et al., 2010). Backgrounds were created by placing randomly geometric cut-outs of the target, therefore preventing breaks in the background patterning. When participants searched unstructured camouflage surroundings the transfer of training to new targets appeared to be much more limited.

Novel objects: Learning

Brady and Kersten (2003) tested the detection of novel camouflaged objects. Already the recognition of familiar objects in cluttered backgrounds seems to be challenging, therefore the authors wanted to investigate how visual systems detect novel objects that are even camouflaged. In their experiment scenes consisted of generated objects, namely camouflaged “digital embryos” that appear to be organic forms but are different from any familiar class of organism (see Fig. 28). After a phase of training, observers were tested on their ability to recognize these objects when presented against a cluttered background with motion-defined, color-defined or ambiguous boundaries. It was hypothesized that learners of novel objects need color or motion segmentation cues, even more when the objects or severely camouflaged. However, in contrary to the expectations it was found that humans can learn to identify and segment a novel target shape, even when the object was camouflaged in training images. Brady and Kersten use the term “bootstrapped learning” to describe the ability of humans of building a shape model from highly ambiguous presentations.

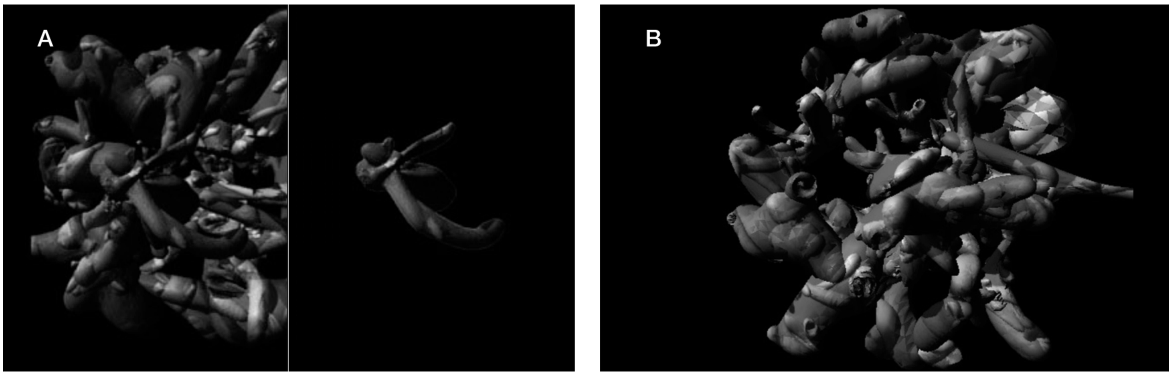

Figure 28. Stimuli for detection of novel camouflaged objects.
Material used by Brady & Kersten (2003). Despite the fact that the object is not hidden, it can´t be detected without prior knowledge of the object. Image A: An artificial morphogenic object (“digital embryo”) with and without background (p. 414). Image B: scene of a training session (p. 416).

Visual search and eye movements

Over, Hooge, Vlaskamp and Erkelens (2007) investigated the eye movement strategy of humans in visual search, suggesting that fixation duration and saccadic eye movements may be used by the visual system as optimizers for visual search success. They analyzed temporal changes in saccade amplitude and fixation duration in two search experiments with constant or varying target conspicuity. The first contains military vehicles in complex natural images with unknown background, type, size and orientation of targets prior to the experiment, in the second experiment only the exact location of the target was unknown. Interpreting the results, Over et al. come to the conclusion that conspicuity seems to have minor influence on oculomotor behavior.

Necessary are computer generated 3D models to test search strategies under naturalistic scenes (Neider & Zelinsky, 2006).

17. Motion

17.1 Perception of motion

The precise representation of motion is an important task of our brain areas. Various studies concentrated on human speed perception or psychophysically aspects of motion perception in the human visual system (Martineau & Cochin, 2003; Mitchell, Kennie, & Kung, 2009; Mysore, Vogels, Raiguel, & Orban, 2008; Pinto & Shiffrar, 2009; Rokem & Silver, 2009).

Chubb, Olzak, and Derrington (2001) recorded that, in human vision a first-order system exist for sensing luminance-defined motion, and one or more second-order systems for correcting the visual input before motion extraction from the signal takes place. Further it is suggested that a third-order system also exists, that sense motion of changes in the salience pattern of the stimulus field. Salience is thought to depend on various factors being part of figure-ground segmentation of the visual field. (Chubb et al., 2001).

Movement attracts attention and allows rapid figure-ground segregation in the visual system of a lot of animals (Zylinski, Osorio, & Shohet, 2009a). When it is not possible to minimize movement through stealth or deceptive resemblance as proposed by Cott (1940), and due to the fact that it is virtually impossible to camouflage a moving body against a non-uniform background, an alternative strategy to avoid detection and targeting of a moving target is necessary (Zylinski et al., 2009a). Possible strategies for this are high-disruptive or dazzle markings. Disruptive markings on some moving creatures may create visual illusions that interfere with motion detection mechanisms (Stevens, Yule, & Ruxton, 2008).

In an psychophysical study comparing visual sensitivity to human and animal motion in point-light displays, it has shown that observers are more sensible to coherent human motion than coherent horse motion (Pinto & Shiffrar, 2009).

However the authors state that the use of configural processing during detection of both motion types would suggest that visual perception of human movement and of nonhuman movement has both its differences and similarities. It has also shown that in healthy children different cortical areas are activated when viewing animated images with human, animal and virtual movement (Martineau & Cochin, 2003).

Mitchell et al. (2009) revealed that the development of global motion perception requires early postnatal exposure to patterned light in a study using kittens.

The recognition of animals' natural motion is part of biological motion (Blake & Shiffrar, 2007; Pinto & Shiffrar, 2009). This is studied by attaching dots to various important points such as ankles, knees and pelvis.

Not just the visual system is important for motion perception. Also the acoustic motion helps breaking the camouflage of a predator or prey, giving information about the future route of an object (Wagner, Kautz, & Poganiatz, 1997), which is also important for non-visual camouflage.

Dorsal V4 neurons seem to possess shape-selectivity for camouflage-breaking dynamic stimuli (Mysore et al., 2008). This was tested by comparing moving shapes (movement of random texture elements) with static shapes (stationary similar texture). Mysore and followers resume that neurons in area V4 show robust invariance for shape preference across different conditions and respond selectively to the moving kinetic shapes.

Concepts like this, and also mechanisms of speed perception (e.g. Van Boxtel, van Ee, & Erkelens, 2006) are the basis to understand how motion dazzle and motion camouflage may work.

17.2. Perception of motion camouflage

Camouflage is normally always associated with motionlessness. Ioannou & Krause (2009) investigated this adaptive function and tested the relationship between movement and crypsis based on larvae and fish. As expected, they showed that Chironomid larvae need both to match the background and to keep still to avoid attacks by the three-spined sticklebacks (Gasterosteus aculeatus L.). Additionally Ioannou and Krause used two forms of colored backgrounds for the prey and demonstrated that more active targets were eaten from cryptic prey groups than from conspicuous ones.

Motion alone can break camouflage by segmenting images into figure and ground, offering by itself sufficient information for detecting the form of a body (Mitchell et al., 2009; Mysore et al., 2008; Shohet, Baddeley, Anderson, Kelman, & Osorio, 2006). Therefore movement can be seen as the enemy of camouflage, because concealment is often revealed by the movement of the target (Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011). Research has shown that even cryptic animals in background matching environments keep still for reducing the risk of being detected (Ioannou & Krause, 2009); hence it seems impossible to camouflage a moving body against a non-uniform background.

Even so motion camouflaged animals indeed move in a certain way for bluffing the perceiver, who thinks it doesn´t move at all (Stevens & Merilaita, 2009a). While appearing stationary the only thing that inevitable changes is the perceived size of the aggressor (Glendinning, 2004). Thus reports of illusions generated by animals, including bodies seeming to be stationary while moving and the difficulty to estimate speed and direction, fall under the category of motion camouflage, although one has to differentiate it from motion dazzle and distractive markings (Stevens, Graham, Winney, & Cantor, 2008; Stevens, Yule, & Ruxton, 2008).

Motion camouflage is of special interest in contexts such as capture of prey by predators and may also be useful for concealment in military and for security applications and computer-games designers (Anderson & McOwan, 2003b; Srinivasan & Davey, 1995).

In general there are various ways of camouflaging motion, ranging from moving as slowly as possible to methods where a predator mimics the optic flow background from the preys' point of view (Troscianko et al., 2009; 2011).

Forms of camouflaging motion

Troscianko et al. (2009) state that motion can be camouflaged through three different ways, namely motion signal minimization (MSM), optic flow mimicry (OFM) and motion disruption (MD).

Motion signal minimization: MSM can function of two different ways (Troscianko et al., 2009). The first is minimizing the motion itself, which results in minimizing the motion signal. This seems like an easy understandable technique and is used by predators which move slowly, therefore minimizing the motion signaled to the prey. The second way is minimizing the motion signal for any given motion, which consists of the signal reduction available to the motion processing system (Troscianko et al., 2009).

Motion camouflage in water is especially interesting because in the sea the current can cause involuntary movements. An example for motion signal minimization are cuttlefish that orient their bodies perpendicular to the the stripes when settling on stripe patterns (Shohet et al., 2006).

Optic flow mimicry: Troscianko et al. (2009; 2011) describe further that optic flow refers to the motion of elements relative to an observer moving through an environment. To apply this successfully the shadower needs to know it´s current position relative to the chosen fixed point, the current position of the shadowee and the motion of the shadowee (see Fig. 29). A shadower refers here to the object that wants to hide its motion while tracking a shadowee (Srinivasan & Davey, 1995). Motion can be concealed if the shadower is moving in a way that emulates the optic flow produced by a stationary object, making approaching a prey possible (Anderson & McOwan, 2003b; Srinivasan & Davey, 1995).

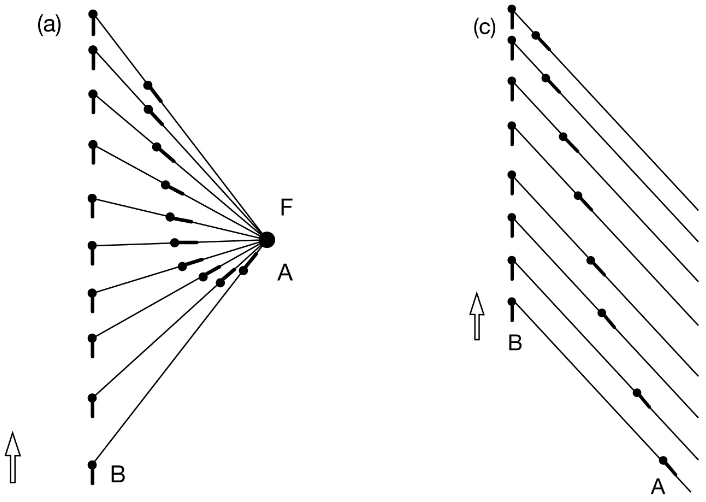

Figure 29. Optic flow mimicry.
Examples of some possible trajectories of a shadower (A) and a shadowee (B). The motion of A can be camouflaged by imitating a static object at a point F, which is located behind (left image) or at infinity (right image) at A´s starting position (Srinivasan & Davey, 1995, p. 20)

Examples of this stealth strategy in the animal kingdom are motion camouflage in dragonflies (Mizutani, Chahl, & Srinivasan, 2003) and the male hoverfly shadowing females in flight (Srinivasan & Davey, 1995). The latter was also demonstrated by a computational model using two- and three-dimensional simulations (Anderson & McOwan, 2003b).

Concerning humans it has shown that we too are susceptible to motion camouflage. Anderson and McOwan (2003a) demonstrated this by developing a three-dimensional computer game with missiles to compare different attack strategies of predators and their distances to the prey before being detected. Their results revealed that motion-camouflaged missiles approach closer to prey than the other missile types, showing its success also in humans observers. Additionally it seems possible that artificial systems determine motion-camouflaged approaches precisely to mislead humans. This results also seem to be of special interest for military engineers (see “Military Camouflage“).

Glendinning (2004) presented a mathematical framework for analyzing motion-camouflage strategies, while analyzing and simulating some cases. With his theory it´s possible to understand the strategy of different target movement patterns and to compute an ideal motion-camouflage path.

Motion disruption: Troscianko et al. (2009) see motion disruption as a manipulation of contours and form for deceiving the perception of motion. For the understanding of motion disruption it is necessary to consider the “aperture problem“ (Adelson & Movshon, 1982). The aperture problem appears when a line or edge is seen moving behind a firm aperture. The motion component parallel to the line cannot be inferred, therefore only perpendicular movement is detectable. The true movement of the line is not clear, and the movement often appears to be at right angles to the line (Bruce, Green, & Georgeson, 2003). This can be an entry point to understand how observers of striped patterns can be misled.

The following remarks overlap partly with motion dazzle. While Troscianko et al. (2009) see motion disruption as subtype of motion camouflage, other authors explain this exclusively with motion dazzle (where markings deceive speed and trajectory estimations), another form of camouflage different from motion camouflage (Stevens & Merilaita, 2009a).

Movement attracts attention and allows rapid figure-ground segregation in the visual system of a lot of animals (Zylinski, Osorio, & Shohet, 2009a). When it is not possible to minimize movement through stealth or deceptive resemblance as proposed by Cott (1940), and due to the fact that it is virtually impossible to camouflage a moving body against a non-uniform background, an alternative strategy to avoid detection and targeting of a moving target is necessary (Zylinski, Osorio, & Shohet, 2009a). Possible strategies for this are high-disruptive or dazzle markings. Disruptive markings on some moving creatures may create visual illusions that interfere with motion detection mechanisms (Stevens, Yule, & Ruxton, 2008).

A good example for deceiving motion perception is the dazzle painted ships during both World Wars (see also chapter 19). This high-contrast geometric patterns should confuse the perceived motion of the ship, among others speed and heading, therefore preventing attacks (Behrens, 1999; Scott-Samuel et al., 2011; Stevens et al., 2008; Troscianko et al., 2011). Troscianko and colleagues however note that a lot of these paint schemes on ships would have created the impression of a false bow, suggesting that part of the effect was figural deception and not motion deception. Scott-Samuel and his colleagues (2011) nevertheless presented the first evidence that dazzle patterns indeed can affect speed perception, showing that when moving rapidly, high contrast patterns (zigzag and checks) produce a speed distortion (see later, chapter 19).

It is disputable whether or not the striping patterns of many animals are motivated by motion disruption. Thinking of the high-contrast patterns of frequently moving animals, these patterns may have a more common function in motion dazzle (Zylinski et al., 2009). High-contrast markings may also be compatible with other strategies such as aposematism, thermoregulation and sexual signaling (Stuart-Fox & Moussalli, 2009). Repeated patterns like motion dazzle can be found in many animals such as zebras, various fish, and snakes. In the context of dazzle painted ships one has to have in mind that they also have functions on some animals and that the zigzag markings of snakes may produce similar optical effects. Such zigzag patterns can supply camouflage or aposematism to a stationary animal and a dazzle coloration or flicker- fusion effect to a moving animal, depending on the viewing distance. The flicker-fusion effect can also be the answer of why some animals with banded markings are cryptic when moving. If they move faster across the visual field than a predators temporal acuity, the patterns may match the background when blurring into a monochrome appearance (Stevens, 2007; Ruxton, Sherratt, et al., 2004).

Cuttlefish *Sepia officinalis* also use a kinetic display known as “passing cloud“, consisting of high-contrast patterns where dark patches are passed at high velocity over the body surface (Hanlon & Messenger, 1996; as cited in Zylinski et al., 2009a, p. 3967).

All in all, there are proves that similar pattern types may have totally different functions in different circumstances and perceivers. The distinction from other related “tricks“ results challenging.

Disruptive camouflage and motion dazzle

The relation between disruptive camouflage and motion dazzle seems to be unclear, although both use high-contrast markings. Disruptive coloration seem to be optimal when it matches the background (see Stevens et al, 2006, Fraser et al. 2007), but dazzle coloration may be best when not matching the background (Stevens, 2007). According to Stevens and colleagues (2011) the protective function of contrasting stripes while in movement and its deception of speed and direction, perhaps spoils camouflage in stationary contexts.

Part III. Camouflage and Humans

18. Overview of camouflage in the human context

It seems that in both human and animal contexts camouflage patterns and the hindrance of detection and/or recognition by opponents are widely studied (Martin Stevens, Searle, Seymour, Marshall, & Ruxton, 2011). Now, after presenting information of camouflage in the animal kingdom and principles of the human perception of camouflage, an insight into the application of camouflage in the human world is given.

It is unknown when camouflage was first practiced, even if one restricts the term to humans. Humans are using quite different forms of deception every day, not only nowadays in their behavior, but also during all periods in all cultures. Historic examples for this lie in the hunting of animals and in religious and social events where humans are disguised as animals, but also in the myth of the Trojan horse with the concealment of Greek soldiers (Blechman, 2004, p. 26).

Humans unlike many species have not evolved obviously protective markings, but often use camouflage forms of the nature in their clothing or military skin paint. Some examples for this are zebra stripes, tiger markings and frog coloration. Apart from military camouflage that will now be presented in more detail, camouflage is also part of various areas such as popular culture and art. Besides new developments in the technological sector, camouflage also developed to be a cult in fashion and in the design world (Blechman, 2004).

19. Military Camouflage

19.1. Introduction to Military Camouflage

Also and especially in war situations the usefulness of camouflage came into view, which is like in other contexts, about fooling the perceiver. It consists in the art of hiding military objects from view, making it harder to see clearly or in deceiving, disguising and misleading the enemy in general (Bauš ys & Danaiti, 2010; O´Carroll, 2009). Moths on tree trunks are difficult to spot because of their camouflage strategies like matching the color of the background and disruptive patterns that are blurring their shape (Wilkinson, 2007). The same methods have been used to conceal military objects and soldiers, developed mainly by professional artists and biologists, starting in the First World War

Like camouflage of animals is not just directed to humans but rather to animals' predators or conspecifics, camouflage in the human context means the intent to be concealed from the point of view of different observers. Enemies should be deceived, but friends should be recognized. To achieve this, coloration, different materials, nets and coverings, but also smoke and noise are used to blend something into its surroundings.

The perception of the viewer is the most important, and modern developments in military camouflage must deceive others form their point of view. Therefore just as insect camouflage has to consider the ultraviolet because birds see it, so must for example modern uniforms deceive night-vision equipment via low infra-red signature (Newark & Miller, 2007; as cited in Cuthill & Troscianko, 2009, p. 9).

Applying and testing the camouflage patterns on military objects against human vision is practical and cost effective in many fighting scenarios. Visual deception has a lot of advantages for survival during battling and the reason for the use of camouflage in the military area is quite obvious: apart from the aim to survive, the attention of an enemy gets drawn away from the real danger and also provokes the enemy to invest its energy and ammunition on a false target (O´Carroll, 2009).

In the last century the military has used the deceptive appearance of a lot of animals for camouflaging their troops, vehicles and equipment and the First World War made a big step with the strategic manipulation of visual information. Also Gestalt psychology influenced the development of camouflage a lot, and with it perceptual organizing principles came up with a theoretical framework for camouflage, helping to make objects more difficult to detect (Blechman, 2004).

In the beginnings of military camouflage, this was conducted by simple field experiments, such as using brush to conceal a truck or earth to hide a gun camp. As the contexts of deception change also the techniques of camouflage have changed (Blechman, 2004). For example the early dazzle painted ships were effective when the human eye, binoculars or periscopes were used to observe the scene. With the beginning of aircraft use, objects also had to be concealed as seen from above and in the modern times more technologically developed techniques that use infrared or other wavelengths have to be cheated. So the effectiveness of camouflage patterns always has to consider the visual and electronical instruments used for observation (Baušys and Danaiti; 2010).

Camouflage in humans is changing all the time and adapts to new developments. Camouflage work always has to respond to its surroundings as war scenes change from jungle to desert to urban areas. Therefore a wide variety of different camouflage patterns in different nations exist. Further the different properties of static and moving objects determine the used camouflage pattern.

19.2 From artists to war

19.2.1. Historical Background

One person who was especially interested in the use of protective coloration and patterns for camouflage in nature as well as in the military was the U.S. artist Abbott H. Thayer. As a sight specialist due to his work as a painter, Thayer - like many artists - was skilled in perfect observation and his three main ideas respective the coloration of animals are countershading, ruptive (now termed as disruptive) coloration and background picturing (Behrens, 1988).

In 1896 Abbott Thayer presented a paper on “The Law Which Underlies Protective Countershading“ and in 1909 published his famous book on “Concealing Coloration in the Animal Kingdom“ (as cited in Behrens, 2009). Although already a few years earlier in 1888, Poulton had written about self-shadow concealment, it was Thayer who got known among friends as “the father of camouflage“. In military history he is still famous for the first practice of countershading and disruptive patterns (Behrens, 1988, 2009).

During experimenting how animal camouflage can be used for military purposes, he worked with stencil cut-outs shaped in the form of animals and with wooden duck decoys to demonstrate countershading (see Fig. 30). Thayer (1918) gives some easy instructions on how to cut out a stencil of the figure which is desired to conceal (e.g. human, ship, cannon) and to “[…] look through this stencil from the viewpoint under consideration, to learn just what costume from that viewpoint would most tend to conceal this figure“ (p. 494). His explanation for this is that when countless details of a background are put across the form of a figure, observers only see the background and don´t recognize the concealed form because of the repetitive background pattern. Following this method, anyone could create appropriate camouflage.

Figure 30. Countershaded material used by Thayer.
Left: A stencil used to demonstrate countershading (Thayer, 1918, p. 484).
Right: Two wooden duck decoys, where the visible left one is of the same color as the floor. The non-visible duck on the right has additionally been countershaded (Thayer, 1908; as cited in Behrens, 2009, p. 498).

As Behrens (2009, 2011) explains, countershading was broadly accepted and many of Thayer´s students later served as camoufleurs in France. Although Thayer was later also critized for his explanation that flamingos are cryptic against sunsets, although their outlines are clearly visible (Wilkinson, 2007), his attribution to the understanding of camouflage is widely honored.

Interestingly, the British-born Australian zoologist and camoufleur William J. Dakin later adopted this method during the Second World War and also published functions of countershading while presenting similar illustrations and using similar wood models to Thayer for the use in military camouflage (Elias, 2008; Rowland, 2011).

In conjunction with George de Forest Brush, Thayer presented for the first time in 1898 the advantages of protective colorated ships and countershaded naval vessels to the U.S. department of Navy (Behrens, 1988). His arguments of the advantages of rendering ships nearly invisible weren´t that accepted. Nevertheless in 1902 the efforts of Thayer and Gerome Brush (the son of Forest Brush) were successful and Thayer obtained an US patent for painting naval vessels using the concept of countershading (Behrens, 1999).

However, a problem of camouflage painted ships consisted in the constantly changing light and weather conditions at sea, hindering the invisibility of naval vessels (O´Carroll, 2009). But soon another solution was found: dazzle camouflage.

19.3. Dazzle camouflage

When the use of camouflage was first established, it was quickly recognized that it is not possible to merge moving vehicles or people entirely with their background. A vehicle cannot always possess the same color like its background when this is constantly changing. The solution of this had been to create a pattern that breaks up the figure intended to conceal, obtained by disruptive patterns (see Fig. 31). By World War I Thayer could make practical use of his theories and also applied the desired effect of discontinuity in protective coloration and military camouflage. It is reported that Thayer noticed while looking at models of ships that a partly painted vessel seems to head in another direction, and that this observation led him to further experiments of deceptive paintings (Behrens, 1988).

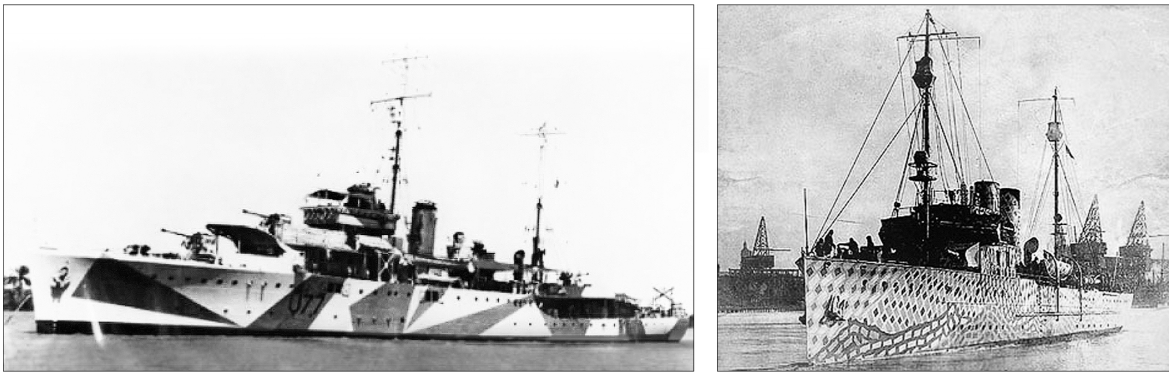

Figure 31: Examples of dazzle camouflage used in the World Wars.
Left: HMAS Yarra, used in World War Two (Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011, p. 2).
Right: USS Isabel painted in dazzle pattern designed by William Andrew Mackay (Behrens, 2012, May).

Thayer´s ideas about ruptive and distractive markings resulted in the application on ships and became commonly known as dazzle camouflage (Behrens, 1988; Dimitrova, Stobbe, Schaefer, & Merilaita, 2009). This consisted in the idea of breaking up dark surfaces of vehicles with white elements, like a zebra. At the same time, also the British naval lieutenant and marine painter Norman Wilkinson came into play. In 1917 Wilkinson recommended that instead of trying to paint a ship so that it could not be seen, which can´t be successful, ships should be painted “[…] not for low visibility, but in such a way as to break up her form and thus confuse a submarine officer as to the course on which she was heading“

(Wilkinson, 1969; as cited in Behrens, 1988, p. 295). Wilkinson is reported as the first who applied dazzle painting at the ships of the Royal Navy and he probably was responsible for installing a few thousand dazzled ship designs (Behrens, 1988).

19.3.1 The effect of dazzle painting

When dark and light color blocks and stripes are put next to each other, the appearance is rendered, the observers´ attention is manipulated, and the exact position can´t be determined that easily (O'Carroll, 2009). When static, such disruptive coloration draws a viewer's attention away from the targeted shape so that this impedes the recognition of more properties, such as the contour, which could reveal the presence of an object (Dimitrova et al., 2009). When the object is moving, the effect of such painting is certainly another: from a distance the size or direction of ships can´t be told.

The design of the geometric patterns were calculated for maximum distortion when viewed using a periscope and the patterns were painted across for example a ship´s hull to confound the usual expectations of light and shade (O'Carroll, 2009; Newark, 2002). Although counterintuitive, this suggests that conspicuous markings enhance inconspicuousness. Distractive markings so far had not received much of scientific interest, maybe due to this seemingly contradictory idea (Dimitrova et al., 2009). Nevertheless, further explanations and visual experiments how the effect of dazzle painting can be tested are given below.

So the successful camouflage of ships consisted of breaking up the continuity of surface and outline of ships by strong color contrasts. Unfortunately, mostly naval officers were responsible for the introduced coloring of ships. Without any scientific or artistic supervision this resulted in absence of the principle and its carrying into practice was often failed in the First World War (Knowles, 1919).

Nevertheless, disruptive coloration or dazzle painting was widely used for military camouflage, although the British Admiralty report no evidence for the effectiveness of dazzle paintings and there exists no real statistical evidence to prove dazzle painting did save ships (Behrens, 1999). However it is supposed that torpedo attacks have been impeded and it was reported that sailors felt safer in them (O'Carroll, 2009).

Later, the adaption of radar probably dissolved the effect of camouflaged ships (Blechmann, 2004).

Note that most of the preserved pictures of dazzled painted ships are in black-white and not in color. Nowadays museum ships are exhibited (e.g. in London (UK), Wilmington (North Carolina, US) and Halifax (Canada), painted in the dazzle camouflage used during the Second World War (Blechman, 2004).

Although unusual, dazzle camouflage is still used as seen by “Steve Irwin“, a ship of the Sea Shepherd Conservation Society in its battle against whaling.

19.3.2 Visual research on dazzle markings

Like described earlier (Chapter 17), moving patterns have a different effect than stationary ones, therefore it is important not to forget that the function of color patterns always depend on the context (Forbes, 2009; as cited in Brodie, 2010). The best example for this is dazzle camouflage, where dazzle markings helped in war time to irritate estimations of speed and trajectory of painted ships by enemies (Behrens, 2009).

In contrast to general camouflage patterns, the investigation of contrasting stripes and motion dazzle is rather rare, despite its fundamental use on warships (Martin Stevens et al., 2011). It is sure that dazzle camouflage does have an effect on the estimations of speed and trajectory (Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011).

The large variety and the range of components used in dazzle camouflage probably mean that different patterns may be optimal for different types of distortion. Some experiments address these questions.

An example motivated by explaining dazzle coloration in nature is the study of Stevens, Yule and Ruxton (2008), programming a computer game that quantifies the capture success of humans detecting variously patterned snakes moving across a background. A single achromatic prey moved across at constant speed but changed unpredictably the direction during the movement to make it more challenging to capture. Participants had to catch the snake by clicking on them with the cursor. In the first experiment Stevens and colleagues used six different prey types using two different backgrounds, as shown in Fig. 32.

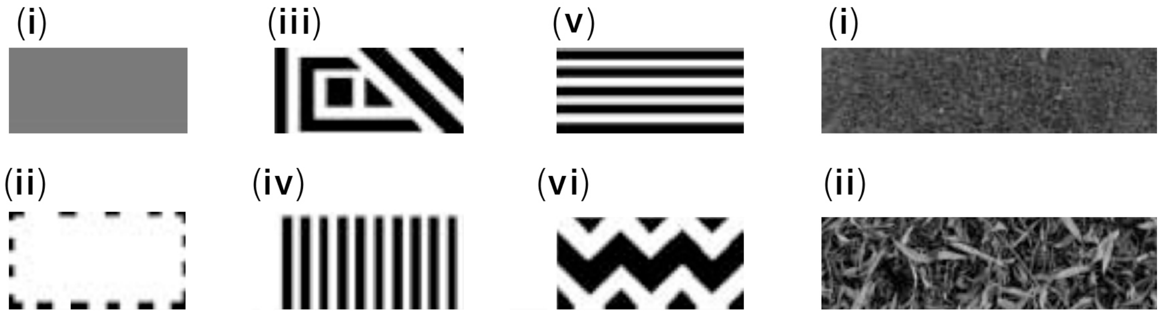

Figure 32: Computer game with dazzle painted stimuli.
Prey types used in the first experiment: camouflaged grey (Ci), conspicuous white (Wii), dazzle (Diii), bands (Biv), stripes (Sv), and zigzag (Zvi). Leafy, heterogeneous (i) and grassy, uniform (ii) background (Stevens et al., 2008, p.2641).

The second experiment investigated the effect of patterns at two different velocities. The main results of both showed that it is harder to capture the prey on the leafy background than on the grass, and prey was easier to catch at low than fast speeds. The capture rates differed between pattern types. The white target was captured the most, the camouflaged grey the least, and there was no significant difference between the other patterned types. Although the study did not show systematic advantages of dazzle camouflage over uniform coloration, some of high-contrast conspicuous patterns (zigzags and bands) were among the hardest to capture.

Due to the fact that the camouflaged grey pattern was matched to the average background luminance, Zylinski, Osorio and Shohet (2009a) later made a comment that because of this it was clear that the grey target had been significantly harder to capture.

Another work that broadened the study design considered the role of contrast, also including either moving or stationary camouflage patterns, was planned by Stevens, Searle, Seymour, Marshall and Ruxton (2011). The interaction of camouflage and motion dazzle was provided using human subjects that had to detect differently patterned targets (see Fig. 33). Apart from the white pattern, all of the subjects had the same average luminance as the background.

The results revealed that moving patterns with stripes were caught less and missed more often, and that stationary patterns with camouflage markings were caught less and caused more false detections. This is in line with the function and intended purpose of dazzled warships. Stevens and colleagues further follow in that context that camouflage and motion dazzle are not complementary strategies, and that the specific coloration on animals depend on the trade-offs between the costs and benefits of these two strategies.

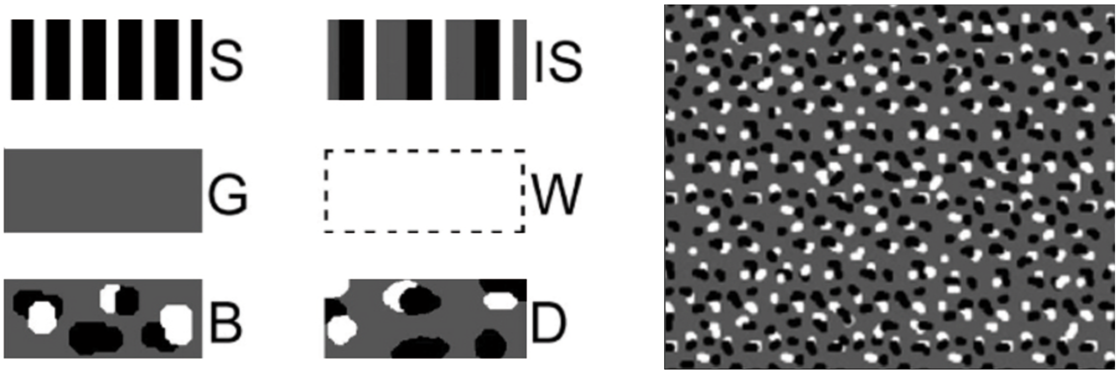

Figure 33: Catching moving patterns.
Left: Black and white stripes (S), interval stripes of gray, white, and black (IS), uniform camouflage grey (G), uniform conspicuous white (W), background matching (B), and disruptive coloration (D). Right: an example background (Some of the stimuli used in Stevens et al., 2011, p.3).

Additionally, in a study mainly motivated by military camouflage**,** Scott-Samuel, Baddeley, Palmer, and Cuthill (2011) presented the first evidence that dazzle patterns apart from range, heading, size and shape, indeed can also affect speed perception. In their experiment different textures were given and subjects had to report which of two stimuli moved more quickly. The stimuli consisted of horizontal black-white stripes, vertical black-white stripes, horizontal black-white zigzag, black-white checks, white plain, and 1-D Gaussian luminance profile as comparison stimulus.

The standard patterns were presented on a mean luminance background, and displayed at two contrast levels (6.25% and 100%). Data were compared with the plain pattern control stimulus, and were plotted as increments or decrements in the perceived speed.

The results show that at high speed, two high contrast patterns (zigzags and checks) were perceived as moving around seven per cent slower than a plain control pattern, showing a significant effect. Patterns with a lower contrast (like in background matching) or with less speed did not produce a speed distortion, indicating that the effect is not simply due to texture. Scott-Samuel and his colleagues further emphasize that high contrast texture as used for dazzle camouflage is necessary to influence the speed perception of an object. For practical military application, the authors also showed that in a situation where handheld weapons are fired from short ranges against a moving Land Rover,

dazzle markings reduce the successful aiming of a grenade. The perceived speed reduction lead to a difference by about one meter (Scott-Samuel et al., 2011).
Still, the exact mechanisms underlying motion dazzle remain unclear.

Dazzle examples from the animal kingdom

Connecting these results with studies on animals gives an interesting insight in the multivariety of motion camouflage. Like presented earlier with information about high contrast patterns, Stevens, Yule, and Ruxton (2008) summarize that stripes, bands and zigzag patterns are common in the natural world, and occur the most in reptiles (Jackson, 1976), mammals (Ruxton, 2002), fishes (Marshall, 2000) and insects. It is likely that some dazzle patterns on real animals that are highly active have evolved these patterns under selection pressure, especially because it is often the easiest to be detected when moving (Stevens, Yule, & Ruxton, 2008). The comparison of capture rates of prey with specific patterns reveals that some seem to be especially effective in making estimation of speed and direction more difficult (Stevens, Yule, & Ruxton, 2008).

Some underwater animals, such as the reef cornetfish seems to be silver colored when it moves, but shows a disruptive pattern when resting (Thomson et al. 2000, as cited in Rosenthal, 2007).

Also to come back again to cuttlefish, they have the potential to teach us our understanding of optimized body patterns when moving, because of their adaptive camouflage capacity. Cuttlefish tune their signals and also body patterns during movement to the visual sensitivities of different viewers and their ability in changing its visual appearance makes it possible to compare the chosen pattern during movement to the predictions of models of motion camouflage (Zylinski et al. 2009).

Zylinski et al. (2009) supposed that the best way pattern for not being detected could be to show low-contrast camouflage markings, when there is no threat nearby. But if the cuttlefish has already been detected, it should be better to produce dazzle markings to reduce the chance of capture during movement.

In their experiment they showed that the body pattern used during movement of *Sepia officinalis* is context-specific and may be distinct from that used when static, relative to the background (eliciting low-contrast mottle patterns or high-contrast disruptive patterns) on which it rests. Further, in cuttlefish high-contrast body pattern components are reduced while moving, meaning that in these experimental conditions the animals do not show high contrast dazzle markings. This suggests that against the expectations, for cuttlefish low contrast and/or smale-scale patterns are likely to protect cuttlefish the best from predators during movement, even when in a static condition the optimal camouflage strategy for that visual environment results in using high-contrast disruptive components.

Zylinski et al. (2009) however explain that this could be due to the fact that moving particles in water rather tend to be of small size and of low contrast, and cuttlefish may try to prevent attracting attention and therefore not chooses high-contrast patterns.

However, comparing these results with that of Stevens et al. (2008) where background matching showed to be the best method of all used target types (see above), Zylinski et al. (2009) assume that probably the body disruptive components used by *S. officinalis* on high-contrast backgrounds are optimal in luminance and spatial matching for this special environment.

The demonstration and the range of different body patterns in the animal kingdom showed that there is possibly more than one solution to reduce movement effects.

19.4 Special unit: Les Camoufleurs

Various artists such as painters, printmakers, sculptors, physicists and art theorists worked together and had been part of camouflage commitment in war time. The need to protect their fellow soldiers from the eyes of the enemies urged many artists to develop new strategies, and the unusual combination of military goals and artistic methods led to the foundation of different divisions of camouflage.

„Les camoufleurs“ (such as André Mare or Georges Braque) had been a special unit that created mass-scale camouflage and camouflage industrial targets with a variety of camouflage forms. This group consisted mainly of painters, decorators, theatre designers and architects and took the chameleon as their sign (O'Mahony, 2010). The camoufleurs were taught different deception methods in the central studio in Paris and later developed specialisms in sub-sections. For concealment of military objects it was for example usual to erect flat covers over them, with green or brown painting, depending on the grass or earth environment. The concealing also addressed every military vehicle (see Fig. 34), so not only ships were painted, also tanks were masked and aircrafts camouflaged (Forbes 2009, as cited in Heethoff, 2010).

Apart from this, the camoufleurs produced anything from fabric to cover military material to gun emplacements and trompe l´oeil painted screens, and were also specialized in “fake“ wood and metal trees, tanks, locomotives, inflatable buildings, and even fake soldiers (see Fig. 35).

O´Mahony further describes that these fabrications were mostly installed whilst under fire, so the conditions under which the camoufleurs worked were challenging. But trees for example, have also been carefully studied in nature, copied in studio, cut down during the night and replaced with fake tree that hid an observation post inside.

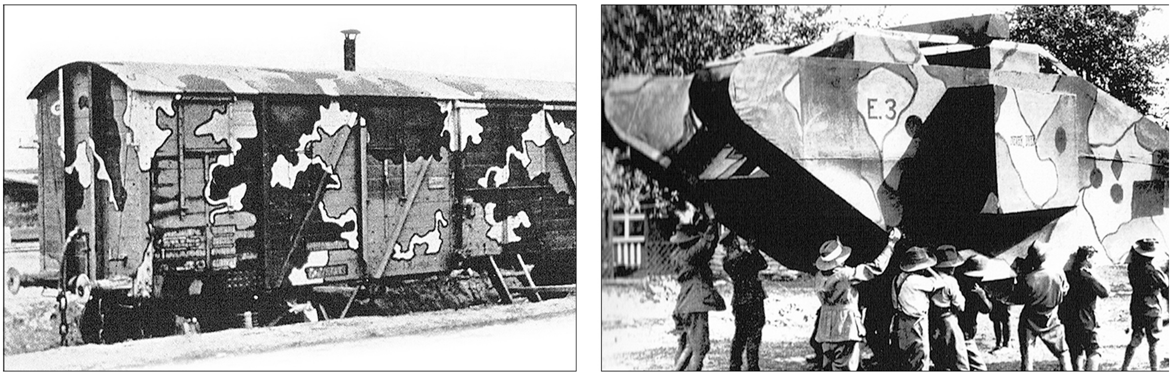

Figure 34: Examples of camouflage painted vehicles.
Left: Disruptive patterned French rail carriages, ca. 1915 (Blechman, 2004, p.342; Roy R. Behrens Collection). Right: Australian troops in the First World War, carrying a dummy tank. The vehicle is painted with a disruptive pattern to draw enemies’ munitions away from real equipment (Blechman, 2004, p. 129).

Figure 35: Observation tree and life size dummy soldiers.
Left: A German observation post in France, 1917 (Blechman, 2004, p. 160).
Right: Life-size silhouettes like this image were installed to give the ilusion of advancing troops, to draw the enemies’ attention away from intended areas of attack (Blechman, 2004, p. 133).

Apart from „Les Camoufleurs“ there existed also other private individual initiatives (e.g. Ernö Goldfinder in London worked with a group of Surrealist artists), who studied different light conditions and nocturnal views. Diverse wartime Home Guard manual has been published, like for example that of the English artist Roland Penrose dedicating one chapter with “How to Turn Yourself into a Hedge“ (Leggett, 2010). By time even teaching institutions responded to the demand for camouflage and offered special courses of camouflage for architects, engineers and designers.

Importance of aerial observation

In general, military information is achieved by horizontal and vertical observation, but especially the vertical observation form airplanes has been of great importance for the camoufleurs (Klein & Mottram, 1919).

Since photographs can reveal much greater detail than direct observation, it was usual to compare photographs that have been taken at different days to detect possible changes and intents of concealing things. Readers of aerial photographs are experts in discovering concealed objects form signs, tracks, moved earth, activities along roads, so that a camouflaged object was likely to be subject to detailed control and the smallest mistake likely to be detected. Therefore, to defeat the aerial camera an exact copy had been required and care in the smallest detail was a necessity, especially because a discovered camouflage otherwise gave false security (Klein & Mottram, 1919). In order to achieve this, also part of camouflage on a basic level was the concealing of tracks of a moving vehicle.

Cott is reported to have painted the fake shade of tanks on the desert ground to deceive aerial reconnaissance by enemies. There also exists the anecdote that later the Germans put a fake wooden bomb on the non-existent tanks (Wilkinson, 2007).

19.5. Camouflage of Architecture

The military also recruited architects directly in addition to general training programs. Architects were called to the special camouflage units because of their geometric skills, and graphic and pictorial techniques had been required to read a built landscape (Cohen, 2011).

The use of camouflage in large cities is an extraordinary example of the gigantism of camouflage projects (Maniaque-Benton, 2011). Urban environments with its landscape of streets, blocks, buildings and monuments are much more complex than any countryside and the intent of deceiving parts of a city results even more difficult. Nevertheless, some buildings, for example governmental buildings or (like in the World Wars) hospitals, must have additional security that disguise them from an aerial point of view (Baušys & Danaiti, 2010).

Camouflage in large cities started indirectly with a censorship of city plans and aerial photographs. Deriu (2004, as cited in Cohen, 2011) gives the example of a 1940 issue of "*L'Architecture d'aujourd'hui*" where views of the port of Marseille were replaced with white spaces. Also for instance in the USSR city plans have been systematically altered.

At groundlevel, the problem of visually detecting buildings had been addressed differently. Urban camouflage aimed to produce large-scale illusions like displacing a recognizable place of interest or disguising characteristic elements like streets and monuments. The German city of Hamburg is a broad example for visual manipulation during the Second World War, where a part of the city should have been visually "displaced" to protect the main railway line from bombing (Deriu 2004, as cited in Cohen, 2011). For achieving this, false islands (in the size of almost ten acres) were installed that covered a part of the lake Außenalster to simulate the nearby lake Binnenalster. Also two bridges have been replicated 600 meters farther away and the main railway station disguised by simulating streets on its housetop.

Camouflage in urban environments is not only an example from the past, but rather is quite actual. The best instance of this is the ongoing research about the camouflage patterned painting of buildings. Further explanations to different patterns in general and to computer-generated patterns have been given earlier (see chapter 14).

There also exists practical interest in questions to depth perception. For example, how it is possible to separate a surface from the floor when both possess the same textures and there is nothing that foretells the boundary of the surface (Ninio, 2007). This is of special relevance for explaining how camouflaged buildings can be discovered with aerial observation (Aschenbrenner, 1954; as cited in Ninio, 2007, p. 562).

Like other kinds of camouflage, the painting on buildings that should be camouflaged must fulfill the main principles of camouflage making it hard to detect or to identify even if it is detected from the air (Baušys & Danaiti, 2010). Therefore its visual properties have to blend with nearby camps or connecting facilities, disrupt the shape of the building and reduce the shine of a building (see Fig. 36).

Figure 36: Two stages of a camouflaged Building.
Building before and after being camouflage painted (Baušys & Danaiti, 2010, p. 855).

Patterns should hinder the interpretation of shadow and shapes. Colors complete this and are used for different purposes, for example matte colors are used to reduce shine (Baušys & Danaiti, 2010; Blechmann 2004).

As greater the distance between an observer and an object gets, the more colors and also brightness changes disappear (Baušys & Danaiti, 2010). Because of this, aerial reconnaissance and observation therefore depend on the color and brightness contrast of a camouflaged facility with the surrounding background.

The big advantage of camouflage patterns on buildings (see Fig. 37) is that they can be adapted to surrounding terrain configuration because in the case of structures the background is not continuously changing.

Figure 37: Examples of camouflaged buildings.

Top left: Camouflaged buildings in Nice, France (one home to Matisse), painted by the Italians in 1943 to protect against US bombers (Toby Ziegler collection; as cited in Blechman, 2004, p. 250). Top right: Harbour Tower, Düsseldorf, finished in 2001. The random colored stripes negate the distinction between the walls and windows of the tower (Blechman, 2004, p. 389). Bottom: The Tours Aillaud (also known as the Tours Nuages or “Cloud Towers´) in Nanterre, a Parisian suburb, were finished in 1977. The buildings shall blend into the surrounding sky and landscape (Blechman, 2004, p. 387).

19.5.1. Culture Architecture

The camouflaging of buildings is not limited to the military, and many civilian structures are designed to be less conspicuous, using “utility camouflage objects“. Transmission stations of the telecommunication industry are often camouflaged with a naturalistic facade, such as various trees, rocks, lamp posts, church spires and building adornments to reduce visual impact and for maintaining nice views in the countryside (Blechman, p. 397).

19.6. Camouflage patterns

19.6.1. Generally

Camouflage patterns are very diverse and the history of camouflage patterns is extensive. To begin with, already Aborigines used camouflage in their war costumes (Thayer, 1918) and camouflage patterns can be adopted from many animals, using their typical skin or fur appearance.

In earlier times, war uniforms had been colorful and soldiers had been detected easily. For example, the French Army used bright red trousers which presented easily detectable targets for snipers and low flying planes (O´Mahony, 2010). Hiding during battle was considered dishonorable, only later military uniforms and material have been changed to blend into the battlefield (Blechman, 2004). During the World Wars military camouflage has been refined thanks to progressing understanding of the use of animal color patterns in nature, but also inspiration derived from modern art (Forbes, 2009; as cited in Brodie, 2010). So a variety of patterns had been produced to conceal humans and objects in outdoor and indoor environments (Baušys & Danaiti, 2010; Behrens, 2009). Through the diversity of camouflage designs however also a problem derived: the need to distinguish friend from foe (Cuthill & Troscianko, 2009, p.9).

The development of camouflage patterns used the advantage of blending in with the battlefield and of being part of the environment. A form of military camouflaging consists in producing artificial boundaries of high contrast within the object that should be hidden. The object is well in sight, but the real shape cannot be recognized (Ninio, 2007).

Camouflage has seemed to be always more effective on equipment than on soldiers, and whole factories disappeared under acres of netting and warships have been covered by cubist-inspired dazzle designs**.** As always, the context is of great importance especially in choosing camouflage patterns. The camouflage of any object that matches the color of its background fails in other differently colored environments, restricting it therefore (Wilkinson, 2007). For example, on sands of a coral beach the natural skin of humans is way better concealed than when painted with dark camouflage cream.

The original green-brown design of uniforms should conceal solders in “natural“ environments like woods and in the countryside, contrary to cities where camouflage with such uniforms fails and special urban camouflage patterns are used.

Camouflage in the desert results particularly difficult, because the context lacks vegetation and cover (Blechman, 2004). This fact has led to various evolutionary studies and to investigations of the conditions under which background matching or more generalized camouflage is demonstrated.

19.6.2. Military Uniforms

Disruptive pattern techniques are used worldwide by different armies, although some confusion exists around the names of military camouflage patterns. As Blechman (2004) states, some countries put official names to their designs, such as the Disruptive Pattern Material “DPM“ (UK), “Woodland“ (USA) or Canadian Disruptive Pattern “CADPAT“ (Canada) and the many different camouflage patterns used in military (see Fig. 38-40) includes also different specific camouflage types such as Civil Camouflage, Army Camouflage, Desert Camouflage, Snow Camouflage, Urban Camouflage, Admiralty Camouflage, RAF Camouflage and so on. Men also seem to identify often with their national patterns like frog skin, oak leaf, chocolate chip and also in many cases the community of camouflage collectors has come up with its own terminology (Blechmann, 2004, p. 24).

Figure 38: Woodland and desert camouflage patterns.
Left: the British DPM (Blechman, 2004, p. 28). Middle: The British ´four color desert DPM´ of which a copy was sold to Iraq. For the Gulf War British Army designed a replacement to be not confused with their enemies (Blechman, 2004, p. 208). Right: The Indian national woodland camouflage pattern, known as the ´cactus´ or ´palm frond´ pattern (Blechman, 2004, p. 202).

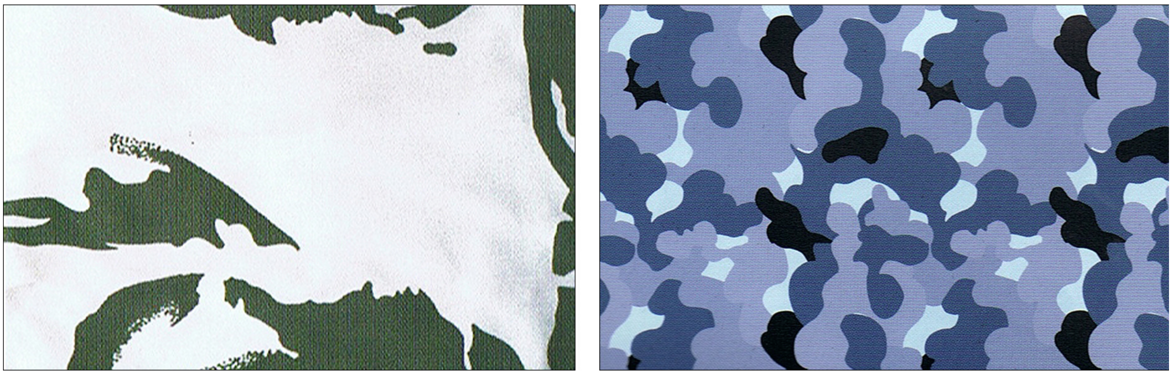

Figure 39: Urban camouflage patterns.
Left: A two-color urban pattern of the South African company Adro Inc., made for commercial use. Right: Supreme´s blue ´bubble´ camo, inspired by the 1950s `clouds` pattern of South Vietnam (both images from Blechman, 2004, p.216).

Recently introduced patterns in the last years are CADPAT and the Multi-Terrain Pattern (MTP). MTP replaces with the use of different colors both the woodland DPM and the desert pattern of the British Army whether CADPAT is the first digital computer-generated pattern and had been designed especially to protect being detected by night vision devices. Another modern digital design that has pixelated patterns is the US Marine Pattern (MARPAT), although there are different opinions about their effectiveness (see Fig. 41).

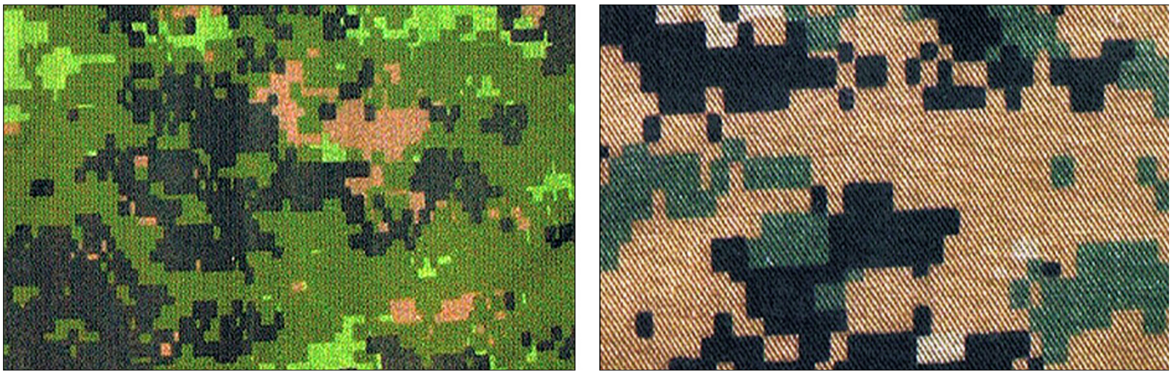

Figure 40: Digitally designed patterns.
The Canadian ´CADPAT TW´ (Blechman, 2004, p. 256; Steve Grammont collection).
The US Marine ´MARPAT woodland´ pattern (Blechman, 2004, p. 256; USMC).

Effectiveness of patterns

Billock, Cunningham, and Tsou (2008) describe that MARPAT and CADPAT use a two-scale scheme that blends better into terrain than a single-scale scheme. They give as an example that detection times for MARPAT camouflaged objects are about 2.5 times longer than of NATO single-scale camouflage patterns, and also the recognition time after detection rises by 20 % (O´Neill et al., 2004; as cited in Billock, Cunningham, & Tsou, 2008, p. 4).

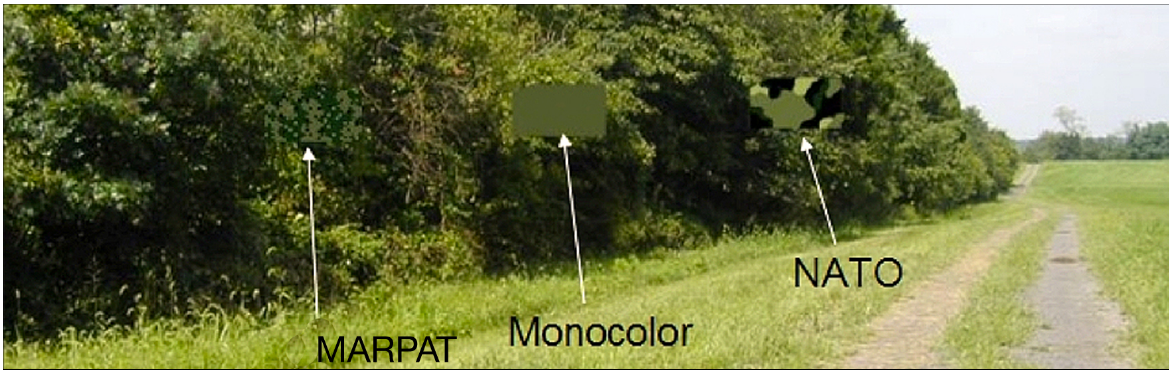

Figure 41: Comparision of camouflage patterns effectiveness.
Comparison of monocolor, NATO single-scale and MARPAT two-scale patterns in a natural environment (Cramer & O'Neill, 2009).

Baušys and Danaiti (2010) also state that digital patterns are more effective than standard uniform patterns because of the human eye interaction with pixelated images (p. 859).

In contrast to that, Cuthill & Troscianko (2009) differ clearly from this explanation and suggest that digital designs don´t have a function in camouflage. They explain that digital patterns rather seem to have a signaling component in telling the enemy that this troop has the best technology available (p. 9).

19.7. Newer Developments

Apart from the exterior appearance of uniform clothing, helmets and shoes, camouflage is also used differently in footwear. So there exist for example shoes that leave impressions of bare feet or shoes with reverse direction soles used to mislead other people (Blechman, 2004).

Many prototype car models wear dazzle camouflage during testing, or use covers. This is especially relevant in hiding the curves of the car before the official release. Further it is reported that a speed trap with dazzle marking exists in Loipersdorf, Austria, probably to confuse the drivers (personal conversation, February, 2012).

Most modern uniforms deceive night-vision equipment and resist radar and infrared detection (Newark & Miller, 2007; quoted by Cuthill & Troscianko, p. 9).

Blechman (2004) names this as another camouflage technique that consists in “blocking the reflection of probing signals“. Current experiment patterns of military uniforms also involve irisdescence and fiber optics (Blechman, 2004).

In general, newer investigation works on invisibility and camouflage methods that adapt automatically to the environment with the help of digital technology. A modern camouflage uniform could be a smart combination of cameras that grab the environment and a lot of projection spaces where these pictures are given, for example on the coat of a soldier, whose surface additionally adapts to the point of view of observers (e.g. see the work of Susumu Tachi, university of Tokyo). This modern “Display-method“ indeed seems to be an option for camouflaging at least buildings or vehicles. Also coats that use electro-optical mechanisms for camouflage are produced (Blechman, 2004).

Military interest is big, so there exists for example a special unit for “Camouflage, Concealment & Deception“. Newly computer generated digital patterns that use fractals mimicking the color distribution in nature make the wearer nearly invisible, providing more time of being concealed (Hambling, 2012).

One design, the “HyperStealth SmartCamo”, is able to change color and to adjust to its surroundings. Also HyperStealth is working on new versions in which the wearer´s movement shall be concealed and on patterns that gives a 3D effect by placing light and dark patches side by side (Hambling, 2012). Despite this, what still seems to be a problem is the shadow of an object, which cannot be concealed that easily like a vehicle (ORF ON Science, 2005).

The military seems also especially interested in the investigation of cephalopods, in the hope that one day similar mechanisms of cuttlefish´s skin dimensionality can be incorporated in the uniforms of soldiers (National Geographic News, 2011).

Most details and technical features are not revealed because of military secret, therefore we probably cannot even assume how developed new inventions are.

20. Camouflage in Human Culture

There is a great interplay between modern military developments and popular culture. Camouflage has changed from concealing a prey or enemy, to being integrated by the public into fashion and also products of daily consummation. Therefore also camouflage is widespread in many areas of everyday life and includes camouflage in art, architecture, clothing, accessory fashion, sports, music, media and toys (Blechmann, 2004). Camouflage itself already has a cultural significance, on that account some of these areas will now be addressed.

20.1. Camouflage and Art

Fraud, hiding and invisibility are some of the concepts that connect art and camouflage, building a big branch of art and war. Dealing with color theory, disruption and abstractiveness but also perfect matching, art continued its relations with camouflage from the beginning of modern military camouflage design in the First World War, throughout the 20th and 21st century. Different movements of Art influenced the development of camouflage (Méndez Baiges, 2007). Thus often the disruptive patterns were described as “cubist“ and also Picasso reportedly stated after seeing in 1914 a camouflaged vehicle on the Boulevard Raspail in Paris “Yes, it is we who made it, that is cubism“. (Stein, 1938; as cited in Cohen, 2011). The camouflaged cannons that had been painted with multicolored zigzags probably have reminded Picasso of the harlequin´s diamond suit in his paintings (Behrens, 1988).

Nevertheless, associations of the camoufleurs with cubism are controversy, because most of the camoufleurs did not use the disruption of geometric form. Rather they had to use naturalistic observations of color and pattern to create perfect screens to be in tune with the surrounding landscape so that no distinction could be seen (O´Mahony, 2010).

Nowadays military camouflage is present among others in Pop art and conceptual art, and the passion of invisibility that characterized once surrealism, is used by actual artists (Méndez Baiges, 2007). As an example, Andy Warhols last major work consisted of the Camouflage-Series, with some camouflage Self-Portraits. Other camouflage artists are, to name just a few, Alain Jacquet, Lee Miller, Annie

Leibovitz, Harvey Opgenorth, Desirée Palmen, William Anastasi, Laurent la Gamba, Toby Ziegler, Lyle Starr, Adelle Lutz, Jennifer Lapham, Paul M. Smith and many more.

So there are lots of examples that show the range of camouflage art, where objects are blended into unusual or also usual backgrounds. A strategy artists often use is to paint themselves or others to resembling their background, to document this in a photography. In this way, Holger Trützsch pictured the painted model Veruschka (Vera von Lehndorff) in and in front of different backgrounds such as a wall, window frame or wooden door. Camouflage can, as commented by Veruschka, "[…] show what exist, and at the same time what does not exist" (Blechman, p.302). For examples of camouflage in Art, see Fig. 42.

Figure 42: Camouflage in Art
All images derived from Blechman (2004). Top left: Let´s Wreck the Party, 2003, Geoff McFetridge (p.371). Top Middle: "The Innermost Mindscape", 2002, Geoff McFetridge (p. 371). Top right: "Green window frame", 1975, Holger Trülzsch (p.302). Bottom left: "Athlon Gamba", 2002, Laurent la Gamba (p.309). Bottom middle: "Somebody Up There Likes Me", 2003, Toby Ziegler (p.310). Bottom right: detail of "Indigenous Interior", 1999, Jennifer Lapham (Blechman, 2004, p.320).

20.2. Camouflage and Fashion

Nowadays camouflage clothes are only used for reducing personal vulnerability, but rather as a fashion statement. Already during the prime of military camouflage in war times, apart from uniforms, some fashion clothes were designed in typical high contrast patterns. Examples for this are dresses and bathing suits in dazzle zebra stripe patterns, influenced by dazzled ship patterns.

Also instructions of how to use camouflage effects in the personal style of dressing were given, with examples of how to improve a slim girl´s or fat girl´s appearance.

The wearing of camouflage patterned clothes in nonmilitary context has become quite normal and also was a real fashion trend a few years ago. So there exists anything from jackets, sweaters, trousers, shirts, skirts and underwear to shoes, bags, hats, jewelry, watches, electronics, eyewear and diverse accessories in varied military designs and colors. Also, maternity pants and clothes for babies and children are on the market, even camouflage accessories, collars and chewable toys for mascots and camouflaged interior design (see Blechman, 2004, Culture Accessories). Various famous designers such as Christian Dior, Louis Vitton, Dolce & Gabbana, Gucci, Jean-Paul Gaultier, Tommy Hilfiger, and many others got inspired by camouflage printings and camouflage also decorates the front pages of diverse fashion magazines.

Action figures, but also non-violent camouflage toys such as plush toys and teddy bears exists that show a typical camouflage pattern. A notable example of camouflage in fashion is also the use of its military patterns for the dress of a “Hello Kittie“ doll. Another example for camouflage dressed culture toys is the Army Barbie (“Boot Camp Barbie“), packaged with military equipment (Blechman, p. 649).

Despite all the trend of camouflage, in some countries such as Barbados, Zimbabwe and Ghana, it is prohibited to wear camouflage clothes by non-military persons (Blechmann, p. 422).

20.3. Camouflage and Media

Cinema and television played an important role in making camouflage pattern popular among civilians. Already Charlie Chaplin´s movie “Shoulder Arms“ from 1917, show two scenes with slapstick effects where Chaplin is disguised as a fake tree (O´Mahony, 2010). Major studies have been involved in promoting camouflage, such as the Walt Disney Studios. Although mainly in military context (e.g. Stanley Kubrick´s movie “Full Metal Jacket“), camouflage has been brought over the screens worldwide. Futuristic methods have been used in films and for some movies a special digital camouflage design was created (e.g. “Avatar“), but also the topic of camouflaging one´s behavior is found throughout the history of film (e.g. “Wag the Dog“; Blechman, 2004, p. 605).

Also, a famous American TV game show “Camouflage“ and its board game vision existed, where people had to find hidden concealed objects.

Camouflage is also frequently used in advertisements, both to promote products (e.g. Coca Cola, Pepsi, Absolute Vodka) and by the military for recruiting new soldiers. For example of Camouflage in film and advertisement, see Fig. 43.

Also in computer and video gaming camouflage is often associated and used with war and military-based action games.

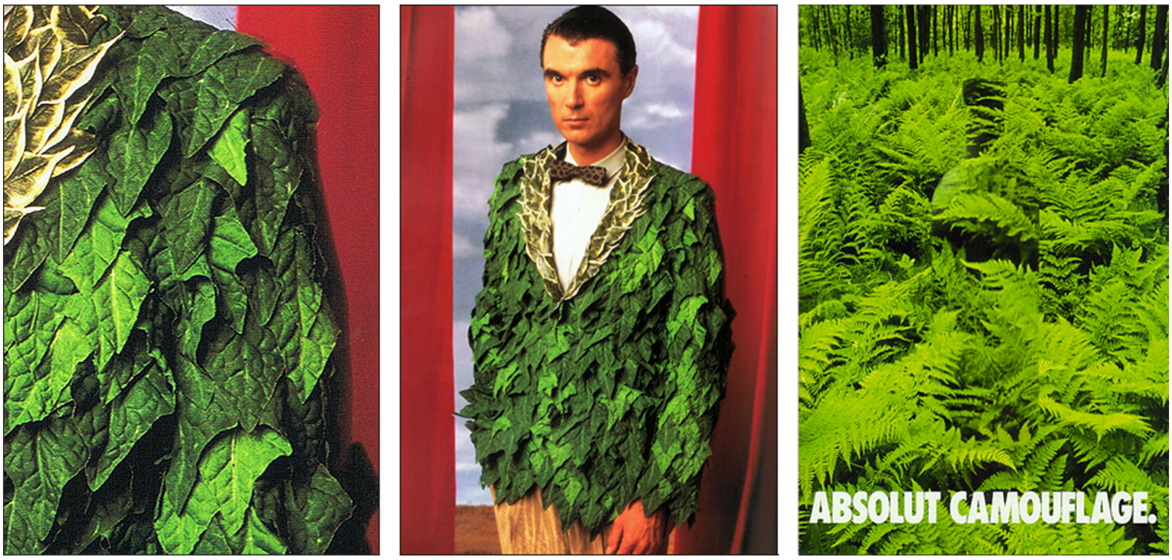

Figure 43: Camouflage in film and advertisement.
Left and middle: Ivy jacket and wood pants for the film **“**True Stories”, 1986 (Blechman, 2004, p. 606). Right: Absolut Vodka advertisement, 1995 (Blechman, 2004, p. 619).

20.4. Camouflage, cosmetics and human behavior

20.4.1. General use

One can draw parallels with camouflage and many different areas of everyday life. Humans are deceiving others all the time while wearing false teeth, quilted shoulders, rugs, hair extensions, plastic nails or high heels to simulate a beauty ideal.

But also placebos, fake fur, plastic flowers and electric candles on the Christmas tree are used to pretend to appear as something different than in reality. Further, humans often imitate the facial expression of their counterparts, called “facial

mimicry“ (Lunau, 2011). Other examples are hunters that imitate the calls of animals, magicians that earn their money with the human attraction for getting deceived, or people that camouflage their gayness (Elder, 2010).
Also, camouflage raises questions about how and why we practise misdirection and can provoke philosophical questions about our reality.

Humans are using cosmetics as a special form of camouflage and deception by altering their natural physical appearance. Apart from military camouflage face paint that often includes an insect repellent (Debboun, Coleman, Sithiprasasna, Gupta, & Strickman, 2001; Lawrence, Benante, Close, & Achee, 2009), the confrontation with and the use of daily color cosmetics is part of the human life. Also beauty operations and facial rejuvenation surgeries are in the broadest sense a form of camouflage, with the frequent aim of camouflaging one´s age.
Further, chemical camouflage and the use of perfume play an important role in the behavior of humans.

20.4.2. Make-up and signaling

Research on the perception of faces has rarely included the effects of adornment. The same way as animals often use color cues to attract conspecifics or to intimidate other animals, humans use color cosmetics to alter their visual features and to increase attractiveness (Etcoff, Stock, Haley, Vickery, & House, 2011).
Russell (2009) suggests that cosmetics probably play a role in exaggerating sexual dimorphic attributes. Female faces with cosmetics possess more facial contrast than the same faces without cosmetics, therefore facial contrast can influence the perception of gender.
When humans see a rouged face, apart from making conclusions based on cosmetic´s effects on the appearance, also opinions about the use of make-up and the user´s personality and intentions are built (Etcoff et al., 2011).
Etcoff et al. (2011) used female faces with three different styles of make-up (natural, professional, glamorous) and without any make-up at all. Participants had to rate these photos for attractiveness, competence, likeability and trustworthiness. The results revealed that cosmetics had positive effects on all of these outcomes.
Authors showed that facial attractiveness together with body weight is the best predictor of physical attractiveness and also represent one of the primary factors

that influence self-esteem (Swami, Furnham, Georgiades, & Pang, 2007). Make-up therefore plays a major role in presenting our external appearance (Korichi, Pelle-De-Queral, Gazano, & Aubert, 2009, 2011). Korichi and al. (2009) conducted a study to investigate the possible relation between two psycho-behavioral make-up profiles (seduction and camouflage) and parameters involved in facial attraction. Women of the group C rather intend to decrease a negative self-perception acting as a form of camouflage, while women of the group S have more desire to please and promote a positive self-image, increasing the powers of seduction. Korichi and al. (2011) then showed that women of group C have a greater asymmetry of the lower face, and women of group S manipulate in a larger range their attractiveness by applying many different colors and maybe because of this, adjust their facial asymmetry and increase their attractiveness more.

20.4.3. Skin camouflage make-up

In general, it has to be distinguished between the use of daily make-up and also permanent make-up such as eye-shadows and lipstick for appearing more attractive, and corrective make-up that is used for camouflaging scars. Skin camouflage make-up is often used by people who have a facial disfigurement, various non-infectious skin conditions (such as dermatoses, vitiligo, plaque psoriasis) or scars as a result of accidents, burn injuries or other causes (British Association of Skin Camouflage [BASC]). Skin camouflage products are designed to blend in with the natural skin color, although the skin structure will remain unchanged. The immediate visual effects of a camouflaged altered appearance can alleviate the psychological and social effects of concerned persons, and can help to regain self-esteem (Saul & Thistlethwaite, 2011). So it was shown that the proper use of camouflage make-up improves the quality of life in patients with vitiligo (Ekwegh, 2011; Kumar & Kaliyadan, 2012; Ongenae, Dierckxsens, Brochez, van Geel, & Naeyaert, 2005).

20.4.4. CV Dazzle

Dazzle make-up (after the dazzle camouflage used in World War I) or “CV Dazzle“ is camouflage from computer vision (CV). CV Dazzle aims to break up the gestalt of a face or object, making it undetectable to face detection and other computer vision programs. Starting as a master thesis work in 2010 of Adam Harvey at the New York University Interactive Telecommunication Program, the project tries to protect privacy in public using ambiguously deceptive fashion. Eye-catching dazzle face make-up and hair styling is combined in limitless variations for altering the contrast and spatial properties of key facial features (see Fig. 44). With the application of make-up on brighter areas that normally are not painted, these face areas are effectively inverted. This can be achieved by applying color on the upper cheek or nosebridge area, instead of around the eyes. Ideally the face becomes an anti-face, which as such is undetectable to machines.

The looks were also tested and validated against environments with automated face recognition systems such as Facebook's Photo Tagger, Google's Picasa, and eblearn (Adam Harvey, 2012).

Figure 44: CV Dazzle
Comparison of detected (left) and not detected (right) faces (Adam Harvey, 2012).

21. Perspectives

One cannot help being impressed by the various ways of camouflage used in order to be not seen. However, understanding the diverse concepts and illusions in terms of human vision and linking them to the coloration, visual systems and behavior of non-human species is challenging (Stevens, Yule, & Ruxton, 2008).

As Ruxton, Sherratt and Speed (2004) state, the natural world is complex, and all the models just represent simplifications. Therefore it is of special importance to be always aware that what humans see is not the same as other creatures see. The mechanisms of how this works need further scientific testing and explanation, and major gaps remain between the knowledge of visual capabilities of most animals, and predator-prey situations in nature. Probably because of the challenges of well-conducted experiments in this area, progress is rather slow.

Since the majority of studies are conducted in standardized systems with rather unnatural ambient conditions, a need for more research in a range of environments exists. Also, more experiments with real animals, of course with considering ethical aspects, are required to deepen an understanding of camouflage mechanisms. As Stevens (2007) claims, a greater knowledge of how strategies may function and how they may be connected, assumes above all also the consideration of the visual and cognitive abilities of the concerned creatures.

Future studies should also connect more specific psychological issues with camouflage appearance. Possible areas of interest including humans are eye-movement studies on the effects of camouflage and attention distraction, but also adressing memory effects, cognitive abilities, and script activation mechanisms.

Further the use of color in general, for protection, and in connection with warning signals and unlearnt avoidness would be of interest, also in human cosmetics to alter properties.

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Appendices

List of figures

Abstract

This work focuses on camouflage in the animal kingdom and in human history. In order to gain a deeper knowledge of mechanisms for avoiding detection or attack and for deceiving predators, the properties of visual systems of different species are explored from the mind and eyes of various perceivers. While inspecting how predators and conspecifics see each other, an overview of several testing material is given, such as manipulations of color patterns and body parts of an object to examine the response of a receiver, manipulation of visual backgrounds, computer simulations and also visual search scenarios. Areas of visual perception that influence camouflage breaking include among others principles of target-background segmentation, object recognition and edge detection in the human visual system, which are compared with animal sensory systems. Mechanisms of camouflage and deceptive coloration from nature have been adopted to the human context. Starting with the broad area of art, military and dazzle painted ships, the connection of camouflage with human culture and recent developments on the technological sector is presented. Despite all that insight, knowledge of how camouflage works is spare but by further examing the interactions of visual systems we can understand perception more precisely.

Zusammenfassung

Die vorliegende Arbeit behandelt Tarnung im Tierreich und der Menschheitsgeschichte. Um die Mechanismen zur Täuschung von Feinden und Vermeidung von Entdeckung und Attackierung besser zu verstehen, werden die Eigenschaften von visuellen Systemen unterschiedlicher Spezies und aus der Sicht verschiedener Wahrnehmer genauer betrachtet. Während der Beschäftigung damit, wie sich Feinde und Artgenossen wahrnehmen, wird ein Überblick über einige Testmaterialien gegeben, wie die Manipulation von Farbmustern oder Körperteilen eines Objektes um die Antwort eines Empfängers zu untersuchen, Manipulation des visuellen Hintergrunds, Computersimulationen und auch Szenarien zur visuellen Suche. Bereiche der visuellen Wahrnehmung welche “Camouflage breaking” beeinflussen, beinhalten unter anderem Prinzipien von Figur-Hintergrund-Segmentation, Objekterkennung und Kantenerkennung im menschlichen visuellen System, welche mit tierischen Sinnessystemen verglichen werden. Mechanismen von Tarnung und Täuschungsfärbung aus der Natur wurden auch im humanen Kontext angewendet. Beginnend mit den umfassendenen Gebieten von Kunst, Militär und “dazzle painted“ Schiffen, wird die Verbindung von Camouflage mit der menschlichen Kultur, und neuere Entwicklungen auf dem technologischen Sektor präsentiert. Trotz allen Erkenntnissen ist das Wissen um die genauen Wirkungsmechanismen von Tarnung spärlich. Durch weitere Forschung auf dem Gebiet der Interaktion von visuellen Systemen können diese jedoch genauer verstanden werden.

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