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1. Chapter 1

1.1 Introduction of dissertation

This thesis consists of 7 psychophysical studies in which the effects of visual stimuli on human cognition are investigated. Pupillary dynamics are measured as a proxy of cognitive neuronal processes. With these studies several questions were answered about how humans perceive, interpret, and handle visual information, and which neural processes are possibly involved. More specifically, this thesis assesses how humans process visual stimuli that are ambiguous and subject to multiple interpretations because of unclear or impoverished conditions. It further assesses why ambiguity leads to changes between being aware or unaware of the existence of particular stimuli in scenes.

1.1.1 Rivalry: from noisy environments to multiple interpretations

Although humans have highly developed skills to process and react to stimuli in our surroundings, noise and ambiguity in our surroundings can cause us to miss visible stimuli or infer incorrect stimulus interpretations. For instance, it may sometimes be difficult to find an item because it is embedded in a cluttered environment, or to determine the physical motion of an object moving in depth. Nevertheless, the human visual system is very skilful in inferring a rich set of information from constrained input that is noisy or incomplete. Humans (and many other species) can, for example, imagine how objects would look in their full entity when they are partially occluded by other objects (Figure 1A).

Sensory information is generally ambiguous that often can be interpreted in multiple ways. Although multiple are available, a single interpretation is often acquired with prior knowledge (e.g., Gerardin, Kourtzi & Mamassian, 2010). Interpretations tend to be based on the strongest and most likely activated memories (Figure 1B) rather than unlikely representations (Figure 1C). However, in situations where there are multiple and equally likely interpretations, the human mind does not seem to have a fixed preference but "resolves" ambiguity by switching between interpretations. Take for example the image shown in Figure 1D in which two gratings with dissimilar colors and orientations overlap (Breese, 1899, Campbell, Gilinsky, Howell, Riggs & Atkinson, 1973). During fixation of this image, fluctuations in luminance for each of the overlapping grating will be observed after several seconds. One grating can be dominant for a specific duration after it is

visually suppressed and perception is "taken over" by the other grating. Thus although their physical appearance remains constant, cognition alters across multiple interpretations. Note that despite their relative equality, these interpretations can have small deviations in likelihood as well. One of the two interpretations may be more likely to be seen than the other interpretation because its features are stronger (Figure 1E).

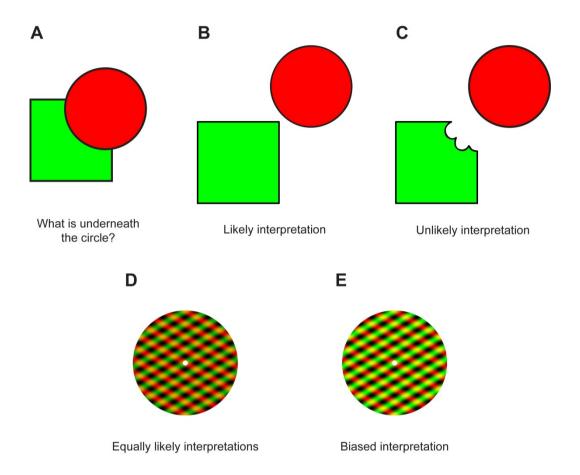


Figure 1. Likely and unlikely interpretations. (A) An example of two occluded objects. The visual system can infer and interpret the lay-out of objects, even if they are partially occluded by other objects. The visual system may for example assume that the red circle is occluding a complete green square. (B) A likely non-occluded interpretation of (A). The most obvious and likely interpretation of the occluded green object in (A) would be a green square behind a red circle. (C) A less likely non-occluded interpretation of (A). It is unlikely that a deformed green square is behind the red circle. (D) Example of a monocular rivalry stimulus. In some rare cases, an object may consist of multiple interpretations that compete (i.e., rival) with each other. By fixating on the white dot in the centre of the stimulus, one observes perceptual rivalry between the red and green overlapping gratings. The luminance of each grating will fluctuate from very bright and conspicuous to hardly visible, and vice versa, while the luminance of the other grating will do the opposite. (E) An example of a rivalry stimulus with small deviations in strength between percepts. Interpretations may be likely or less likely depending on which features they represent. In this example, the luminance of the green grating is increased. Consequently, the green grating is stronger and will be dominant and visible more often than the red grating.

Such ambiguous images are called multi-stable stimuli because they induce multiple alternating percepts and Figure 2 depicts just a couple examples of an extensive collection of stimuli that have been described during the last couple of centuries (Boring 1930, Breese, 1899, Necker, 1832, Schröder, 1858). The actual

phenomenon of ongoing alterations between dominant interpretations over time is called perceptual rivalry and several types can be observed across sensory modalities, including visual (images; Blake & Logothetis, 2002 for review), auditory (sounds; Van Noorden, 1975, Warren & Gregory, 1958), olfactory (odours; Zhou & Chen, 2009), and tactile rivalry (skin pressure; Carter, Konkle, Wang, Hayward & Moore, 2008). This suggests that perceptual rivalry is a very general phenomenon and perhaps a generic property of how a brain handles ambiguous information. Moreover, the phenomenon on itself is of importance to the scientific field of perception as multiple representations exist in parallel while the sensory input remains constant. Hence, the effect of having more states during perceptual rivalry is purely a cognitive process. This has been an important factor for several studies of this dissertation in which we tested how the cognitive interpretations of visual stimuli affected behavior although their physical properties were fixed (Chapter 4 and 5). Why perceptual rivalry is useful for perceptual sciences and what its implications have been so far will be clarified in the following paragraph.

1.1.2 Unresolved issues in perception: Rivalry and its applications

When viewing a rivalrous bi-stable stimulus, you are basically aware of one of the two interpretations and unaware of the other rivaling interpretation at any given time point. This phenomenon is quite remarkable because even though it is obvious that both interpretations are available, only one percept dominates awareness at the expense of the other. Perceptual rivalry can be categorized in two types: monocular and binocular rivalry. Monocular rivalry is induced by presenting the same stimulus to both eyes (i.e., normal viewing conditions; Figure 1D and E, and Figure 2). The stimulus itself contains multiple interpretations that consist of particular features that can rival for dominance (i.e., for visibility or visual awareness). Alternatively, binocular rivalry is induced by presenting dissimilar stimuli to each eye separately. Both types induce changes in visual awareness. It has been, however, very challenging to perform reliable and nonconfounded measurements of rivalry because so many processes affect it, including attention, motor responses, performance, and feature binding. Despite these potential confounds have some limitations, as discussed in Chapter 4, rivalry is a good basis for research of awareness because it exemplifies how perception can change as a function of time without modifying stimulus design. This is why rivalry has often been used as a tool to investigate the neural correlates of visual awareness or consciousness.

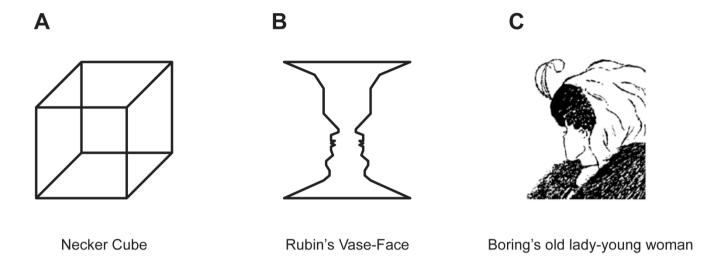


Figure 2. Three examples of perceptual rivalry. (A) The Necker Cube. It induces two percepts of a cube that can be orientated to either the bottom-left or the top-right. (B) Rubin's Vase-Face bi-stable figure. It can be interpreted as either a vase in the centre or two faces at the sides. (C) Boring's old lady-young woman picture. It can be seen as either an old lady with a big nose and a sharp chin that faces towards the front-left, or a young woman with a necklace that faces to the left away from the viewer. This figure is taken from Blake & Logothetis (2002).

Perceptual rivalry can also be employed to study feature or stimulus strength. Rivalry occurs between two percepts that each have specific features such as luminance and color (Figure 1D). Varying these features has an effect on the dominance periods during rivalry. For example, if the perceived contrast of one percept is higher, the other rivaling percept with a relatively lower perceived contrast is less likely to dominate perception (Levelt, 1965). By measuring the dominance durations of each percept (i.e., how long a percept is visible until the rivaling percept takes over perceptual dominance), it can be examined which percepts and the features they are made off are "stronger". But what does it mean when a percept has a higher strength? Does it receive more attention or does it recruit on increased levels of visual processing? Recent studies indicate that perceptual dominance is indeed closely intertwined with attentional processes (Kanai, Bahrami & Rees, 2010, Paffen, Alais & Verstraten, 2006, Paffen & Van der Stigchel, 2010) and saliency (Paffen, Naber & Verstraten, 2008, Stuit, Verstraten & Paffen, 2010a). Saliency is here used in a purely bottom-up, i.e., stimulus-driven, meaning that assumes that a highly salient feature automatically retrieves increased resources or priority from brain processes (Hopfinger & Ries, 2005, Koch & Ullman, 1985). The terms stimulus strength and saliency are often used to describe how sensitive an observer is for a percept and its constituting features. These are also terms for the probability that an excess of resources is deployed to a particular brain mechanism that processes a visual attribute. Salient features attract visual attention and many studies use saliency models to predict where observers will fixate when a particular image is shown (e.g., Einhäuser, Spain & Perona, 2008a, Itti & Koch, 2001). For example, saliency models may weight specific features in an image (Figure 3A and E), such as orientation (Figure 3B), intensity (Figure 3C), and color (Figure 3D), to subsequently end up with a saliency map (Figure 3F) that indicates which areas in the image will most likely be attended and fixated by observers. Note that features alone cannot explain all fixations as formations of higher-level object representations are also important (Einhäuser et al., 2008a). It has remained elusive, however, whether saliency is a mechanism that can not only be assessed by measuring both fixations during free viewing of images, *but* also dominance durations during rivalry (Paffen et al., 2008). Salient features that attract visual attention could similarly increase dominance during rivalry. As will be demonstrated in Chapter 2 and 3, rivalry seems to be an excellent tool to study feature strengths and the visual mechanisms that process them.

Lastly, rivalry can be used to diagnose and treat medical and psychiatric disorders. For instance, amblyopia ("lazy eye"), a disorder of the visual system that results in degraded vision of the neural pathways coming from one eye, can be both measured and treated through the application of binocular rivalry. During binocular rivalry, dissimilar images are separately presented to each eye (Figure 4A). Thus, the left eye receives for example a green grating and the right eye a red grating. This induces rivalry between the eyes (and colors) and perception will switch dominance between red and green percepts over time. If one eye and its related neural visual pathway strongly dominates the other, as is the case in amblyopia, this can be determined by simply inducing binocular rivalry, asking the patient to report visual dominance of both patches, and determine whether there is a strong bias in dominance for one percept (i.e., one eye) (e.g., Huang, Zhou, Lu, Feng & Zhou, 2009). Furthermore, amblyopia can be treated by adding a dark eye-patch to the healthy "eye". As the healthy eye will then be less likely to dominate the other unhealthy eye because of lacking input (extremely low levels of luminance, contrast, color, etc.), the unhealthy eye is consequently forced to dominate vision. This eventually results in a process that facilitates the slow development and recovery of vision for the eye that initially had poor vision (e.g., Holmes, Repka, Kraker & Clarke, 2006). Binocular rivalry has further been suggested as a diagnostic test for patients with bipolar disorders (Hunt & Guilford, 1933, Krug, Brunskill, Scarna, Goodwin & Parker, 2008, Miller, Gynther, Heslop, Liu, Mitchell, Ngo, Pettigrew & Geffen, 2003, Nagamine, Yoshino, Miyazaki, Takahashi & Nomura, 2009, Ngo, Mitchell, Martin & Miller, 2011, Pettigrew & Miller, 1998). Euthymic (i.e., with neutral mood) patients diagnosed with a bipolar disorder tend to have a slower rate of switches between percepts. Unfortunately, populations of healthy controls and patients are not fully dissociable based on binocular rivalry rates as both groups depict large overlapping ranges of alternation rates. Nonetheless, further development of such rivalry tests may result in reliable, fast, and objective diagnoses of such psychiatric disorders.

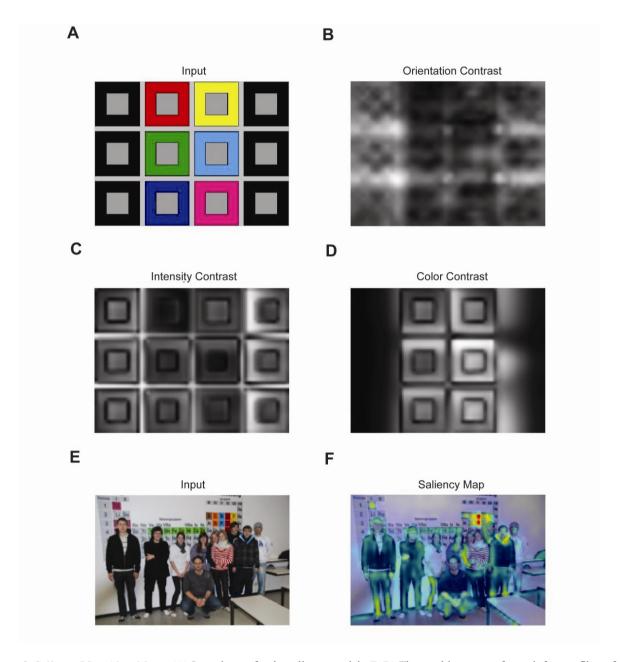


Figure 3. Saliency Map Algorithms. (A) Input image for the saliency model. **(B-D)** The resulting output for each feature filter of the saliency models' algorithm. Areas with highest orientation contrast (i.e., where borders of lines clearly cross), intensity contrast (i.e., strong local differences in luminance), and color contrast (i.e., strong local differences in color) are indicated as most salient areas. **(E)** Another input example of an image for which a saliency map is calculated. This picture of a local gymnasium school class was taken in a lecture hall of the Philipps-University Marburg. **(F)** The resulting overlaying saliency map of the linearly added feature filters outputted by the algorithm. Red colored areas are the most salient.

1.1.3 Measuring perceptual rivalry

As mentioned, several types of rivalry exist, each with their own characteristics. The types of rivalry described in this dissertation are restricted to the visual domain and we use both monocular (Chapter 2 and 5) and binocular rivalry (Chapter 3 and 4). Monocular rivalry can simply be induced by presenting the stimulus on a screen and asking experimental participants to observe the stimulus. Binocular rivalry can be induced with a stereoscope (Wheatstone, 1838). A stereoscope stimulates both eyes with dissimilar stimuli by adding mirrors in front of each eye that reflect light coming from two screens. In one study of this thesis we wanted to assess how changes in perception during binocular rivalry affected pupil size and the direction of gaze (Chapter 4). This approach led to the development of a novel stereoscope with the following characteristics (Figure 4A): First, two images that ranged over a large visual field were presented with two monitors to each eye separately. The monitors were positioned left and right from the observer, 90 degrees rotated from the view point of the observer, facing each other, and the light they emitted was reflected towards the observer with a 45 degree rotated mirror located between them. This setup resulted in a viewing distance of ~30cm and ranged across a large visual field (height: 50.6 deg, width: 37.1 deg). Second, an eye-tracker camera (EyeLink 2000, SR Research, Osgoode, ON, Canada) could monitor pupil size and gaze direction through the mirrors. The mirrors were reflective to visible light and transparent for infra-red light (i.e., cold mirrors) such that observers could not see the eye-tracker setup and that the infra-red sensitive camera could capture light reflected from the eyes. An array of infra-red diodes was installed next to it for illumination of the observers' eyes. The final stereoscopic setup could thus induce binocular rivalry, and measure pupil size and gaze direction.

Binocular rivalry consists of the perceptual rival between the eyes, or strictly speaking, between the features at the local areas of the visual input to each eye. Rivalry results in dominant percepts that may consist fully of the stimulus presented to one eye (Figure 4B and C), or components of both the dissimilar images that are presented to each eye (i.e., piecemealing or fractionation; Figure 4D and E). Remarkably, if components of two rivaling figures are distributed between the two eyes (e.g., Figure 4D and E are jigsaw puzzles of Figure 4B and C), these components are likely grouped into coherent percepts (i.e., interocular grouping; Kovács, Papathomas, Yang & Fehér, 1996). Thus although each eye receives incoherent input, the visual

system combines it into a coherent figure. Interocular rivalry – a term for the local conflict between merely the visual areas captured by the two eyes – occurs when information processed by each eye separately start to rival. Rivalry between the visual fields of each eye can be described as an additional rivalry modality to feature modalities (Knapen, Kanai, Brascamp, van Boxtel & van Ee, 2007a). However, note that not only the eyes but the features of which the percepts are made off can rival for dominance in binocular rivalry as well. In sum, percepts are not strictly separated (i.e., changes in perception do not have an all-or-none nature) and changes in visual awareness can be driven by rivalry between features and the eyes. Visual dominance fluctuates between percepts and a percept is merely a subjective categorization of what is presented. Figures that are presented to each eye separately during binocular rivalry may thus not always result in a coherent visible percept and separate parts of both rivaling figures can dominate locally at the same time. More details on the properties of piecemeal rivalry processes will follow later (Chapter 3 and 4).

The principle process of rivalry consists of alternations between two or more percepts over time (Figure 4F). The previously suppressed percept becomes dominant by "spreading" over the rivaling percept (Wilson, Blake & Lee, 2001), and this process continues between the percepts as long as the stimuli are observed. Perceptual alternations are generally measured by having observers report which percept is dominant. Thus, through introspection, an observer may, for example, hold down buttons, each assigned with a percept, to report dominance during rivalry. The net result of such a measurement is a timeline that indicates the observed perceptual dominance of an observer (Figure 4F; reaction times are not taken into account).

Percepts have inherent stimulus properties that determine their dominance "strength", that is, how easily they are rendered invisible or visible. To measure the stimulus strength of each percept, the distribution of dominance durations is computed per percept (Figure 4G). If one percept has longer average dominance durations, it is indicated as stronger and more dominant than the other rivaling percept. Note that dominance duration distributions are typically leptokurtic (supra-Gaussian) and thus more robustly described by their median rather than their mean. Another calculation that is similar to the median dominance duration is the dominance rate. The dominance rate is based on the ratio of time a percept was dominant during a fixed time interval (e.g., a percept was visible for 60 out of 100 seconds).

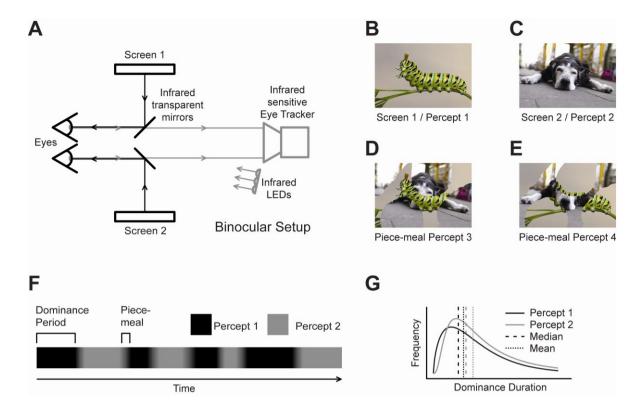


Figure 4. Rivalry methods. (A) A stereoscope that can be used to induce binocular rivalry. This particular setup was developed for this thesis and used in several of the reported studies. It was special in the sense that it enabled the independent stimulation of both eyes to induce binocular rivalry, in combination with the measurement of gaze direction of the eyes and pupil size with an eye-tracker. Two (cold) mirrors reflect light coming from two screens to each eye separately (black lines). Both mirrors are reflective for normal light and transparent for infrared light (>750nm). Both eyes are lit with infrared emitting diodes and light reflects back to the eye-tracker (grey lines). (B-C) Examples of dissimilar images that can be presented by each screen of the binocular setup. If two dissimilar images are shown to each eye separately, binocular rivalry is induced and two dissimilar percepts of each image emerge. (D-E) Examples of piecemeal percepts. Percepts from the eye of origin are not always fully dominant and piecemeal percepts may occur occasionally. (F) Example of alternations between percepts over time. Full dominance occurs more often than piecemeal, especially if both images are substantially dissimilar and small. Both images are either dominant (visible) or suppressed (invisible) at any given time, and after being dominant for a particular period, it will be "taken over" and the previously suppressed image will visually "spread over" the previously dominant image until the reversed process starts. (G) Heavy-tailed distribution of dominance durations. For each rivalry stimulus, periods of short dominance durations occur more often as compared to long dominance durations.

After the dominance durations are calculated, it can be determined whether subsequent dominance durations depend on each other. Surprisingly, dominance periods that follow each other in time correlate in durations (van Ee, 2009). Such serial correlations provide information about whether it is likely that a dominance period of a percept with a particular duration is followed by a dominance period of the other percept with a similar duration. Serial correlations may thus give an indication of how strong percepts are related and how processes, such as attention, affect the overall dominance durations during a given time period. Furthermore, when a rivalry stimulus depicts more than two percepts, it can be determined how often a particular percept is followed by each of the other percepts (e.g., percept A is followed by percept B in 60 of

100 alternations, and followed by percept C in 40 of 100 alternations). Such alternation or switch probabilities cannot be computed for bi-stable rivalry because the probability to go from one percept to the other is 1.0. Hence, more complex analyses can be applied to tri-stable rivalry (i.e., rivalry between three percepts) as is shown in Chapter 2. It is demonstrated that both dominance durations and switch probabilities depend on perceptual stimulus strength, and that perceptual sequences indeed correlate over time in both durations and switch probabilities.

Alternations in dominance may sometimes seem to be abrupt, that is, a percept can be rendered invisible by a rapid change in dominance to the rivaling percept. Especially if stimuli are small and dissimilar, rivalry may appear to be an all-or-none process (Blake, O'Shea & Mueller, 1992, O'Shea, Sims & Govan, 1997). A percept is then either fully visible or fully invisible. As mentioned above, however, transitions in dominance are not necessarily abrupt but often consist of piecemeal rivalry: a gradual change in perceived transparency or spatial fractions of dominance across several percepts. So far only button presses were used to report changes in rivalry. It is conceivable that part of the abruptness is a consequence of a discrete response mode, which is often used to report rivalry. To assess gradual transitions, we offered observers a continuous scale by having them use an analog joystick (Chapter 4), also touching upon the more general issue of action to perception transfer in rivalry (Beets et al., 2010). An observer can deflect the joystick fully to the left to indicate full dominance of a percept, fully to the right to indicate full dominance of the other percept, or somewhere in between to indicate partial dominance of either one of the percepts. Importantly, the amount of piecemealing during rivalry could be an indication of local inhibition between features and depends on the dissimilarity between the rivaling percepts (i.e., distance in feature space; Knapen et al., 2007a). In other words, more piecemealing is observed when both percepts look alike. Thus, the amount of piecemeal rivalry depends on stimulus similarity rather than on stimulus strength.

In conclusion, there are a variety of rivalry measurements possible and each has its own implications on how the brain processes and represents stimuli, multiple interpretations, ambiguity, and changes in awareness. Perceptual rivalry is a unique method to measure cognitive processes and how the brain processes ambiguous information, interprets our surroundings, and eventually organizes these interpretations in meaningful behavior, are key issues that can be tested with it. Despite a tremendous pool of information on rivalry is available, there are several issues that have remained unclear. For example, what happens to alternation

sequences when more than two interpretations are available (**Chapter 2**), how do ambiguous stimuli drive the alternations in percepts over visual space (**Chapter 3**), how does introspection affect these processes (**Chapter 4**), and can ambiguity change the way we perceive objects (**Chapter 5**)? The following paragraph extends on this by evaluating how the visual system processes and labels interpretations of feature constitutions as items and objects when these are ambiguous due to brief presentations.

1.1.4 Impoverished object representations

A percept is an interpretation of a sensory appearance, event, or experience. Similarly, an object is an interpretation of a relatively complex sensory experience that consists of one or more features. The color red in Figure 1A is often referred to as a low-level feature rather than an object. But when the color is paired with an enclosed circular shape that contrasts the red color with its background, an object is formed. It seems that the binding of for example color and shape results in the subjective interpretation of an object. But it is not clear which processes turn a set of features into a cognitive representation of an object. This binding process is also subject to ambiguity and depends on the features and context of the objects. The binding of features into the conscious perception of objects or *gestalts* is a well-known but still not fully understood phenomenon (Revonsuo & Newman, 1999). How is it possible that the separate feature analyses by our visual system create the subjective impression of coherent percepts and objects? If features such as color, motion, and shape are functionally processed in anatomically separate brain areas (Livingstone & Hubel, 1988, Zeki, Watson, Lueck, Friston, Kennard & Frackowiak, 1991, Zeki, 1978), how is each separate analysis combined into a bound object label (Chapter 5), representation (Chapter 5-7), or memory trace (Chapter 7)? Furthermore, how are these representations encoded (Chapter 7), how are they activated and retrieved, and what is the role of separate features in these processes (Chapter 6)? These questions all relate to the "binding problem", an intriguing phenomenon that has several implications on some of the studies in this dissertation. By meticulously adjusting features and presentation time of items - a commonly applied technique in psychophysics – the effects of object formation, detection, categorization, and identification can be measured. Such methodological approaches can be used to gain insights in the underlying mechanisms of feature binding and ambiguity. For example, very brief and presentations of many objects will demand high processing capacities of already limited resources. Such an approach results in ambiguous neural

representations of the presented objects and subsequently the observer has difficulty determining what was shown. This type of ambiguity, is however, not explicitly visible as is the case with perceptual rivalry, but occurs on a decision-making level. What have I seen and which is the most likely interpretation when there are multiple available? The impoverishment of the stimuli by for example limiting the presentation time is thus another method to induce ambiguity (Chapter 6). It has remained challenging, however, to assess the actual neurological processes of feature binding and ambiguity with merely psychophysical methods. Alternatively, physiological methods can also determine how certain components and stages are represented in the brain. Recent studies have therefore focused on neurophysiological measures of feature binding and object formations (e.g., Ostwald, Lam, Li & Kourtzi, 2008, Seymour, Clifford, Logothetis & Bartels, 2009). Such physiological measures may reveal the underlying cognitions related to visual interpretations of ambiguous stimuli and impoverished objects. Another advantage is that these measures do not necessarily rely on human introspection and are thus objective indications of cognition (Chapter 4). The next paragraph focuses on several popular neurophysiologic methods that enable measurements of cognitive brain processes. It is explained why specifically the dynamics of the pupil – an important physiological measure for the studies presented in this dissertation – are so useful regarding research on the visual system.

1.1.5 Pupillometry: An open window into our minds

To understand cognition, it is necessary to study how the brain projects information within its complex network of neurons. There is a vast array of tools available to measure information processing in the human brain and generally they consist of methods that probe neuronal activity. For example, functional magnetic resonance imaging (fMRI) studies measure the oxygenation of blood in the brain with sophisticated MRI scanners. Increases and decreases in oxygenated blood (i.e., BOLD responses) can be measured at a three-dimensional scale of approximately 1-3 mm in each dimension. BOLD responses are often assumed as indirect indicators of increased or decreased activation of neuron clusters. The advantage of fMRI is the relatively high spatial resolution, but the disadvantages are noisy measurements and the slow time course of changes as BOLD responses have approximately a 4 second latency. Other examples of methods that measure activity are electro-encephalography (EEG) and magneto-encephalography (MEG) and these can probe brain activity through electric currents and magnetic dipoles measured close to the scalp of the head. These

methods have a much lower spatial resolution than fMRI but can measure at much higher temporal resolution.

This enables scientists to focus in on the temporal dynamics of cognitive processes.

Despite the tremendous informative nature of these methods, they are very expensive, subject to a variety of noise sources (e.g., head movements for fMRI), and can have limited resolution in either spatial or temporal domains. An alternative and nowadays often neglected measure is the pupil (Figure 5A). Changes in pupil size reflect brain processes and are much more practical indicators of cognition because pupil size can be accurately recorded at high temporal resolutions with a simple camera setup. It is generally known that pupil size adapts to changes in illuminance on the eyes' retinas. Surprisingly, pupil size is controlled by a much more complex network of brain pathways that is also intertwined with neural areas responsible for higher-level cognitive processes. As such, pupil size has been correlated with many behaviors and cognitive states such as attention (Daniels, Hock & Huisman, 2009, Kahneman, 1973, Karatekin, 2004, Karatekin, Couperus & Marcus, 2004), arousal (Bradshaw, 1967), alertness (Yoss, Moyer & Hollenhorst, 1970), decision-making (Einhäuser, Koch & Carter, 2010, Simpson & Hale, 1969), anxiety and emotions (Bitsios, Szabadi & Bradshaw, 2002, Charney, Scheier & Redmond, 1995, Nagai, Wada & Sunaga, 2002, Simpson & Molloy, 1971, Steinhauer, Boller, Zubin & Pearlman, 1983), deception (Dionisio, Granholm, Hillix & Perrine, 2001, Wang, Spezio & Camerer, 2006), task-engagement (Gilzenrat, Nieuwenhuis, Jepma & Cohen, 2010, Jepma & Nieuwenhuis, 2011), mental effort, resource allocation, cognitive or working memory load (Ahern & Beatty, 1979, Beatty & Wagoner, 1978, Bijleveld, Custers & Aarts, 2009, Cabestrero, Crespo & Quirós, 2009, Granholm, Asarnow, Sarkin & Dykes, 1996, Hess & Polt, 1964, Kahneman, 1973, Kahneman & Beatty, 1966, Karatekin, 2004, Reinhard & Lachnit, 2002b, Verney, Granholm & Dionisio, 2001), target onset probabilities (Friedman, Hakerem, Sutton & Fleiss, 1973, Privitera, Renninger, Carney, Klein & Aguilar, 2010, Raisig, Welke, Hagendorf & van der Meer, 2010, Reinhard, Lachnit & König, 2007), and, particularly interesting in the present context, perceptual alternations in rivalry (Einhäuser, Stout, Koch & Carter, 2008b). With so many factors affecting the pupil (Andreassi, 2000, Beatty & Lucero-Wagoner, 2000, Janisse, 1977, Loewenfeld & Lowenstein, 1993, for review), this outwardly visible part of a sensory organ is an excellent measure for the temporal dynamics of cognition, as demonstrated in Chapter 4, 6, 7, and 8. From a neuroscientific perspective, it may also provide information about particular neurotransmitters that are responsible for cognitive processes (Chapter 7).

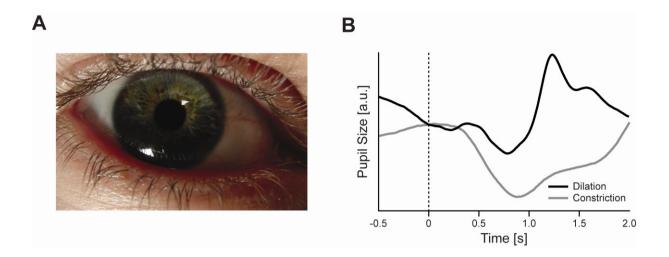


Figure 5. The pupil. (A) Example image of an eye with a slightly constricted pupil. **(B)** Pupil size as a function of time around the onset of a stimulus or change in cognitive state. In this example, pupil size was measured as a function of time around the onset of either an image on a screen (grey) or a reported transition between percepts during perceptual rivalry (black). Pupil size can either constrict (i.e., decrease in size) or dilate (i.e., increase in size). Note that the pupillary constriction as a response to stimulus onset is fast with an approximate latency of about 300-400ms, while pupil dilation as a response to a change in a cognitive state is slow with much longer latencies of 600-1100ms. Pupil dilations can also be preceded by small constrictions, and constrictions are often followed by a pupil size increase back to baseline.

Most studies on pupil size and behavior or cognitive states report a facilitated (i.e., stronger) or attenuated (i.e., weaker) dilation (mydriasis) or constriction (miosis) during a particular task, stimulus presentation, or change in cognitive state (Figure 5B). There are two main pathways that may separately contribute to both the dilation and constriction of the pupil (Loewenfeld & Lowenstein, 1993). Dilation of the pupil can be accomplished by the excitation of the smooth radial muscle and the inhibition of the sphincter muscle. Conversely, inhibition of the smooth radial muscle and excitation of the sphincter muscle results in pupil constriction. The dilatory radial muscle is controlled by the sympathetic nervous system through the posterior hypothalamic nuclei. The constrictory sphincter muscle is driven by the parasympathetic nervous system through the Edinger-Westphal complex of the oculomotor nucleus in the midbrain. Each neural pathway is characterized by the sensitivity for specific neurotransmitters that either activate or inhibit nerves in these pathways, and eventually the constriction or dilation of the pupil. The administration (e.g., with cholinergic drugs) of acetylcholine (ACh) leads to a constriction of the pupil as ACh acts on the muscarinic receptors of the sphincter muscle (Elliott & Carter, 1989, Fountoulakis, Fotiou, Iacovides, Tsiptsios, Goulas, Tsolaki & Ierodiakonou, 1999, Fountoulakis, St Kaprinis & Fotiou, 2004, Loewenfeld & Lowenstein, 1993).

Furthermore, Alzheimer studies have also shown indirect evidence of ACh's contribution to pupil constrictions as Alzheimer patients have reduced levels of ACh (e.g., Francis, Palmer, Snape & Wilcock, 1999) and attenuated, thus weaker, pupil constriction (Fotiou, Fountoulakis, Tsolaki, Goulas & Palikaras, 2000, Prettyman, Bitsios & Szabadi, 1997). The release of ACh also consequences in the inhibition of norepinephrine (NOR) related activity (Yoshitomi, Ito & Inomata, 1985). NOR is a neurotransmitter that is released from the brain nucleus "locus coeruleus" and acts on alpha-adrenergic cell receptors that regulate activity of the dilator muscle (Loewenfeld & Lowenstein, 1993, Yoshitomi et al., 1985). In contrast to ACh, release of NOR results in the dilation of the pupil (Elliott & Carter, 1989), and inhibition of NOR activity, by for example ACh, leads to a constriction of the pupil. Activation of the sympathetic pathway, and thus dilation of the pupil, has been indicated as an effect caused by cognitive states (Steinhauer & Hakerem, 1992, Steinhauer, Siegle, Condray & Pless, 2004). Also the inhibition of the parasympathetic pathway, and thus the attenuation of constriction, has been similarly indicated as an important factor during cognitive demand (Steinhauer et al., 2004). In sum, both the constriction and dilation of the pupil seems to be a trade-off between the release and inhibition of ACh (cholinergic) and NOR (noradrenergic). This delicate balance – as reflected in the pupil – will play an important role in the elucidation of several results presented in this dissertation. How the pupil behaves during the processes of perceptual rivalry (Chapter 4), object detection (Chapter 6), identification (Chapter 6), memory formations (Chapter 7), and decision-making (Chapter 8) is explained in the following outline of experiments.

1.2 Outline of dissertation chapters

As described in the Introduction, the general gist of this dissertation is the investigation of how the visual system infers interpretations from ambiguous information. With the help of the phenomenon perceptual rivalry and the physiological measure of pupillary dynamics, important insights in the role of ambiguity, visual awareness, object formations, features, introspection, memory, and decision-making were gained. Here follows a concise outline of the studies in which these insights are reported.

The first two studies of this dissertation consist of psychophysical papers about perceptual rivalry and its dynamics. With only a few exceptions, almost all studies on ambiguity during perceptual rivalry have used stimuli that induce two percepts (bi-stable stimuli; Figure 2). For the first study (**Chapter 2**), several tri-stable

stimuli were developed to assess how rivalry behaves if observers may have three instead of just two separate percepts. Tri-stable stimuli further enabled us to not only measure dominance durations, but also switch probabilities (the probability to switch from one percept to the other during bi-stable rivalry is trivially 1.0). These stimuli were presented to observers who were asked to report their perception. They indicated, with three buttons, which of the three percepts was dominant. It is found that switch probabilities between and dominance durations of percepts depended heavily on the preceding history of perceptual dominance. Furthermore, by varying the luminance of a percept across experimental trials, it was discovered that these results depended on stimulus strength.

As mentioned before, resolving ambiguity is not all-or-none and switches or changes between percepts in rivalry may occur gradually. Rivalry is, however, often assumed to be and measured as a discrete process. On the contrary, a switch in visual dominance between percepts is a "spread-like" or "wave-like" event. These perceptually traveling suppression or dominance waves may start at a certain location inside the stimulus and travel towards another location with a specific direction and speed. In a second study the dynamics of traveling dominance waves during binocular rivalry were investigated (**Chapter 3**). Two main questions were answered: 1) whether the speed of such gradual switches in perceptual dominance depended on the spatial direction of the change and the stimulus strength of the stimulus that initiates the switch, and 2) the generality of these speed dependencies across two different phenomena. Results showed that dominance wave speeds indeed depend on their direction as they decelerated towards the visual fovea while they remained at constant speed when moving towards the periphery. In addition, the speed was determined by the luminance of the stimulus that was used to initiate the wave. These two novel characteristics of binocular rivalry were also observed in a related but different phenomenon termed *generalized flash suppression*. This indicates that traveling suppression waves might be a phenomenological property of a very general process that causes changes in visual awareness in a variety of visual illusions.

Besides rivalry's usefulness regarding the initiation of multiple cognitive states and interpretations during a constant display, it is further often used to study the neural mechanisms underlying visual awareness. The search for the neural correlate of consciousness is a popular topic in contemporary neuroscientific studies. However, these studies face the challenge to extract the mere neural process strictly related to changes in visual awareness. Such processes are inevitably confounded by a variety of processes that occur

during perceptual rivalry, such as attention, motor responses, and other cognitive functions. More specifically, changes in visual awareness can be induced by monocular or binocular rivalry but the actual timing of perceptual switches is typically measured through introspection and button presses by observers. Experimental participants have to report which percept is dominant at a given time point. Rivalry studies are thus limited to and by subjective interpretations and response latencies. In the third dissertation study (Chapter 4), these problems were circumvented by the development of a new objective measure of rivalry (i.e., pupil dynamics) and comparing it with an existing objective measure (i.e., optokinetic nystagmus, OKN). By varying luminance and movement direction of gratings separately for each percept, and by inducing changes in dominance through binocular rivalry, pupil size and the OKN direction were modulated accordingly. Thus unlike to pupil dilations induced by the actual switch in perception (Einhäuser et al., 2008b, Hupé, Lamirel & Lorenceau, 2009), when a percept with a high luminance was dominant during rivalry, pupil size decreased, and when a percept with a low luminance was dominant, pupil size increased. It was shown that pupillary dynamics were relatively reliable indicators of rivalry dynamics and could be used as an alternative to the OKN to objectively measure changes in visual awareness. In addition, reflexive signals such as pupillary dynamics and the OKN were examined to estimate whether they provide more information about rivalry dynamics than conventional introspective measures. By using these reflexes as objective measures of rivalry, we revealed that the process underlying switches in perceptual interpretations is gradual rather than abrupt, is sped up by overtly reporting perception (i.e., introspection), and that some of the switches can slip away from awareness. Future studies can now filter out confounding factors of activity related to motor responses and attention with the aim to extract the "pure" neural correlate of visual awareness by applying this pupil method in combination with sophisticated brain imaging tools. All together, these results are strong motivators to use objective measures of rivalry and ambiguity in future studies on visual awareness.

In a fourth study, ambiguity was applied as a tool to examine how the visual system processes and interprets objects (**Chapter 5**). There are two views on how objects are represented in the brain and how object-based attention is allocated to them. First, objects consist of features such as luminance, color, collinearity of borders, and closure. If these features are combined in the right formation, attention can be deployed to them and then an object representation is formed through a bottom-up process. An object can then consequently be labeled and categorized by our visual system. Alternatively, features may automatically

draw attention, but a unique top-down formed object representation is needed to deploy attention. The main difference between these two views is thus the order of how attention is deployed to parts in a scene: View 1 suggests that specific feature combinations drive and allocate attention to the object while view 2 argues that the mere concept and neural representation of an object allocates attention to these features. Whether just one of the two views can explain object-based attention effects and whether features play a role in the deployment of attention to parts in a scene per se, was tested with a special rivalry stimulus termed as the ambiguous moving diamond. The moving diamond induces two percepts, one of a single, bound, and coherently moving object (i.e., a 45 degree rotated square or diamond), or multiple unbound, independently- and incoherentlymoving objects. This stimulus enabled the dissociation between a cognitive single and multiple object interpretation while the physical appearance remained unchanged. In other words, the cognitive state of the observers and not the presented stimuli determined whether a single or multiple objects were seen. Results showed that the state of seeing a single object lead to a facilitated detection and discrimination of targets on this object. Thus, if a single rather than the multiple object state is perceptually dominant, attentional allocation to the object is activated. In conclusion, specific features combinations are not necessary to allocate attention but object-based attention effects are controlled by a top-down allocation of attention through an object interpretation that is stored as a higher-order representation. This finding would not have been possible without the use of the elegant phenomenon of perceptual rivalry.

Combining the issues of Chapter 4 and 5, it was next investigated whether pupil dynamics could give insights into how the brain processes objects and which features can help to resolve ambiguity connected to interpretations of objects (**Chapter 6**). The stages that relate to detection and identification of animals in rapidly presented natural scenes were elucidated by looking at pupil responses to image presentations. Furthermore, image features were analyzed and tested for their effects on detection and identification performance. The effect of anxiety for the depicted animals on performance was also assessed. Surprisingly, anxiety had a small but negative effect on performance as animals were detected faster and identified with higher confidence when they were less frightening. Features, such as luminance, contrast, saturation and color contrast also strongly affected performance, and especially the contrast between the object and its background turned out to be an important predictor of performance. Pupil size correlated with detection, identification, and anxiety judgments at different time-points after image presentation. In sum, rapid visual processing

depends more on target pop-out features than on overall visual context, is negatively affected by anxiety, and finds its processing stages differentially reflected in the pupillary response. Measurements of pupil size show herewith that it can reveal the timing and strength of rapid visual processing of objects in natural scenes. The results further suggest that features are highly important for object recognition during the rapid bottom-up processing of ambiguous visual stimuli, and that higher-order features such as anxiety have less effects than previously suggested.

The fifth study reported that pupil dynamics provide information about how the brain processes objects that are only shown for short periods. The sixth study focuses on how the viewing of objects and scenes affects pupil responses during memorization and retrieval and whether the subjective and ambiguous nature of deciding whether an image is old or novel is similarly reflected in the pupil (Chapter 7). The memorization of visual objects and natural scenes consists of the storage of a memory trace (i.e., a representation), and is known to be imperfect and prone to mistakes due to perceptual ambiguity. The retrieval of object representations from memory during the task to judge whether an image is new or old (familiarity memory), is a difficult task and subject to ambiguity as it is often unclear whether an object has been seen before or not. In this study it is found that the pupil constricts more when an image is successfully encoded and later remembered, and when an image is recognized as novel during retrieval. These results are explained in the context of the encoding of novel items and the release of the acetylcholine (ACh) and norepinephrine (NOR) – two neurotransmitters known to be responsible for both the constriction and dilation of the pupil.

The seventh and last study discusses the effects of decision-making on pupil size and tests the ability of human observers to use pupil size as an informative signal about another person's cognition during a game (**Chapter 8**). Movies of the eye of several participants ("opponents") were recorded while they played several trials of a game of rock-paper-scissors during which they had to make a decision within a certain interval. These opponents had to choose one of three options (rock, paper, or scissors) per trial that were serially presented with four second intervals in between. Pupil size tended to briefly dilate during an interval following a decision, and was a reliable indicator of when and thus which option was chosen by the opponent on a trial-by-trial basis. A new group of participants ("players") were allowed to watch these movies (viewing conditions were made as life-like as possible) and had to determine which one of the three options had been

chosen by the opponent. Remarkably, only one player was able to extract useful information from the pupil shown in the video of the opponents'. Other players were "distracted" by other potentially informative cues such as eye-brow movements and blinks. Only when informed to look for pupil dilations, all players were able to considerably increase their performance. This is a good example of how multiple visual cues can be available to an observer and that after correct instructions, observers are able to resolve ambiguity and focus on the relevant cues. In conclusion, observers can interpret a person's cognitive state by looking at pupil dynamics.

2. Chapter 2

Tri-stable stimuli reveal interactions among subsequent percepts: Rivalry is biased by perceptual history

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Abstract

In rivalry, constant stimuli allow several interpretations ("percepts"). Percepts are characterized by their probability to occur and by the duration of their dominance. During continuous presentation of *bi*-stable stimuli, both percept probabilities are trivially 50%. To disentangle the processes triggering a percept from those stabilizing it, we introduce *tri*-stable stimuli having three percepts. We find the probability and dominance duration of a percept independently adjustable. Percept probabilities and dominance durations show mutual dependencies across several perceptual switches. Consequently, the current perceptual experience depends on perceptual history; therefore, rivalry - even for continuous presentation - is not a memory-less process.

2.1 Introduction

Signals arriving at our sensory system typically contain incomplete or ambiguous information about their sources in the real world. The system is then faced with the challenge to infer a unique and consistent interpretation. If several interpretations are equally probable, the perceptual experience tends to switch between several alternatives over time, while at any given time point one interpretation dominates. This phenomenon, termed rivalry, is observed for a huge variety of stimuli (Blake & Logothetis, 2002 for review), ranging from geometrical figures (Necker, 1832; Schröder, 1858), faces (Boring, 1930), structure from motion (Ullman, 1979), binocular (Wheatstone, 1838), tactile (Carter, Konkle, Wang, Hayward, & Moore, 2008), auditory (Warren & Gregory, 1958; Van Noorden, 1975), and olfactory stimuli (Zhou & Chen, 2009). Although these stimuli differ substantially across features and modalities, they induce a strikingly similar rivalry process: continuous and stochastic perceptual alternations between two interpretations of an ambiguous sensory stimulus (e.g., Brascamp, van Ee, Pestman, & van den Berg, 2005; Rubin & Hupé, 2003; Sheppard & Pettigrew, 2006; Pressnitzer & Hupé, 2006; Naber, Carter, & Verstraten, 2009; O'Shea, Parker, Rooy, & Alais, 2009).

In rivalry, successive dominance durations (i.e., the time period a certain percept is visible) are generally considered as independent and the exact timing of rivalry switches as unpredictable (Fox & Hermann, 1967; Levelt, 1967; Blake, Fox, & McIntyre, 1971; Borsellino, De Marco, Allazetta, Rinesi, & Bartolini, 1972; Walker, 1975). However, several outwardly accessible physiological measures, such as eye position, saccades, eye-blinks, and pupil size have been found to relate to rivalry states (Wundt, 1898; Becher, 1910; Glen, 1940; Eure, Hamilton, & Pheiffer, 1956; Ito, Nikolaev, Luman, Aukes, Nakatani, & van Leeuwen, 2003; Einhäuser, Martin, & König, 2004; van Dam & van Ee, 2005, 2006; Einhäuser, Stout, Carter, & Koch, 2008; Hupé, Lamirel, & Lorenceau, 2009) and may potentially serve as predictors for dominance durations and switch times.

Even without the use of physiological markers, independence and unpredictability of perceptual states have received considerable challenge. By carefully accounting for noise effects in reporting the perceptual state, van Ee (2009) has recently reported a non-zero correlation between successive dominance durations in rivalry. On long and on very brief time-scales, perceptual history also is known to affect the speed of rivalry

switching: Suzuki & Grabowecky (2007) find a brief initial decrease of dominance durations during the first 6 trials of 20-s rivalry presentations and a feature-specific long-lasting effect of daily exposure to a rivalry stimulus. Most evidence against the stochasticity of rivalry, however, has resulted from studies using interrupted presentations of rivalry stimuli. In such a setting the order of percepts and their dominance durations also contain information about subsequent percepts (e.g., Maloney, Martello, Sahm, & Spillmann, 2005; Brascamp, Knapen, Kanai, Noest, van Ee, & van den Berg, 2008; Pastukhov & Braun, 2008). More specifically, if a bi-stable stimulus presentation is interrupted by a blank presentation period, the chance that the preceding percept returns after the blank is related to the length of its previous dominance duration. Some of the resulting theories and models of multi-stable perception that take into account these facts, have denoted a significant role of an internal bias and memory (Leopold, Wilke, Maier, & Logothetis, 2002; Maier, Wilke, Logothetis, & Leopold, 2003; Kanai, Knapen, van Ee, & Verstraten, 2007; Brascamp et al., 2008; Pastukhov & Braun, 2008; Brascamp, Pearson, Blake, & van den Berg, 2009). These studies generally imply that a perceptual bias cumulatively builds up during the dominance periods of a percept and the larger the bias for this percept (i.e., the longer its preceding dominance durations), the higher the probability to turn dominant again after interruption. An exogenously controlled factor, such as blanking the stimulus, however, may itself affect rivalry dynamics. Indeed, during discontinuous presentation of bi-stimuli, the process of alternations can, depending on the duration of blank interruptions, either be sped up (Orbach, Ehrlich, & Heath, 1963) or slowed down (Leopold, et al., 2002). In addition, the effect of an intermittently presented stimulus depends on whether the interrupting stimulus itself is ambiguous and on its similarity to the interrupted stimulus. If an ambiguous stimulus interrupts a percept, this percept is less likely to survive as compared to an unambiguous interrupting stimulus (Pearson & Clifford, 2005). If the interrupting and the interrupted are dissimilar, the interruption has effects comparable to a blank; increasing similarity between the features of the rivalry stimulus and the interrupter, however, decreases the survival probability of the percept preceding the interruption (Pearson & Clifford, 2005; Kanai et al., 2007). The probability of a percept to survive an interruption furthermore depends on the contrast of the rivalry stimulus (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007). These studies show that intermittent presentation of a rivalry stimulus reveals important features about the process of rivalry. However, here we are interested in the dynamics of rivalry without any

exogenous events (such as interruptions). Hence we here aim at studying effects of perceptual history on the current perceptual experience by using the continuous presentation of an uninterrupted stimulus.

Most stimuli used in rivalry research are *bi*-stable, that is, they allow exactly two distinct percepts. For continuously presented *bi*-stable stimuli, the probability to experience one of the two percepts at an arbitrary point in time is proportional to the average dominance duration of this percept. Only considering the percept sequence, both percepts occur equally often (provided the sequence is sufficiently long to neglect edge effects from start and end of the sequence). If we refer to the percentage of occasions in which a percept becomes dominant as percept probability, percept probability will thus be exactly 50% for any uninterrupted bi-stable stimulus by definition. (Note that the average TIME a percept is dominant, i.e. the dominance duration, is distinct and can be substantially different between the two percepts of a bi-stable stimulus). Hence, the factors underlying the stabilization of a given percept and those subserving its (re-) occurrence cannot be disentangled in bi-stable stimuli, unless perceptual states are exogenously interrupted. To keep presentation continuous, while nevertheless dissociating dominance durations from the probability of entering a percept, we here use *tri*-stable stimuli (i.e., figures that induce three distinct interpretations of a constant stimulus).

Stimuli with more than two interpretations have been studied before. Burton (2002) used a quad- (or tetra-)stable perceptual rivalry stimulus and showed an effect of instructions on the percept sequences, but did not report relations between dominance durations and switches. Other studies on multi-stable stimuli combined binocular rivalry with other forms of rivalry. O'Shea, Tep, Roeber, & Schröger (2008) showed different perceptual rivalry stimuli to each eye to achieve a tri- (to hex-)stable percept ("trinocular rivalry"). Suzuki & Grabowecky (2002) asked subjects to report four different dominance states during bi-stable rivalry in which the percept could have exclusive dominance (i.e., one eye was fully dominant) or was intermixed with its rival to achieve 4 different percepts through instruction. Despite several similarities between perceptual and binocular rivalry (Andrews & Purves, 1997), both might differ from each other in other respects, in particular with regard to the dependence on perceptual history (van Ee, 2009). Hence it is well conceivable that using binocular rivalry or a combination of binocular and perceptual rivalry stimuli, may yield substantially different results as compared to using a rivalry stimulus without binocular conflict. To assess whether multi-stable perception without binocular conflict reveals similar dependencies between

dominance durations and transition probabilities, we use different tri-stable stimuli without inducing binocular rivalry.

With our stimuli, rivalry is either induced in the motion (Experiments 1 and 2) or in the color domain (Experiments 3 and 4). Within each domain, slight modifications of the stimulus allow us to bias the stimulus such that either one of the three percepts dominates (experiments 1 and 3) or all are about equally strong (experiments 2 and 4). Hence we can measure the relation between dominance duration and percept probabilities and check whether any perceptual history effect is contingent on a specific parameter choice. In addition to analyzing the sequence of percepts, we measure dependencies between dominance durations and percept probabilities, and identify a new relation between these measurements. Our data support the view that, even under continuous viewing conditions and without binocular conflict, rivalry is not a memory-less process, but biased by perceptual history.

2.2 Methods

2.2.1 Observers

Author M.N. and 7 naive observers (age 18-31) participated in each experiment. Observers had normal or corrected to normal vision. Each observer gave written informed consent to participation; all procedures adhered to national standards on experiments with human observers and with the Declaration of Helsinki.

2.2.2 Stimuli

We used four different tri-stable stimuli in four separate experiments. In Experiment 1 and 2, the stimulus was a moving plaid consisting of two superimposed gratings (Wallach, 1935; Adelson & Movshon, 1983) (Fig. 1A). These plaid stimuli allowed three distinct alternating percepts: coherent upward motion (U), incoherent transparent motion in which the leftward motion is perceived on top (L), and incoherent transparent motion with rightward motion on top (R). In Experiment 1 the gratings were tilted ± 120 degrees against the vertical midline. In Experiment 2 the tilt was increased to ± 140 degrees. The latter parameter change generally increased the relative stimulus strength of the incoherent sideward motion percepts. In both experiments, gratings were square-waves, had a spatial frequency of 0.73 cycles per degree, a peak luminance (white) of 84.2 cd/m², a minimum luminance (gray) of 23.3 cd/m², a 5 degree circular aperture, and drifted outwards at a speed of 1.73 deg/s.

Stimuli in Experiments 3 and 4 consisted of three stationary overlapping color gratings (for bi-stable version: Breese, 1899) in a 5-degree circular aperture (Fig. 1B). Despite the fact that luminance remained physically constant throughout the experiment, the stimulus induced alternating shifts in perceived luminance per color, with one of the 3 colored gratings clearly dominating (i.e., appearing brightest) at any given point in time. Each grating's color was produced by a single gun of the screen only. For Experiment 3 the gratings had CIE coordinates (x, y, Y) of (0.623, 0.332, 17.7 cd/m²), (0.298, 0.598, 60.6 cd/m²), and (0.153, 0.068, 8.99 cd/m²), respectively. In Experiment 4 the luminance (Y) of the green grating was lowered to 25.1 cd/m² with otherwise identical settings. This made the perceived luminance of the green grating closer to that of the other gratings and therefore increased the relative stimulus strength of the red and blue gratings. Gratings were square-waves and had a spatial frequency of 1 cycle/degree. Orientations relative to the vertical midline were -120 degrees (red grating), 0 degrees (green), and +120 degrees (blue). For consistency of notation with

Experiments 1 and 2, we referred to the red, green and blue gratings by their tilt to the midline, i.e. by L (red), U (green) and R (blue), respectively.

2.2.3 Setup

Stimuli were generated using Matlab (Mathworks, Natick, MA) with its Psychophysics toolbox extension (Brainard, 1997; Pelli, 1997; http://psychtoolbox.org) running on an Optiplex Dell computer and presented with a 21 inch EIZO Flexscan monitor on a gray background with 1280x1024 pixels at a refresh rate of 100 Hz. Mean luminance of the background was 23.3 cd/m², minimum luminance (black) of the screen as well as ambient light levels were negligible. Head position was stabilized using a chin and forehead rest that assured a steady viewing distance of 82cm.

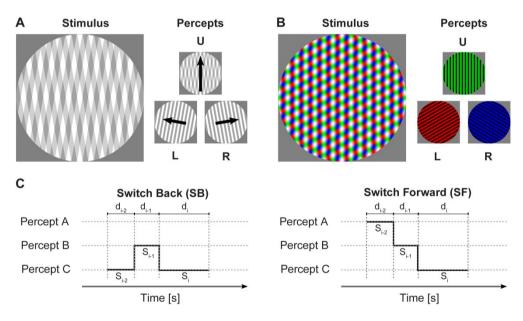


Figure 1. (A) Moving plaid stimulus used in experiments 1 and 2. Two superimposed gratings move sideward, inducing three possible percepts: coherent upward motion (U), transparent (incoherent) motion with leftward moving grating in front (L), or transparent motion with rightward-moving grating in front (R). **(B)** Static color grating stimulus used in experiments 3 and 4. Perceptually one color grating of the stimulus dominates at any given point in time (red=L, U=green, R=blue). Note that the figure's color and luminance values might differ dramatically from the actual presentation and that it takes several seconds before rivalry initiates. (C) Considering triplets of percepts, two sequence types can be observed: "switch forward" (Si is different from Si-2) and "switch back" (Si is the same as Si-2). Si denotes the state (percept), di denotes the corresponding duration of the percept being dominant (dominance duration), and i denotes the index of the percept in the sequence.

2.2.4 Procedure

Observers were instructed to indicate the percept by holding down one of three arrow keys of a USB-gamepad (Left, Up, or Right) per percept. Observers were asked to always press one button even if their

perceptual dominance was weak. Since during transitions the button for the preceding percept had to be released, while the button for the new percept had to be pressed, in the transition period either two or none of the buttons were pressed. In 30% of the cases this transition was below the resolution of the input device (36 ms). In the remaining cases, the overlap periods lasted on average (medians) 80ms (two buttons, 31% of cases) and 130ms (no button, 39% of cases), which is very short compared to the overall dominance durations (median: 2750ms). This indicates that the transitions between percepts were experienced as sharp. In both cases, the period with two or no button were allotted to the second percept. Only very rarely (3% of all transitions) did observers release a button and press the same one again. For the reported data, we aggregated the periods if the release lasted less than 10s and excluded the whole period otherwise. Neither exclusion nor inclusion of all these periods, however, changes any of the reported results or conclusions (data not shown).

Each experiment consisted of three 5-minute blocks. Experiments were taken on separate days and observers were allowed to take breaks between blocks. Before the actual experiment observers were familiarized with the stimuli and apparatus.

2.2.5 Notation

We denote the sequence of perceptual states ("percepts") by S_1 , S_2 S_N where ... The dominance duration corresponding to the i-th state is denoted by d_i . To enable analysis across observers, we normalized distributions of dominance durations by dividing them through the median dominance duration within blocks and observers. These *normalized dominance durations* are denoted as d_i^* . We also analyzed relative dominance durations; i.e. how much longer was percept d_{i-2} relative to d_{i-1} . Hence we defined *relative dominance duration* as $(d_{i-2}-d_{i-1})/(d_{i-2}+d_{i-1})$. The experimental setting only allows transitions between different states (as same-state transitions, if existent, would not be reported as "switch"), that is $S_i \neq S_{i-1}$. Consequently, given S_{i-2} there are only two alternatives for S_i . If $S_{i-2} = S_i$, we will refer to a (S_{i-2}, S_{i-1}, S_i) triplet as "switch back" (SB), otherwise we refer to $(S_{i-2} \neq S_i)$ as "switch forward" (SF, Fig. 1C).

2.2.6 Test for Markov property

If rivalry were a memory-less process, the probability to transit from a current state to another should be independent of any preceding state other than the current one. In other words, the sequence of perceptual states would have the so-called Markov property. In the Appendix, we devised a test of the null-hypothesis

that a given finite sequence fulfills the Markov property; p-values in Results section 3.4 (denoted as p_{Markov} to avoid confusion with the transition probabilities) refer to this test. A low p_{Markov} implied that the null-hypothesis, and thus the hypothesis of a memory-less process, is likely to be refuted.

2.3 Results

2.3.1 Tri-stable stimuli show the same dominance-duration statistics as bi-stable stimuli

We investigated tri-stable rivalry with four different stimuli in four separate experiments. First we assessed, per experiment, whether general properties of tri-stable stimuli, in particular the distribution of dominance durations, match those typically observed for bi-stable stimuli. At visual inspection, the sequence of perceptual states and associated dominance durations appears irregular and random (Fig. 2A), similar to the typical observation for bi-stable stimuli. To facilitate comparison and pooling across observers, we consider normalized dominance durations d_i* (see 2.5; Table 1 for raw durations). As for bi-stable stimuli the distribution of dominance durations has a leptokurtic (i.e., heavy-tailed) distribution, which can be approximated well by a Gamma or a Log-normal distribution (Fig. 2B). Hence the 0th order properties of all our tri-stable stimuli, namely the distribution of dominance durations, are similar to the bi-stable case.

2.3.2 Dominance durations and percept probabilities are independently adjustable

In bi-stable stimuli the probability of both percepts to occur in the sequence is exactly 50% (neglecting initial / final percept). In tri-stable stimuli, however, percept probabilities may range from near 0 (only the other two percepts are observed) to 50% (the percept re-occurs after every other switch). Dominance durations, in turn, need not be coupled to these percept probabilities (consider for illustration a case, where the sequence of percepts is ABACABACA, but B's and C's duration is twice that of A's). If the processes underlying stabilization and (re-)occurrence of a percept, however, would be the same, we would predict percept probabilities and dominance durations to be proportional to each other. To test this hypothesis, we analyze whether stimulus parameters can adjust percept probability independently from average dominance duration. First, we compare the two drifting plaid stimuli (Experiment 1 and 2). In Experiment 1, both the mean dominance duration of the up percept (Fig. 2C) and its probability (Fig. 2D) are higher than the other two percepts. Note that compared to Experiment 1, the motion direction of the gratings was deliberately changed to "weaken" the U percept in Experiment 2. In Experiment 2, however, the up-percept still has (marginally) the highest average dominance duration, while it occurs substantially less frequent than the left and right percept. Consequently - although we cannot exclude some coupling between dominance duration and percept

probability; the relation that trivially holds in the bi-stable case, does indeed not hold for tri-stable rivalry. We observe a similar result for the color stimuli of Experiment 3 and 4.

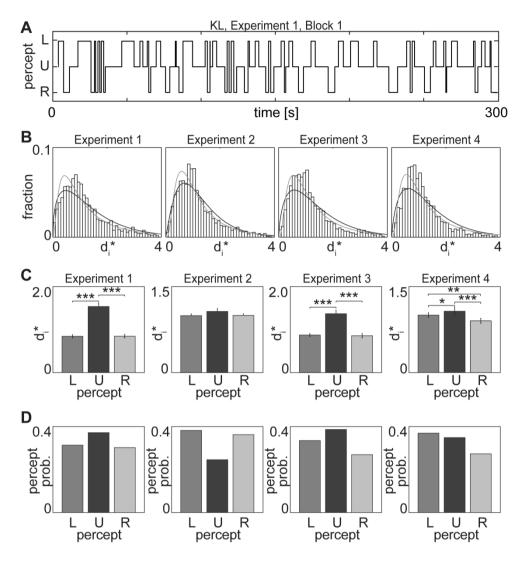


Figure 2. (A) Example sequence of reported percepts over time (observer KL in first block of Experiment 1), illustrating the seemingly stochastic nature of rivalry. **(B)** Distribution of normalized dominance durations, pooled across observers and normalized to unit integral (probability densities). Gamma (black) and log-normal (gray) distributions are shown with the same mean and variance as empirical data. **(C)** Median and standard error of pooled normalized dominance durations per percept. Since dominance duration distributions are non-Gaussian (panel B), significance markers refer to a non-parametric Wilcoxon test on equality of medians. **(D)** Probabilities for each percept to occur, data pooled across observes.

The U percept is dominant in both mean dominance duration and percept probability in Experiment 3. In contrast, the U percept still has significantly higher dominance durations in Experiment 4, but is only second to the L percept in terms of percept probability. Again, percept probability and dominance duration are not proportional. In conclusion, the processes determining the probability of a percept to occur and the processes subserving the persistence of its dominance are – at least partly – distinct.

2.3.3 First-order transition probabilities

For all experiments, we analyzed the first-order transition probabilities between the 3 percepts (Fig. 3). No comparable measure exists for continuously presented bi-stable stimuli, as the probability to switch to the other percept is always 1 if only two percepts exist. In the tri-stable case, however it is relevant to see whether certain transitions are preferred. As illustrative example, consider a case in which all percepts had equal occurrence probability. With this example all transition probabilities could be 0.5, but, on the other extreme, could also be 1 for $L \rightarrow R$, $R \rightarrow U$, $U \rightarrow L$ and 0 for the other ($L \rightarrow U$, $U \rightarrow R$, $R \rightarrow L$). In the former case, switch back and switch forward would be equally likely, while in the later case only switches-forward would exist.

In Experiment 1 (Fig. 3, left), it is more likely to switch from an incoherent percept (L or R) to the coherent percept (U) than between the incoherent percepts. This is not surprising, given that the U percept is most probable to occur (Fig. 2D). Conversely, in Experiment 2 the transition from incoherent to coherent is less likely than between incoherent percepts, although there is a slight asymmetry in favor of the R to L transition (Fig. 3, 2nd from left). In Experiment 3 there is a bias to switch from U to L (rather than to R), while in Experiment 1 and 2 the incoherent to coherent transition probability is independent of whether the incoherent percept was L or R (Fig. 3, 3rd from left). The preference to go from U to L is preserved in Experiment 4 (Fig. 3, right). In both cases this is consistent with the overall more likely occurrence of L as compared to R (Fig. 2D). In sum, there is an effect of stimulus properties on first-order transition probabilities. However, this effect is mostly accounted for by the effects on the (0th order) percept probabilities and beyond this, there is no evident preference for any specific first-order transition.

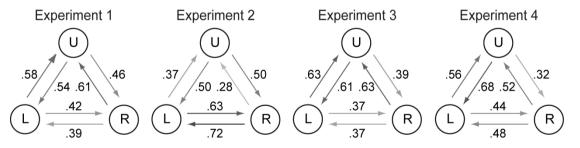


Figure 3. First-order transition probabilities between the different percepts for the 4 different experiments, data pooled across all observers. Gray value of arrows is negatively related to the size of probabilities.

2.3.4 The sequence of percepts is non-Markovian

If rivalry were a memory-less process, percept sequences induced by the tri-stable stimuli should have the Markov property (cf. Methods). To test this, we calculated for each possible triplet (see Appendix) the probability that a particular sequence is Markovian (p_{markov}). When calculating p_{markov} for all observers and experiments, we find that in Experiment 1, the null-hypothesis of the sequence being Markovian can be refuted (at $p_{\text{markov}} < 0.05$) in 4 out of 8 observers (Fig. 4, top-left). In Experiment 2 even 6 out of 8 observers violate the Markov assumption (Fig. 4, top-right). With the exception of observer KG in Experiment 1, the violation consistently occurs when U is the intermediate percept (S_{i-1}) in a triplet sequence (S_{i-2} , S_{i-1} , S_i) and is symmetrical with respect to the two possibilities for S_{i-2} . In all significant cases (at p < 0.05) the switch forward is more likely than the switch back. Again for 3/8 observers in Experiment 3 (Fig. 4, bottom-left) and 4/8 observers in Experiment 4 (Fig. 4, bottom-right) the Markov property is violated. Since we perform 192 individual comparisons, (4 experiments * 8 observers * 6 transitions), an adjustment of the alpha-level of the test is needed. When adjusting the expected false discovery rate (FDR) to 0.05 by using the Benjamini & Hochberg (1995) method, the corrected level across all experiments is 0.006. Using this corrected level, we still find significant preferences for the switch forward in 3/8 observers in each experiment.

It should be noted that the lack of significant Markov violation in the remaining observers does not imply that their sequences are indeed Markovian. First, we only checked violations of the Markov property in the transitions up to S_{i-2}. Second, for particularly short sequences, like in observer SG with only 66 switches, the statistical power to reject the Markov assumption is low. In sum, we find the Markov property to be violated in all experiments, which is clear evidence against a memory-less process in continuous rivalry.

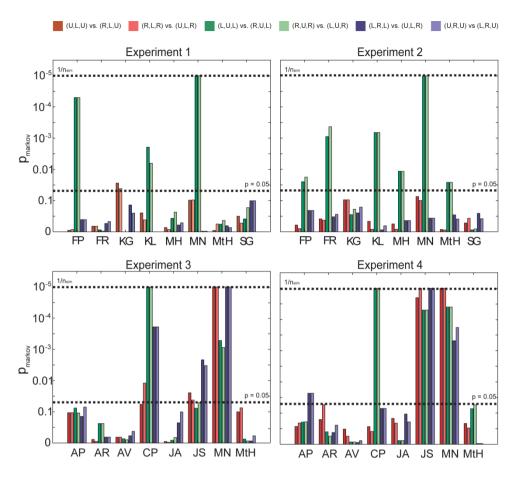


Figure 4. Estimated p-values for the null-hypothesis that a sequence of perceptual states has the Markov property (i.e., is memoryless). Each bar represents the data of one particular transition per experiment and observer. A bar exceeding the p=.05 line indicates that for this particular sequence, the Markov assumption is violated and the probability to switch from the current percept (Si-1) to the next percept (Si) depends on the preceding percept (Si-2). The y-scale is logarithmic and significance increases towards the top (log10 p represented).

2.3.5 Dominance durations are influenced by the preceding percept

Next we address whether the dominance duration of a given percept depends on which percept preceded it. Again, this question cannot be posed for continuous presentation of a bi-stable stimulus, as there is only one possible preceding percept. Separately for each experiment and each percept (L, U, R), we compared the median dominance durations between the two different preceding percepts (Fig. 5). Since the distributions of dominance-durations are non-Gaussian, the non-parametric Wilcoxon test for the comparison of medians is used. In all experiments, we find a significant effect of the preceding percept on median dominance duration for at least one of the percepts. In experiments 1, the incoherent percepts (L or R) are significantly longer when preceded by the coherent (U) percept than when preceded by the other incoherent (R or L) percept (Fig. 5 left panel; $p=7.65*10^{-4}$ for $S_i=L$, p=0.04 for $S_i=R$). The same and even stronger pattern is observed for

Experiment 2 (Fig. 5, 2^{nd} panel from left; $p=1.99*10^{-5}$ for $S_i=L$, $p=9.81*10^{-11}$ for $S_i=R$). In experiments 3 and 4, when there is no obvious hierarchy of the percepts (coherent vs. incoherent), we nonetheless observe a similar dependence of the dominance duration on the preceding percept for some percepts (Fig. 5 right panels; Experiment 3: $p=8.79*10^{-3}$ for $S_i=U$; Experiment 4: $p=4.90*10^{-3}$ for $S_i=L$: $p=7.31*10^{-3}$ for $S_i=U$). Note that while the reported p-values are uncorrected, all but one of the significant effects survive an individual Bonferoni-adjustment within each experiment (0.05/3=0.0016) and most of the significant effects survive an adjustment to an expected FDR of 5% across all experiments (adjusted alpha level: 0.0088). In sum, there is a significant dependence of dominance duration on the preceding percept.

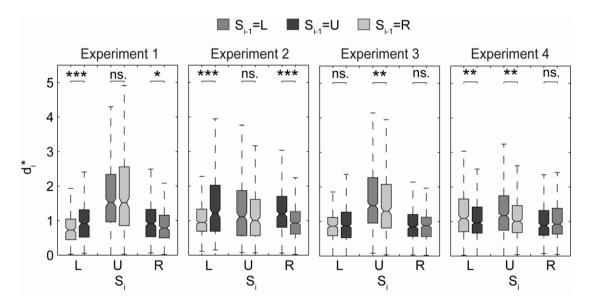


Figure 5. Boxplots of median normalized dominance durations (d*i) per experiment. Any difference within a pair of bars indicates that the median dominance duration (d*i) of the current percept (Si) depends on the preceding percept (Si-1). Current percept is labeled on x-axis, the preceding percept (Si-1) is encoded by gray values (legend on top). Boxes represent the lower quartile, median, and upper quartile of the data, whiskers the extent of the data. Significance markers refer to uncorrected results of two-sided Wilcoxon-test on equality of the medians.

2.3.6 Subsequent percept depends on preceding dominance durations

We have demonstrated that dominance durations depend on the preceding percept. Does in turn the probability to switch to a certain percept depend on the dominance durations of the preceding percepts? To answer this question, we consider the effect of preceding dominance durations on the subsequent switch probability in triplets of percepts: for an identical pair of $S_{i,2}$ and $S_{i,1}$ (i.e., identical 2^{nd} order history) does S_i

depend on d_{i-1} and/or d_{i-2} ? As before, we compare two distinct cases (Fig. 1C): the switch-back (SB, $S_i = S_{i-2}$) and the switch forward (SF, $S_i \neq S_{i-2}$) across all experiments and all (S_{i-2} , S_{i-1}) pairs (4x6=24 data points). To achieve sufficient amounts of data, we pool across all observers and consider normalized dominance durations d_i^* . If switch probabilities were associated with the duration of preceding percepts, then we would expect that the median dominance duration per condition is different between the switch back triplets and switch forward triplets. Data show that for switches back the dominance duration d_{i-1}^* is longer than for switches forward in 18/24 cases (points below diagonal in Fig. 6, left panel). This fraction is significantly larger than expected by chance, even when the absolute size of the durations is neglected (p=0.02, sign-test). Conversely, d_{i-2}^* is shorter if $S_{i-1} \rightarrow S_i$ is a switch back than if it is a switch forward (22/24 cases, Fig. 6 middle, $p=3.6x10^{-5}$). The relative dominance duration ($d_{i-2}-d_{i-1}$)/($d_{i-2}+d_{i-1}$), which was computed individually at each switch and thus not affected by normalization, confirms this result (Fig. 6, right): in 21/24 cases, a longer d_{i-2} (as compared to the following d_{i-1}) is observed for switches back than for switches forward. In sum, this shows that the shorter a percept has lasted and the more time has elapsed since it disappeared, the more likely it is to reappear. This result is consistent with a slowly adapting bias that persists across several percepts and is not reset by a perceptual switch.

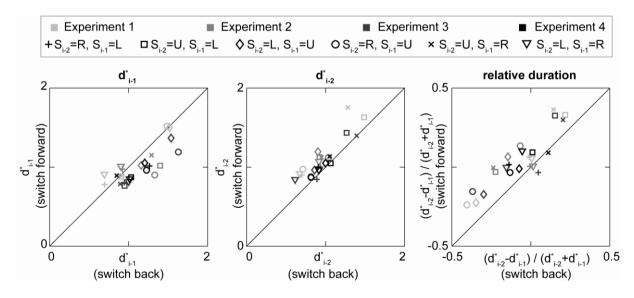


Figure 6. Effect of preceding dominance durations on transition from preceding state (Si-1) to current state (Si). Median values for d*i-1 (left), d*i-2 (middle), and relative duration (right) on y-axes for switches forward (Si-2≠Si), on x-axis for switches back (Si-2=Si), cf. Fig. 1C. Gray values denote experiment, markers denote pairs of subsequent states (Si-2, Si-1) as given in the legend on top. Points above the diagonal imply higher durations for switches forward. Note that for each data point the two preceding percepts, whose dominance durations are considered (Si-2, Si-1), are identical on both axes, only the current state (Si) differs between the axes.

2.4 Discussion

To dissociate the probability of a certain percept to occur from the duration of its dominance, we introduced *tri*-stable stimuli. Indeed, dominance duration and occurrence probability can – at least to some extent – be adjusted independently of each other. Furthermore, the sequence of percepts is non-Markovian. This implies that the perceptual history of at least two percepts back influence the current perceptual experience. Further analysis revealed that also dominance durations and percept probabilities are coupled across subsequent perceptual states, extending previous work on multi-stable percepts. These effects were independent from stimulus domain (motion or color) or specific stimulus features (i.e., motion direction and color luminance), and insensitive to one percept being dominant. In sum, we find that perceptual state and dominance durations are related to more than just the current and immediately preceding state. Hence, we demonstrate – for the first time during continuous presentation of an unchanged stimulus without binocular conflict – that neither the sequence of percepts nor their dominance durations are generated by memory-less processes; instead both are biased by perceptual history.

In our experiments 1 and 2, dominance durations of the incoherent percepts (L, R) were significantly shorter if preceded by the other incoherent percept (R, L) as compared to being preceded by the coherent percept (U). One possible interpretation of this finding is that switches between percepts of different quality (here: coherent versus incoherent) prolong the subsequent dominance duration. Such an interpretation would be in line with a high-level "fatigue" (adaptation) account of rivalry (Attneave, 1971; Taylor & Aldridge, 1974; Lehky, 1988; Blake, 1989): stimuli with more similar properties fatigue overlapping neuronal populations. It should be noted, however, that adaptation in a single population of neurons with simple direction preferences ("component cells") would generate the opposite prediction: by itself upward motion is more similar to left- and rightward motion than the two side-wards directions are to each other. Neurons reflecting the percept (rather than only the stimulus) with—say—a left-ward motion preference would also partially encode the U percept. They should therefore be adapted more by U than by R, and thus an L percept following a U percept should be comparably shorter. Instead our findings require distinct populations for encoding U, L and R. Higher areas in the dorsal stream of visual cortex (such as MT) indeed tend to code coherent pattern motion separately from component motion, while lower areas such as V1 almost exclusively

encode the components (Movshon, Adelson, Gizzi & Newsome, 1985; Gizzi, Katz, Schumer, & Movshon, 1990). A fatigue account of rivalry thus – at least for the plaid stimulus –would need to involve not only early visual areas but also higher areas. This argues in favor of rivalry originating at more than one level of the visual hierarchy (Blake & Logothetis, 2002).

In rivalry, the function of interruptions is an ongoing puzzle. It is known that interruptions tend to stabilize the percept (Leopold et al., 2002), although this effect reverses when interruptions are sufficiently short (Orbach et al., 1963). In the present context it is tempting to speculate that the middle percept of each triplet acts as endogenous analogue to the exogenous interruption with respect to the other two percepts. At first glance our results support this interpretation: a longer d_{i-1} (equivalent to the interruption) makes switches back more likely (Figures 4, 6). However, some recent studies have found a positive correlation between the probability of a percept to "survive" after an interruption and the preceding duration of its dominance (Brascamp et al., 2008; Pastukhov & Braun, 2008). In the "middle percept (S_{i-1}) equals interruption" interpretation, this would predict a positive relation between the duration of di-2 and the probability to switch back, contrary to our actual findings. Nonetheless, the present results might provide some hint on the role of interruptions. In the view that prolonged experience of a percept makes it less likely to return to a percept without actively destabilizing it, a short blank would render a switch more likely (one cannot return to the percept after the blank), while a long blank allows for recovery. In any case, our results are in line with the general finding of Brascamp et al. (2008) and Pastukhov & Braun (2008) in that perceptual history modulates percept probabilities. Our stimuli in Experiment 1 and 2 as well as in Experiment 3 and 4 differ only in one feature value (the relative direction of the drifting gratings and the luminance of the green grating). These subtle differences mainly reduce the relative bias towards one dominant percept. However, we also observe that the coupling between state and subsequent dominance duration becomes somewhat more pronounced (Fig. 5). Since the feature change affects both the interrupting and the interrupted percept, this effect might be related to the findings that survival probabilities are modulated by stimulus features (Brascamp et al., 2007) and by the similarity between interrupted and interrupting percept (Pearson & Clifford, 2005; Kanai et al., 2007). To assess the role of feature similarity and to fully uncover the role of the interruptions as compared to intervening ("middle") percepts, a combination of tri-stable rivalry and independently varied interruptions seem a promising approach, which is, however, beyond the scope of the present study.

The dissociation of percept probabilities and dominance durations suggests that at least partially distinct processes are responsible for either. In other words, there is a different mechanism determining whether a percept is (initially) chosen as compared to those controlling its persistency. Interestingly, this qualitative distinction has been predicted by a theoretical account of rivalry (Noest, van Ee, Nijs, & van Wezel, 2007) that models initial choice of percept and later switches without the necessity for a high-level decision stage. Although this model aims primarily at explaining the effect of stimulus interruptions, an extension to the tri-stable case is well conceivable.

Multi-stable stimuli with more than two percepts have been described earlier (Burton, 2002; Suzuki & Grabowecky 2002; O'Shea, Tep, Roeber, & Schröger, 2008), but either included binocular rivalry or were designed for different analyses. Closely related to the current study is the phenomenon of "trapping" described by Suzuki & Grabowecky (2002). In a tetra-stable (4 percepts) condition, these authors find a violation of the Markov property ("path dependence" in their terms). In addition, they report an increased probability to stay within a pair of percepts. The probability to stay in this "trap" decreases with the length of the "trapped" sequence, while dominance durations tended to increase within the trapped sequence. This result argued in favor of a long-term ("post-selection") adaptation, but against an adaption of the currently available stimulus. The method employed by Suzuki & Grabowecky (2002) is different from the one used here in various respects. Most importantly, these authors used binocular conflict, while in our paradigm rivalry is purely perceptual. Furthermore, they separated "exclusive" from "intermixed" percepts by instruction, thus combining binocular rivalry with binding features into objects. Our stimuli, in turn, operate in distinct feature domains (motion or color). Despite obvious commonalities, it is unclear, to what extent binocular rivalry and perceptual rivalry are comparable; these potential differences particularly pertain to the dependence on perceptual history (van Ee, 2009) and to the transition between dominant states, which in binocular rivalry often spreads in wave-like manner (Wilson, Blake, & Lee, 2001) and is feature-dependent (Knapen, van Ee, & Blake, 2007; Naber, Carter, & Verstraten, 2009). In the light of these differences it is remarkable that Suzuki & Grabowecky (2002) arrive at similar conclusions. First, both studies observe a violation of the Markov property ("path dependence" in Suzuki & Grabowecky's terms, Fig. 4). Second, we find a dependence of the switch probability on dominance durations of preceding percepts (Fig. 6), which is well in line with Suzuki & Grabowecky's finding of "post-selection" adaptation. In conjunction with Suzuki &

Grabowecky's (2002) results, our data suggest the following interpretation: experiencing a certain percept does not *per se* destabilize it (simple adaptation); instead, prolonged experiencing of a percept reduces the probability to return to this percept once it has been left (thus the dependence on d_{i-2}. in Fig. 6). This reduction in probability then relaxes over time (thus the converse dependence on d_{i-1} in Fig. 6). In the case of trapping, the reduction in the probability to switch back to the preceding percept is most evident for transition between closely related percepts, which - after a while in the trap - can drop below the between-trap transition probability and thereby release trapping (Fig. 6 in Suzuki & Grabowecky's study). Our results both confirm and generalize these earlier results for multi-stable stimuli without binocular conflict.

The trapping phenomenon depends on the similarity between percepts and can be affected dramatically by comparably subtle changes of instruction (Burton, 2002). Consequently, it is important to show that the effect of perceptual history on the current percept does not need a particular trapping pattern. By varying stimulus parameters, we here modulate several of the parameters affected by trapping: dominance durations, percept probabilities and first-order transition probabilities. Since results on perceptual history, in particular the coupling between dominance durations and percept probability, are qualitatively similar across all our experiments, our findings also generalize beyond the trapping stimuli.

In sum, we find effects of perceptual history on the current perceptual experience. This history dependence is reflected in percept probabilities, dominance durations and the coupling between the two across subsequent percepts. This general finding is neither contingent on binocular conflict nor on trapping. Taken together with the aforementioned studies, our results therefore demonstrate that the dependence of the present perceptual experience on perceptual history is a general property of rivalry, which is independent of whether rivalry is induced through binocular conflict, motion, shape or color. This is further support for the view that rivalry is to some extent predictable by perceptual history, occurs at multiple levels of perception with similar properties, and that the encoding and eventual resolution of rivalry might be as ubiquitous in the sensory systems as ambiguity is in real-world stimuli.

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2.7 Appendix – Test for Markov property

To consider a process memory-less, the sequence of perceptual states S_1 , S_2 , ... S_N would need to fulfill the Markov property. That is, the conditional probability of a state S_i may only depend on the directly preceding state S_{i-1} but not on any other preceding state S_j ($j\neq i$, $j\neq i-1$), that is $p(S_i|S_{i-1}) = p(S_i|S_0,...S_{i-1})$. In other words, if the Markov property is fulfilled, this conditional probability would be the same independent of preceding sequences. In the present context, we considered triplets of sequences which could only either constitute an SB - (C,B,C) - OC or an SF - (A,B,C) with $C \neq A$ (Fig. 1C). If the Markov property holds, it follows that

$$p(S_i=C|S_{i-1}=B,S_{i-2}=C) = p(S_i=C|S_{i-1}=B,S_{i-2}=A) [C \neq A].$$

By the definition of the conditional probability this can be rewritten (under the assumption that $p(S_{i-1}=B,S_{i-2}=A)\neq 0$ and $p(S_{i-1}=B,S_{i-2}=C)\neq 0$):

$$\frac{p(S_i = C, S_{i-1} = B, S_{i-2} = C)}{p(S_{i-1} = B, S_{i-2} = C)} = \frac{p(S_i = C, S_{i-1} = B, S_{i-2} = A)}{p(S_{i-1} = B, S_{i-2} = A)}$$
(1)

or for the counts of the respective triplets and pairs in the sequence:

$$\frac{\#(S_i = C, S_{i-1} = B, S_{i-2} = C)}{\#(S_{i-1} = B, S_{i-2} = C)} = \frac{\#(S_i = C, S_{i-1} = B, S_{i-2} = A)}{\#(S_{i-1} = B, S_{i-2} = A)}$$
(2)

The discrepancy between the left-hand side (LHS) and right-hand side (RHS) of equation (2) provides a measure as to what extent a sequence of perceptual states violates the Markov property. Even if a Markov process underlies the generation of state sequences, only infinite sequences will be guaranteed to fulfill equations (1) and (2) perfectly. For finite sequences deviations from equation (1) and (2) are to be expected due to random fluctuations. Since the length of an observed sequence is necessarily finite, we thus need a baseline to estimate which discrepancy from equation (2) can be expected for a finite sequence by chance. Accordingly, we tested the Markov property by computing the discrepancy between the conditional probability $p(S_i|S_{i-1},S_{i-2})$ of SB and SF triplets of subsequent states (S_{i-2},S_{i-1},S_i) .

We exemplify this procedure for observer KL in Experiment 2 for the pair (S_{i-1},S_i)=(U,R). This analysis shows that the switch back is less likely than the switch forward (Fig. 7A, dot), that is $p(S_i=R|S_{i-1}=U,S_{i-2}=R)$ < $p(S_i=R|S_{i-1}=U,S_{i-2}=L)$. Consequently, in this example the Markov property is clearly violated. To assert the significance of this discrepancy, we compared it with a baseline, that is the same discrepancy computed on simulated sequences. To compute this baseline, we performed 10⁵ simulations for each observer and experiment to create surrogate sequences under the Markov assumption, whose first-order transition probabilities $p(S_i|S_{i-1})$ and sequence lengths were matched to the actual data. When testing for the Markov assumption, the data for most of these simulated chains falls closer to the diagonal than the actual data (histogram represented as heat map in Fig. 7). In the example of observer KL 99934 of 100000 simulated chains fall closer to the diagonal than the actual data, yielding an estimate for the probability of p=1-99934/100000=6.6*10-4 that the actual data can occur under a Markov assumption. In contrast, when comparing a switch back and a switch forward for the data for (S_{i-1},S_i)=(R,U) in the same observer (Fig. 7B, dot), there is no evidence against the Markov assumption, as estimating the p-value from the respective simulations yields p=1-13644/100000=0.86. These p-values provided an estimate of the probability to obtain the actual sequence from a Markov process. Hence the fraction will be referred to as p_{markov} and indicates the significance level for the null-hypothesis that the state sequence has the Markov property. These data are given for all observers, transitions and experiments in figure 4 of the Results section.

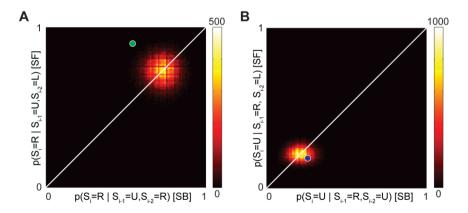


Figure 7. Example to illustrate the test for Markov property in Experiment 2, data from observer KL. Colored dots show the actual data for the conditional switch probabilities; heat maps represent a histogram of the results for 10^5 simulated surrogate sequences that share length (N=456) and first-order transition probabilities with the actual data. Left: S_i =R, S_{i-1} =U; Right: S_i =U, S_{i-1} =R. The maximum significance of rejecting the null-hypothesis, that a sequence has the Markov property, is reached when all 10^5 simulations fall closer to the diagonal than the actual data (dashed line).

2.8 Tables

Exp. 1	FP	FR	KG	KL	MH	MN	MtH	SG
L	3.89±2.24	1.94±1.14	1.76±1.92	2.17±1.22	3.27±1.88	1.91±0.91	1.06±3.81	4.09±12.0
	(061)	(067)	(096)	(079)	(084)	(101)	(056)	(025)
U	3.34±6.53	6.43±5.11	3.29±3.05	3.62±2.67	4.71±4.75	3.93±2.14	3.19±6.75	19.6±15.2
	(084)	(077)	(099)	(115)	(072)	(108)	(092)	(025)
R	3.32±2.67	1.82±1.30	2.04±1.83	2.19±1.63	2.41±1.72	2.38±1.12	0.99±3.59	5.38±3.44
	(055)	(077)	(097)	(083)	(063)	(092)	(066)	(018)
Exp. 2	FP	FR	KG	KL	МН	MN	MtH	SG
L	4.83±3.78	1.34±0.80	1.68±1.86	1.94±2.25	3.36±3.22	2.57±1.36	2.93±2.68	6.20±10.7
	(079)	(177)	(136)	(123)	(096)	(118)	(104)	(027)
U	1.62±2.55	3.17±1.78	2.78±2.59	2.77±2.22	4.40±2.64	2.18±1.25	1.10±2.07	14.2±13.3
	(054)	(085)	(083)	(078)	(028)	(102)	(094)	(024)
R	3.63±2.88	1.39±0.85	1.78±1.95	1.85±1.85	2.45±3.35	3.07±1.31	3.00±2.07	5.74±9.15
	(063)	(197)	(122)	(116)	(093)	(107)	(097)	(020)
Exp. 3	AP	AR	AV	CP	JA	JS	MN	MtH
L	2.66±2.09	2.66±4.11	1.43±11.54	2.12±1.15	2.55±1.94	1.11±1.54	0.94±0.48	1.54±2.70
	(084)	(037)	(036)	(102)	(081)	(184)	(223)	(099)
U	3.38±2.64	9.31±9.77	3.48±14.12	3.48±1.84	5.06±3.78	1.57±1.69	1.52±0.97	3.19±4.33
	(112)	(039)	(042)	(115)	(090)	(199)	(252)	(117)
R	1.81±2.13	6.25±6.61	1.41±13.58	2.46±1.20	2.01±1.66	1.01±1.81	1.02±0.56	0.94±2.33
	(075)	(018)	(045)	(077)	(038)	(152)	(219)	(062)
Exp. 4	AP	AR	AV	CP	JA	JS	MN	MtH
L	3.33±2.93	5.10±8.91	1.84±3.53	2.34±0.93	2.31±3.60	1.31±3.59	1.22±0.83	1.90±1.97
	(117)	(039)	(052)	(111)	(114)	(156)	(218)	(130)
U	1.45±0.94	6.92±13.17	3.71±11.55	2.89±1.45	2.90±2.43	1.51±1.90	1.28±0.80	2.13±3.93
	(076)	(041)	(062)	(143)	(117)	(108)	(205)	(130)
R	2.33±1.81	3.10±3.81	1.61±6.05	2.19±0.90	1.44±1.97	1.22±2.11	1.38±0.74	1.19±2.18
	(108)	(026)	(042)	(086)	(032)	(154)	(187)	(057)

Table 1. Median and standard deviation of dominance durations for individuals and number of occurrences.

3. Chapter 3

Suppression wave dynamics: visual field anisotropies and inducer strength

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Abstract

We used binocular rivalry and generalized flash suppression to identify several new shared properties of traveling suppression waves. A strong relationship was found between suppression wave speed and induction pulse strength: increasing the contrast or dot density of the induction pulse led to an increase in wave speed. Evidence of visual field anisotropies in wave propagation speeds were also seen, with suppression waves decelerating as they travel towards the fovea. This deceleration could not be accounted for by cortical magnification in lower level brain areas, suggesting an important role for other, yet to be identified, factors.

3.1 General introduction

As any good magician or pickpocket will attest, people are often unaware of many of the objects and events that surround them. Experimentally, it has been shown that even when attention is focused intently on an object, that object can be rendered perceptual invisible with a few simple stimulus manipulations. One such method used to suppress stimuli from conscious awareness is binocular rivalry (BR) (Wheatstone, 1838; Levelt, 1965; Blake & Logothetis, 2002). Binocular rivalry arises when one eye receives a significantly different image than the other eye. These incompatible images compete for perceptual dominance, causing them to perceptually alternate. Many studies have used BR to investigate the neural mechanisms underlying conscious experience. However, until recently, little was known about the complementary process of conscious suppression. Here we are interested in the mechanisms by which perceptually salient stimuli come to be suppressed, with the specific aim of identifying the dynamic properties of perceptual suppression.

Although the mechanisms underlying suppression are still poorly understood, it is clear from observation that the transition from suppression to dominance is often gradual and appears to propagate in a wavelike fashion. A recent study showed that it is possible to control the starting point of this transition by generating a brief contrast increment (pulse) at one location of the suppressed image. At the point of the pulse, the previously suppressed image will generally break through and its dominance will spread and travel in a wavelike manner (Wilson, Blake, & Lee, 2001; Lee, Blake, & Heeger, 2005). This technique has opened up the possibility of systematically studying suppression propagation. However, there is one important limitation with BR: suppression of one target image is necessarily accompanied by dominance of the alternate image in the corresponding region of visual space. This makes it impossible to measure the spread of suppression independent of dominance and, more importantly, to dissociate the relative interacting contributions of the suppressed and dominant visual input.

Wilke, Logothetis, and Leopold (2003, 2006) developed a paradigm, called generalized flash suppression (GFS), which overcomes this problem by generating perceptual suppression in an area spatially adjacent to the suppression inducing stimulus. In order to induce disappearance of targets, GFS combines the dichoptic viewing of binocular rivalry flash suppression (BRFS: Wolfe, 1984) and large monoptic motion

fields typical of motion induced blindness (MIB: Bonneh, Cooperman, & Sagi, 2001). In GFS, a target stimulus is presented to one eye. After several hundred milliseconds, a mask pattern consisting of small moving dots is suddenly presented to both eyes. Even though the mask pattern does not overlap the spatial location of the targets, they are perceived to disappear for periods of seconds (Wilke et al., 2003). The fact that the latency of the perceptual suppression in GFS increases with the target's distance from the mask pattern suggests that suppression propagates successively through adjacent areas of the visual field.

Despite these differences, the obvious parallels between the suppression seen in BR and GFS lead Wilke et al. (2003) to suggest that suppression in GFS may propagate in a wave-like manner similar to that in BR (Wilson et al., 2001; Lee et al., 2005). While the labeling of these suppression effects as wave-like is convenient and allows for an intuitive description of the perceptual experience, the primary characteristics of and the degree to which these are shared between suppression phenomena remain unknown. As researchers continue to investigate how the brain generates perceptual suppression, one critical question is whether there are multiple mechanisms or only one. By carefully manipulating properties in both BR and GFS, the present study attempts to: 1) identify the factors responsible for the spatio-temporal pattern of suppression; 2) determine whether these factors are common for GFS and BR.

3.2 Experiment 1

Previous studies show that it is possible to create a suppression wave with a constant speed. A psychophysical study using BR (Wilson et al., 2001) measured cortical brainwave speeds of 2.24 cm/s and an fMRI study (Lee et al., 2005) reported similar speeds between 1.6 and 2.0 cm/s. Despite the consistency of the speeds measured, it was also noted that the inducer does not always trigger a wave at the time or location of the pulse. It is not clear from these studies which features of the inducer influence either the probability that a wave is initiated, or the speed of its subsequent propagation. As it is known that increasing stimulus contrast increases the alternation rate during binocular rivalry (Levelt, 1965), it is possible that this increased alternation rate reflects an increased likelihood of suppression wave initiation or propagation rate. Here we investigate the effect of changing the contrast of the induction pulse on the initiation probability and dynamics of traveling suppression waves during BR.

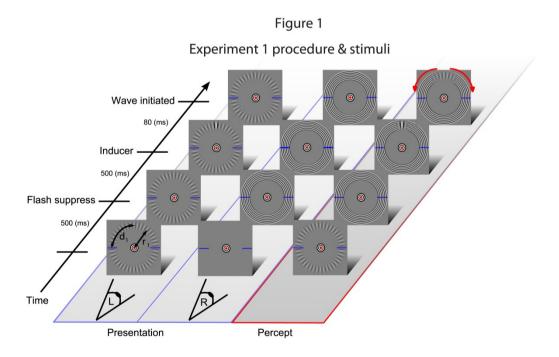


Figure 1. Experiment 1 stimulus consisted of two annuli with a 3.0° radius (r_1) and a 1° width with a gaussian contrast adjustment. One annulus with radial gratings was presented to one eye followed by the second annulus containing concentric gratings presented to the other eye. This procedure resulted in a dominant percept of the newly introduced concentric grating. A brief inducer pulse (60% or 90% contrast increment) was then presented at the top of the radial annulus gradually returning dominance to the radial grating which is perceived to spread out over the concentric gratings $(d_1 - 4.7 \text{ deg})$ in a wave-like manner from the inducer location (shown in the right column). The subject's task was to report when the dominance of the radial grating had reached either of the horizontal blue lines transecting the annulus (the distance from the inducer to each blue line was 4.7°).

3.2.1 Methods

3.2.1.1 Participants

Two authors (MN & OC) and three naïve observers took part in this experiment. All participants had normal or corrected to normal vision and were experienced psychophysical observers recruited from the Vision Sciences lab at Harvard University. The experiments were approved by the Harvard University Committee on the Use of Human Subjects in Research, and conformed to the standards of the Declaration of Helsinki.

3.2.1.2 Stimuli

Stimuli were generated in MATLAB 7.1 using Psychtoolbox (Brainard, 1997; Pelli, 1997) and presented on a 17" monitor (60Hz, 1024x786 pixels) with a grey background. The stimuli used in the experiment were based on those used by Wilson et al. (2001) and Lee et al. (2005). Stimuli consisted of either high contrast concentric, or low contrast radial, sinewave gratings presented in an annulus around fixation (Fig. 1). Background and mean stimulus luminance was 22 cd/m². The radial grating had a 30% Michelson contrast, a spatial frequency of ~6.5 cycles/deg. The concentric grating had a 70% Michelson contrast, a spatial frequency of ~0.5 cycles/deg. Each annulus had an inner and outer radius of 2.5° and 3.5° respectively with the edges of the annulus smoothed using a Gaussian function. Two 0.05° x 1.0° blue lines transecting the annulus along the left and right horizontal meridian were presented dichoptically. The inducer was a 0.4° x 1° contrast increment to either a 60% or 90% Michelson contrast presented in the upper-most (12 o'clock) region of the low contrast radial annulus. The distance around the annulus from the inducer to either of the blue markers was approximately 4.7°.

3.2.1.3 Procedure

Observers viewed the stimuli through a mirror-stereoscope and were asked to maintain fixation on a central red dot, while head position was stabilized using a chin rest that assured a steady screen distance of 40cm. Participants were first presented with the low contrast radial grating to one eye. After 500ms a similar size high contrast concentric annulus was presented in the corresponding retinal location of the other eye (BRFS – Wolfe, 1984) which generally resulted in perceptual suppression of the low contrast radial annulus and dominance of the concentric annulus. An additional 500ms later, the inducer was flashed for 80ms, causing

the previously suppressed image to become perceptually dominant in a wave propagating away from the induction point. The observer was instructed to press a button when the wave reached either one of the transecting blue marks. The button response caused the trial to end.

Next, the observer was asked whether a complete wave-like event was experienced from the location of the inducer to the blue test line. The trial was repeated if participants failed to respond within 2s or if they reported that the wave was either incomplete or irregular. Observers initiated the next trial by pressing the space bar. The experiments consisted of two blocks of 100 successful trials (approximately 15min each) and the two contrast conditions were randomly presented throughout each block. Paired t-tests were performed on the mean traveling wave latency and initiation probability.

As reaction times lengthen the measured suppression wave latencies, we ran a control experiment in which observers were instructed to press a button as soon as they detected the onset of the inducer pulse. The mean RT measured in the control experiment was subtracted, per observer, from the mean traveling wave latency in each condition. Reaction times (RTs) outside the range of 3 standard deviations from the mean were discarded.

3.2.2 Results & discussion

The mean travel latency (travel latencies were normally distributed for 4 out of 5 observers) was 512ms in the low contrast condition (SD: 244ms) and 466ms in the high contrast condition (SD: 241ms) (Fig. 2). The mean difference between the disappearance latencies for the low and high contrast pulse was a significant 46ms (SD: 20ms) [t(4)=5.2382, p<0.01] which corresponds, depending on the observer, to an increase of speed between 8-32% with a high contrast induction pulse as compared to a low contrast pulse. Note the large differences between observers in wave speeds (5.9-18.0 deg/s), but that all subjects showed the same effect of decreasing wave speed with the low contrast inducer (Fig. 2A) The likelihood that an appropriate wave was initiated (incomplete or irregular waves were not included in the initiation probability) was also much lower in the low contrast pulse condition than in the high contrast pulse condition for all subjects (Fig. 2B). The mean initiation probability was 92.46% for a high contrast inducer (SD: 4.90) and significantly lower for the low contrast inducer at 83.15% (SD: 10.88) (t(4)=3.3663, p<0.05).

Our results are the first to illustrate this tight link between the traveling suppression wave inducer and the following wave speed. As it has recently been shown that motion in the suppressed eye's stimulus can speed up the traveling wave (Knapen, van Ee, & Blake, 2007), we were curious whether wave speeds could be modified by other factors, once the wave had begun propagating across visual space.

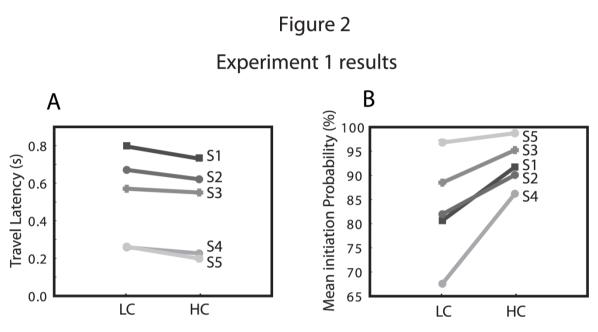


Figure 2. The effect of inducer strength on traveling wave propagation. Low contrast (LC) and high contrast (HC) pulses are shown on the x-axis respectively. (A) Mean travel latencies and (B) initiation probability of the traveling waves for each observer. Both travel speed and initiation probability of a wave is respectively faster and greater in the high contrast inducer condition for all participants.

3.3 Experiment 2

Experiment 1 showed that the induction probability and subsequent speed of suppression waves is not fixed but depends on the strength of the inducer (i.e. the contrast). This raises the question of whether suppression propagation shows similar variability across different areas of the visual field. An earlier study fixed the eccentricity of the wave's path and found that it had a constant speed (Wilson et al., 2001). To test whether the speed remains constant at different eccentricities, we measured the propagation of traveling waves towards the fovea.

3.3.1 Methods

MN, OC and two naive observers participated in experiment 2. To create a traveling wave in BR that propagates towards the fovea, we used a rectangle extending from the periphery to the fovea (Fig. 3). The inducer had a fixed contrast (90%) and was presented as a brief pulse at the outer-most point of the rectangle 6° from fixation. Wave latency was measured at four different eccentricities (1.2, 1.6, 2.0, & 2.4° of visual angle from the fixation point). All other aspects of the apparatus and procedure used were identical to that described above in experiment 1.

As wave latencies were measured at different distances from fixation, it is possible that any observed differences in response times may reflect a difference in speed at which people are able to detect and report the arrival of the wave at different locations in the visual field. To make certain that wave latencies were not influenced by the effects of spatial anisotropies on response latencies, we ran a control experiment with four new naïve observers in which waves were simulated at a fixed speed that was randomly chosen per trial from a 15-30 deg/s range (all other aspects of the apparatus, stimuli and procedure were identical to that described for the main experiment 2). Median values were analyzed using a repeated measures ANOVA to compare the travel latencies per eccentricity condition. Trend tests were performed to analyze the development of the median travel latencies as a function of eccentricity.

Figure 3
Experiment 2 stimuli

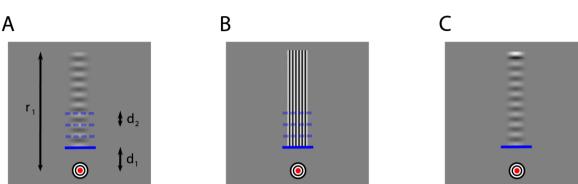
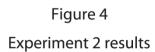


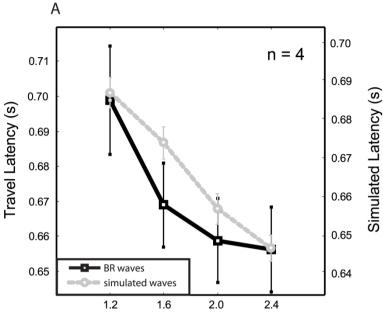
Figure 3. Experiment 2 stimuli. A) A low contrast horizontal sinewave grating was first presented to one eye and this was followed by B) a high contrast vertical grating presented to the other eye. C) After a period of time an inducer pulse was presented, triggering a suppression wave that travels from top at an eccentricity of 6.0° (r_1), to bottom at an eccentricity of 1.2 (d_1). To find out whether the wave has a constant speed as it travels towards the fovea, the travel latency was measured at four different locations; each separated by a 0.4° (d_2) difference in eccentricity (indicated by the dashed lines in A and B). Only one eccentricity was tested in each trial.

3.3.2 Results & discussion

Figure 4A shows the latency of the suppression wave as a function of eccentricity for all observers. There was a significant increase in median latency values 656ms, 659ms, 669ms and 699ms at eccentricities closer to the fovea away from the inducer (F(3)=9.554, p=0.004). For three of the four observers, this increase in latency towards the fovea appeared to be quadratic (data not shown). Indeed, trend analysis over all observers showed that a cubic fit achieves a higher significance level (F(1)=29.061, p=0.013) compared to a linear fit of the same data (F(1)=12.533, p=0.034). Propagation speeds between the four distances (1.2, 1.6, 2.0, & 2.4 and distal from the fixation point) are estimated at 13.4 deg/s, 39.5 deg/s and 157.0 deg/s respectively (Fig 4B), and indicate a clear deceleration of suppression waves. As activity in visual brain area V1 is found to spatiotemporally reflect traveling suppression waves (Lee, Blake, & Heeger, 2007), it is a plausible neural locus for the initiation and processing of suppression waves. Because central visual regions are overrepresented in areas such as V1 (also known as the cortical magnification factor, Daniel and Whitteridge, 1961), the observed deceleration could be absent in V1 activity patterns when asymmetric cortical distances are taken into account. In other words, if the spread of activity in V1, caused by traveling suppression waves,

progresses with a constant velocity towards the relatively larger brain regions that process the central field of vision, the cortical magnification factor could explain the perceptual experience of deceleration. Using cortical magnification values from Larsson & Heeger (2006) we calculated the predicted speed across the three eccentricity differences based on a constant cortical speed of 16.62cm/s. At this cortical speed the corresponding differences in degrees of visual angle would only be 13.4 deg/s, 17.19 deg/s & 19.86 deg/s. The minimal deceleration found in these values indicates that the difference in speed cannot be accounted for by cortical magnification in V1. Also in contrast to the retinal speeds, the simulated wave latencies showed a significant linear increase (F(3)=29.411, p<0.001; linear trend: F(1)=85.346, p<0.001) (Fig 4A). The calculated propagation speeds for the simulated waves were 38.69 deg/s, 23.47 deg/s, and 30.62 deg/s (Fig 4B). The fact that these propagation speeds were relatively consistent across eccentricities indicates that changes in speed reported for the illusory suppression waves, are unlikely to be due to response error. In summary, the results of experiment 1 and 2 show two new characteristics that influence the speed of traveling suppression waves: the strength of its inducer; and its location in the visual field. The following two experiments focus on the generality of these characteristics by measuring suppression effects induced by a different experimental paradigm, namely GFS.





Target Distance from Fixation Point (deg)

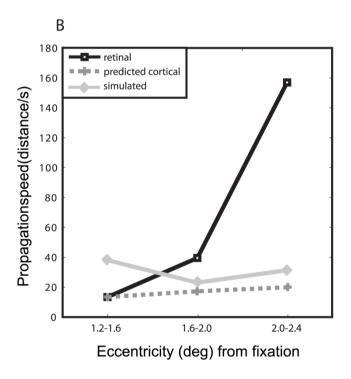


Figure 4. (A) Median traveling wave speed (s) with standard errors, as a function of eccentricity for the real (left y-axis) and simulated control (right y-axis) experiments. The linear function of the simulated waves shows that reaction times did not account for the deceleration of waves found in the BR wave experiment. **(B)** The median traveling wave propagation speeds (s) based on travel latency as a function of eccentricity (deg of visual angle in respect to the retinal image) presented in solid black. The propagation speed increases as a function of eccentricity which indicates that a wave slows down as it travels towards the fovea. The speeds were calculated between the target locations that match the locations used in experiment 2. The dashed light grey line illustrates the change in wave speed predicted on the basis of cortical magnification alone (with a constant speed of 16.62cm/s). The solid light grey line presents the calculated speeds of the simulated waves in the control experiment.

3.4 Experiment 3

As mentioned in the introduction, the BR paradigm makes it impossible to measure the spread of suppression independent of the corresponding spread of perceptual dominance. In contrast, the GFS paradigm allows us to investigate the spread of suppression independent of any changes in perceptual dominance. Wilke et al. (2003) argued that suppression waves could underlie their GFS results. It is unclear, however, whether these suppression waves are identical to those seen in BR, or whether they are simply wave-like. In experiment 3 we looked at whether the wave characteristics found in BR are the same in GFS. Wilke et al. (2003) previously reported that GFS waves traveled at a cortical speed of 0.5cm/s, which is slower than the slowest speed calculated for BR in our experiments as well as those reported previously in other studies (Wilson et al., 2001). Here, we were interested to see whether these apparent differences in travel speeds can be explained by properties of the inducing stimuli.

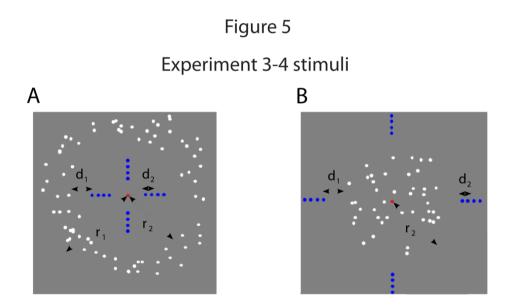


Figure 5. (A) The targets were presented at one of four eccentricities from fixation and the distances between targets (d_2) were the same as in experiment 2. The induction stimulus was presented in a surrounding annulus 3.6 (r_2) to 6.3 (r_1) degrees from fixation. (B) In experiment 4, the opposite configuration was used with the induction stimulus presented centrally between 0 and 3.6 (r_2) degrees from fixation. The targets were presented at one of 4 eccentricities extending towards the periphery and the minimum distance between the targets and the induction stimulus was 1.2 degree (d_1) . In all cases, 4 targets were presented at the specified eccentricity (1 target along each of the 4 cardinal axis).

In previously reported studies, the inducer in GFS consisted of randomly moving dots with a certain density. Since it is known that increasing the density of the inducer results in an increase of the suppression effect (Wilke et al, 2003), it is an appealing thought that the "strength" of the inducer influences the suppression strength and the speed of the wave. If GFS suppression waves are similar to waves in BR, inducer strength should influence their speed and initiation probability and perhaps their duration of disappearance as well.

3.4.1 Methods

Authors MN, OC, and three naive observers took part in experiment 3. In the first condition, four blue target dots were presented centrally along the vertical and horizontal axis at either 1.2, 1.6, 2.0, or 2.4° eccentricity. These eccentricities corresponded to four different distances (2.4, 2.0, 1.6, & 1.2°) distal from the inducer flash. The GFS inducer consisted of randomly moving dots (speed=3.00°/s, maximum angle of deviation = 45°/frame) presented in a surrounding annulus that extended between a radius of 3.6° and 6.3° from fixation (Fig. 5A). Dots going out of bounds were relocated at the opposing boundary at the same visual angle. Targets and moving dots each had a diameter of 0.27°.

Three different suppressor dot densities (0.25, 0.50, or 1.00 dots/deg²) and the four target distances were randomly varied between trials (12 conditions). Targets were viewed monocularly and after 1s a stimulus (inducer/suppressor) was flashed to both eyes dioptically. If one or more targets disappeared after the presentation of the inducer, observers were asked to immediately indicate this initial disappearance of any target by pressing a button. The button was then released as soon as this same target reappeared. The trial ended when observers reported the reappearance of the targets. If no disappearance was reported for 8s the trial was automatically terminated. The experiment consisted of 288 trials divided in two blocks of 144 trials and each block contained 12 trials of all 12 conditions, presented in a random order. The apparatus and all other aspects of the methodology were identical to that described in the preceding experiments.

Median values were analyzed using a repeated measures ANOVA to compare the disappearance latencies and disappearance durations across eccentricities and inducer strengths. Trend tests were performed to analyze how the median disappearance latencies and disappearance durations developed towards higher eccentricity.

3.4.2 Results & discussion

Figure 6 presents both median disappearance latencies (A) and median disappearance durations (B) as a function of inducer density and target location. There was a significant difference in disappearance latency as a function of distance towards the fovea (F(3)=30.161, p<0.001). A trend analysis confirmed that the increase of disappearance latency was quadratic (F(1)=8.229, p<0.05), indicating that the wave of suppression slows down systematically as it moves towards the fovea. From these results we estimated that our GFS inducing annulus caused retinal propagation speeds of 0.28, 0.35, and 1.70 deg/s and cortical speeds of 0.34, 0.34, 1.34cm/s between distances of 1.2, 1.6, 2.0, and 2.4 deg distal from the induction point respectively. The target distance also had a significant effect on disappearance duration, with closer targets disappearing for a greater time (F(3)=5.982, p<0.01). A trend analysis showed a linear decrease in disappearance duration, for target locations further from the inducer and closer towards the fovea (F(1)=9.512, p<0.05).

Increasing the dot densities of the surrounding inducer from 0.25 to 0.5 and 1.0 dots/deg, resulted in mean disappearance probabilities of 85.6% (SD: 14.2), 91.0% (SD: 8.6), and 92.1% (SD: 7.5) respectively. This relationship between disappearance probability and dot density showed a clear positive trend but differences in disappearance probabilities between the dot densities did not reach significance (F(2)=2.302, p=0.162). The density of the inducer also had an overall effect on disappearance latencies (F(3)=2.715, p=0.126) but not on the duration of disappearance (F(3)=1.212, p=0.347). Although the observed trend towards lower density flashes taking longer to produce a target disappearance than higher density flashes did not reach significance, the findings mirror significant effects previously reported (Wilke et al., 2003). The lack of significance in the current study likely reflects a ceiling effect. In the previous study (Wilke et al., 2003), density had an effect on disappearance probabilities in the range of 0-80% but not for probabilities between 80-100%.

These results show that like BR induced suppression waves, GFS suppression wave speed is not fixed during propagation, but slows down as the wave travels towards the fovea. In the following experiment we investigated whether this slowing down was specific to the foveal direction of the wave.

Figure 6 Experiment 3-4 results

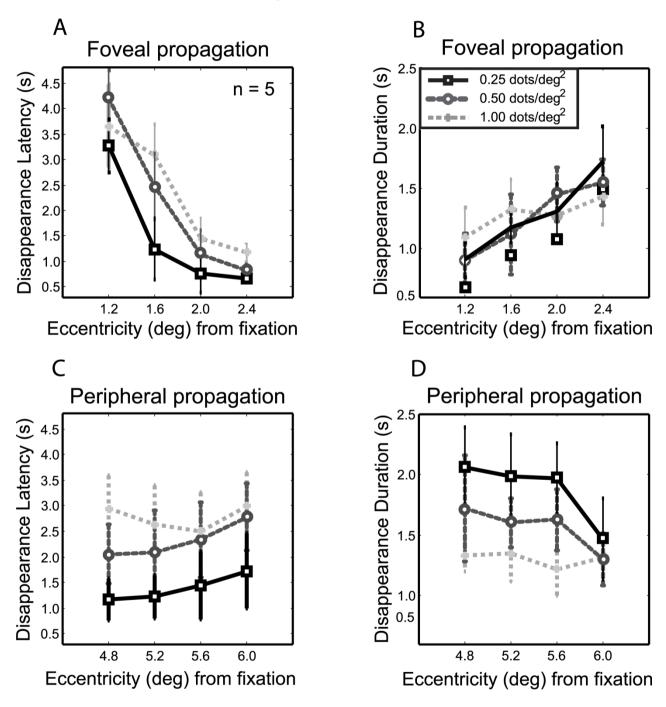


Figure 6. The disappearance latency (A and C) and duration (B and D) of the targets when the dot pattern is either flashed in an annulus around the targets (A and B) or centrally with the targets located in the periphery (C and D). Latencies quadratically decrease if waves travel toward the fovea (A) and inducer density seems to influence both disappearance latencies and durations (A, C, and D). Data points and error bars represent the medians and standard error of data pooled across all subjects.

3.5 Experiment 4

To investigate whether this deceleration was specific to propagation towards the fovea, or whether we had identified a more general principle for traveling waves, a fourth experiment measured the propagation of suppression waves away from the fovea, towards the peripheral visual field.

3.5.1 Methods

In this experiment the observers, stimuli, apparatus, and procedure were as described in experiment 3, the only difference being that the inducer was presented centrally, and the targets in the periphery (Fig. 5B). Target eccentricities were 4.8, 5.2, 5.6, or 6.0° and their relative distances from the inducer were the same as in experiment 3 (i.e. 1.2, 1.6, 2.0, & 2.4°).

3.5.2 Results & discussion

Changing the dot density of the central inducer from 0.25, 0.5 and 1.0 dots/deg had a systematic effect on the disappearance latencies (Fig. 6C), with lower density flashes taking significantly longer to produce a target disappearance than higher density flashes (F(3)=7.251, p<0.05; linear trend: F(1)=8.247, p<0.05). Inducer density also had a significant effect on the disappearance duration (F(3)=7.440, p<0.05) wherein higher densities produced longer disappearance durations (linear trend: F(1)=12.083, p<0.05) (Fig. 6D). Inducer density had no effect on disappearance probability (F(2)=0.331, p=0.727).

Target eccentricities had a minor but non-significant effect, leading to slightly increases in disappearance latencies (mean: $4.8^{\circ} = 2.06s$; $5.2^{\circ} = 1.98s$; $5.6^{\circ} = 2.10s$; $6.0^{\circ} = 2.50s$. F(3)=2.816, p=0.084), and decreases in disappearance duration respectively (mean: $4.8^{\circ} = 1.70s$; $5.2^{\circ} = 1.65s$; $5.6^{\circ} = 1.60s$; $6.0^{\circ} = 1.36s$; F(3)=1.497, p=0.265).

These results suggest that increasing the strength of the central inducer results in both strengthening of the inhibitory effects of the waves and the speed of the propagation, but there is negligible slowing between the ranges of peripheral eccentricities used in the current experiment. The deceleration of waves appears to be specific to foveal propagations.

As the target sizes in experiment 3 were held constant at different eccentricities, the parts of cortical area V1 responsible for processing the more foveally presented targets was larger than the cortical area that processed the peripherally located targets. Because the foveal targets received more visual processing, this cortical magnification effect might have biased the results making the foveal targets slower and less likely to disappear than the peripheral targets. The following experiment investigated this possibility.

3.6 Experiment 5

To assess whether differences between foveal and peripheral representation of the targets may have contributed to the reduction in propagation speeds calculated in experiment 3, we performed a final experiment in which the targets were kept constant and the inducer was presented at variable eccentricities.

3.6.1 Methods

MN and 4 naïve subjects participated in this experiment. Across the different trials, the target eccentricity was kept constant at 1.2° and inducer eccentricity (i.e. the inner boundary of the annulus) was randomly varied between 2.0 and 4.0°. In order to ensure that the inducer was stimulating a similar sized area of visual cortex, the width of the inducer's annulus was adjusted such that it equated to approximately 8mm of primary visual cortex. In all other respects the stimuli, apparatus, and procedure were identical to that used in experiment 3 and 4. Trials were ended as soon as subjects reported target disappearance by pressing a button. Median values were analyzed using a repeated measures ANOVA to compare the disappearance latencies per eccentricity condition. An additional analysis was performed to test for a trend of disappearance latencies across eccentricities.

3.6.2 Results & discussion

Differences in target disappearance latencies between foveal inducers were larger than between peripheral inducers (Fig. 7). The nonlinear development of the latency function indicates a decrease of speed when suppression waves travel towards the fovea (F(7)=24.518, p<0.001; quadratic trend: F(1)=5.171, p<0.05). Because the deceleration is present in the data while we controlled for the size of the cortical area that processes the target and mask, it seems unlikely that cortical magnification effects are responsible for the speed values found in experiment 3. Together with the results of experiment 2, this adds further evidence that suppression waves slow down as they travel towards foveal regions of visual space.

Experiment 5 results (a) 4.0 2.0Mask eccentricity (deg)

Figure 7. Target disappearance latencies (s) as a function of mask eccentricity (deg) for all 5 subjects. Medians and standard errors were calculated by dividing pooled data into 8 bins. The nonlinear increase of the function indicates the deceleration of waves when traveling towards the fovea. As target eccentricity was kept constant and the annulus width was adjusted to the cortical magnification, these results exclude the possibility that stimulus sizes underlie the very similar results found in experiment 3.

3.7 General discussion

In conclusion, we report a number of new characteristics of suppression wave propagation. Firstly, we have demonstrated that the latency and duration of perceptual suppression is systematically influenced by the "strength" of the inducer. Secondly, the suppression wave decelerates as it travels towards the fovea. Thirdly, as these effects were seen in both BR and GFS, it is tempting to suggest that the two phenomena may share a common neural origin. The most surprising result of this study, though, was the finding that the deceleration could not be accounted for by cortical magnification alone.

Our findings fit within a new body of research suggesting that perceptual suppression is propagated in a wave-like fashion throughout the cortex. Studies that used voltage sensitive dye imaging to image waves evoked by electrical pulses in brain slices of animals, found wave propagation speeds in the range between 1-5 cm/s, values that are very close to the speed values found in this study (Bai, Huang, Yang, & Win, 2006; Sanchez-Vives & McCormick, 2000). In support of the proposed existence of traveling suppression waves underlying GFS, recent electrophysiological recordings from awake monkeys found that the latency of V1 cell responses to a surround onset increased systematically as the distance between surround and receptive field border increased (M. Wilke, personal communication). Evidence of similar wave-like effects in V1 was seen in a recent human fMRI study that found activity in V1 to be correlated with the observation of a traveling wave in binocular rivalry (Lee et al., 2007). While the current GFS propagation speeds are similar to those found by Wilke et al. (2001), it is noteworthy that our calculated BR speed values are approximately 10 fold faster than the 1.6–2.24cm/s reported in earlier studies (Wilson et al., 2001). Although the general pattern of slowing was seen consistently across observers, it is difficult to know how much significance to place on the difference in speeds calculated between BR and GFS when taking the stimulus-related differences into account. Beyond the potential differences in wave speed, it is also possible that small errors in reported latency (that varied only by a few milliseconds) would have resulted in large overestimations of the calculated speed. Therefore, while the overall pattern of results stand, the exact speed values reported here should only be considered as estimates. We are also confident about our consistent finding of a non-linear decrease of foveal wave speeds in both BR and GFS. In further support of this decrease in wave speed, several observers

reported seeing waves slowing down until they stagnated and flipped back to the top of the stimulus during experiment 2.

The dissimilarity between the foveal and peripheral disappearance durations, and the finding that waves slow down as they propagate towards the fovea, was surprising and in need of some explanation. The most obvious possibility was cortical magnification - the amount of brain tissue in the occipital lobe responsible for foveal visual processing is much larger than that for peripheral processing (Tootell, Silverman, Switkes, & De Valois, 1982; Horton & Hoyt, 1991; Engel, Glover, & Wandell, 1997; Sereno, Dale, Reppas, Kwong, Belliveau, Brady, Rosen, & Tootell, 1995; Duncan & Boynton, 2003; Larsson & Heeger, 2006). Related to this difference in cortical representation are neuronal receptive field (RF) sizes. Neurons that represent the fovea have significantly smaller RFs than neurons in the periphery in each of the brain areas V1, V2, V3, and V4 (Dow, Snyder, Vautin, & Bauer, 1981; Smith, Singh, Williams, & Greenlee, 2001). It is possible that these neuronal characteristics underlie the wave's substantial deceleration when it is propagating towards the fovea. As the results in experiment 2 show, however, the cortical magnification factor can only explain a small fraction of the observed deceleration. The cortical magnification factor varies substantially between subjects (Duncan & Boynton, 2003) and could as such have been exceptionally prominent in all subjects. Although we cannot exclude this possibility, the total number of 11 different observers that performed in experiments 2, 3 and 5 makes it very unlikely that all observers' cortical magnification factors in V1 deviated strongly from the mean. Therefore, it appears that feedback from higher cortical areas or long range lateral connections within visual cortex may also play a role (Bringuier, Chavane, Glaeser, & Frégnac, 1999; Grinvald, Lieke, Frostig, Hildesheim, 1994). Lee et al., (2007) concluded that attention plays an important role in promoting the V1 neural activity of waves to higher visual areas. Given that waves travel faster in the absence of attention (Lee et al., 2007), it is tempting to suggest that when waves enter the fovea and the spatial acuity becomes higher, attentional processes further reduce the spread of activity in V1. Unfortunately, it is only possible to speculate as to the likely causes of the observed visual field anisotropies and inducer dependencies in wave propagation. Exactly how the brain's complex networks of distributed neural assemblies coordinate and generate transitions in perceptual awareness, remains one of the biggest mysteries in visual neuroscience. Adding further complexity to this question, a recent study found that the relative contribution of factors such as thalamic and lateral inputs can vary considerably depending on the

strength of sensory input (Nauhaus, Busse, Carandini, & Ringach, 2009). Luckily, the fact that BR and GFS provide a means to experimentally control and measure the dynamics of perceptual transitions, suggests these phenomena may be ideal for further exploration of this question.

Our finding that inducer strength can influence propagation speed and initiation probability complements recent work showing that the spatial origin of traveling suppression waves can be predicted by contrast, spatial frequency, and motion of the inducer (Paffen, Naber, Verstraten, 2008). It is interesting to speculate whether there is any functional significance to these systematic effects of inducer strength on the rapid propagation of new perceptual information at the expense of the previously perceived stimulus. As features such as stimulus contrast are known to be relevant to measures of visual salience, the increase in suppression wave propagation speed may be one reason why salient features appear to reach awareness faster than non-salient features of the environment. Contemporary theories have not yet linked visual saliency and suppression together so further experiments are needed to investigate how, and to what extent, the dynamics of suppression waves relate to other visual processes known to be influenced by the salience of visual features.

The similar pattern of results obtained in the GFS and BR experiments presented here, provides strong evidence that they may share the same underlying mechanism. Confirming whether or not there is only one means by which sensory information is temporarily rendered inaccessible to consciousness, is clearly critical for accurate interpretation of future research into the neural correlates of unconsciousness. Again, more work is needed before any conclusions can be drawn on this point. If further testing continues to reveal such large individual variation in the speed and strength of suppression waves as that observed here, individual differences may provide one avenue through which to investigate the relationship between these different phenomena.

The current study focused on BR and GFS, however, there are many other methods known to render stimuli consciously unavailable (for review, see Kim & Blake, 2005). With increasing effort being directed to these investigations, it is hoped that this study will shed light on why and how stimuli are rendered unconscious. The finding that dynamics of suppression waves vary as a function of inducer strength and direction of propagation relative to the fovea suggests a possible involvement of cognitive factors (attention), or a role for specific neural populations (feedback or long range lateral connections) in constraining the

transitions between perceptual awareness and suppression. The recent finding that visual phantoms also propagate in a similar wave-like manner (Meng, Ferneyhough, & Tong, 2007), raises the exciting possibility that these widely varying visual phenomena are all tapping into the same basic mechanism.

3.8 Acknowledgements

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4. Chapter 4

Perceptual Rivalry: Reflexes reveal the gradual nature of visual awareness

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Abstract

Rivalry is a common tool to probe visual awareness: a constant physical stimulus evokes multiple, distinct perceptual interpretations ("percepts") that alternate over time. Percepts are typically described as mutually exclusive, suggesting that a discrete (all-or-none) process underlies changes in visual awareness. Here we follow two strategies to address whether rivalry is an all-or-none process: first, we introduce two reflexes as objective measures of rivalry, pupil dilation and optokinetic nystagmus (OKN); second, we use a continuous input device (analog joystick) to allow observers a gradual subjective report. We find that the "reflexes" reflect the percept rather than the physical stimulus. Both reflexes show a gradual dependence on the time relative to perceptual transitions. Similarly, observers' joystick deflections, which are highly correlated with the reflex measures, indicate gradual transitions. Physically simulating wave-like transitions between percepts suggest piece-meal rivalry (i.e., different regions of space belonging to distinct percepts) as one possible explanation for the gradual transitions. Furthermore, the reflexes show that dominance durations depend on whether or not the percept is actively reported. In addition, reflexes respond to transitions with shorter latencies than the subjective report and show an abundance of short dominance durations. This failure to report fast changes in dominance may result from limited access of introspection to rivalry dynamics. In sum, reflexes reveal that rivalry is a gradual process, rivalry's dynamics is modulated by the required action (response mode), and that rapid transitions in perceptual dominance can slip away from awareness.

4.1 Introduction

While the signals arriving at the human sensory systems typically provide only noisy and ambiguous information about their sources in the real world, introspectively perception seems unified and coherent. Introspection suggests further that at any point in time one can either be aware of a distal item or not, but such awareness cannot be partial. Whether this all-or-none nature of awareness is objectively justified is, however, subject to debate (Alais, Cass, O'Shea & Blake, 2010a, Overgaard, Rote, Mouridsen & Ramsøy, 2006, Sergent & Dehaene, 2004) and points to the principled difficulty of relying on introspection (but see Ericsson & Simon, 1980, Nisbett & Wilson, 1977).

Studying changes in perception and awareness in the real world presents the challenge that changes in the stimulus (bottom-up signals) interact with changes in their interpretation. To circumvent this bottom-up "confound" we use different variants of rivalry, a phenomenon known for at least a quarter of a millennium (Breese, 1899, Dutour, 1760, Wheatstone, 1838). In rivalry, a constant stimulus evokes distinct (usually two) perceptual interpretations ("percepts"). Rivalry occurs when two distinct stimuli, that cannot be fused, are presented to either eye (binocular rivalry, Wheatstone, 1838) or when the stimulus itself allows different interpretations, such as the famous Necker cube (Necker, 1832) or the stimulus shown in Figure 1A (monocular rivalry, Breese, 1899). To distinguish binocular rivalry from other forms, we here follow the usual convention and subsume the latter as "monocular rivalry" despite simultaneous presentation to both eyes. Rivalry is not restricted to vision, but also observed in touch, audition and olfaction (Carter et al., 2008, Van Noorden, 1975, Zhou & Chen, 2009). The extent to which all these forms of rivalry exhibit the same phenomenology is subject to debate (Klink, van Ee & van Wezel, 2008b, Knapen et al., 2007a, Meng & Tong, 2004, O'Shea, Parker, La Rooy & Alais, 2009, Wade, 1975) as is the neural origin of rivalry.

While rivalry is often described as an all-or-none process, a variety of physiological markers show a *gradual* modulation around the time of transition between two percepts: eye-position (Einhäuser, Martin & König, 2004, van Dam & van Ee, 2005, van Dam & van Ee, 2006), (micro-)saccade frequency (Glen, 1940, van Dam & van Ee, 2005), pupil dilation (Einhäuser et al., 2008b, Hupé et al., 2009), blink frequency (van Dam & van Ee, 2005), or gamma-band activity

(Doesburg, Green, McDonald & Ward, 2009, Doesburg, Kitajo & Ward, 2005). As with awareness in general, however, this conflict between discrete phenomenology and continuous physiology, may be a consequence of relying on introspection and subjective report. Hence we here combine rivalry with objective measures to probe visual awareness without relying solely on introspection.

Numerous studies have attempted to pinpoint neural processes underlying rivalry. Conceptually, local and modality specific processes have often been put forward: the representations of each percept mutually inhibit each other and loss of dominance follows from neuronal adaptation ("fatigue") of the dominant percept (Attneave, 1971, Blake, 1989, Taylor & Aldridge, 1974). In addition, evaluative higher-order processes could account for the reversals between percepts as these trigger changes in visual awareness by reorganization of activity (e.g., Leopold & Logothetis, 1999). Several studies support a low-level account of rivalry, linking transitions between percepts to spatial activity patterns in V1 (Lee, Blake & Heeger, 2005, Lee, Blake & Heeger, 2007, Lee & Blake, 2002) or indicating correlations between fluctuations of early visual activity and changes in visual awareness (Lee & Blake, 2002, Leopold & Logothetis, 1996, Polonsky, Blake, Braun & Heeger, 2000, Tong & Engel, 2001). Other studies, however, have shown that higher brain areas are linked to awareness (Leopold & Logothetis, 1999, Lumer, Friston & Rees, 1998, Sheinberg & Logothetis, 1997, Tong, Nakayama, Vaughan & Kanwisher, 1998). To reach consensus on the subject, several authors have argued that rivalry may occur at different levels of the visual hierarchy (Blake & Logothetis, 2002, Freeman, 2005, Long & Toppino, 2004, Sterzer, Kleinschmidt & Rees, 2009, Tong, Meng & Blake, 2006, Wilson, 2003). Supporting this proposition, Haynes and Rees (2005) show that different forms of rivalry (in their case between eyes or between colors) have representations at distinct locations in the visual processing stream. It seems thus likely that both high and low level mechanisms contribute to initiation of rivalry (Sterzer et al., 2009).

One possible reason for the lack of consensus on the neuronal origin of rivalry and awareness is the effect of attentional and motor processes that add an additional difficulty to the interpretation of imaging data. For example, attention could selectively activate or modulate distinct regions; subjectively attending a specific feature, such as one orientation in two overlapping gratings with

different orientations, activates neurons processing that feature in early visual areas (Kamitani & Tong, 2005). Similar to attending one feature, the allocation of attention to one percept could result in the activation of neurons processing the features tied to the corresponding percept. The activated brain regions during rivalry could thus be a consequence of attentional processes rather than the actual process involved with visual awareness. Attentional mechanisms are indeed known to affect brain regions differently during rivalry (Lee et al., 2007). Regions responsible for the allocation of attention to salient events (Corbetta & Shulman, 2002) seem to be involved with spontaneous perceptual switches as well (Britz, Landis & Michel, 2009, Lumer et al., 1998, Sterzer & Kleinschmidt, 2007, Sterzer, Russ, Preibisch & Kleinschmidt, 2002). Also, decreasing attentional resources to a rivalrous stimulus slows the rate of alternations in rivalry (Alais, van Boxtel, Parker & van Ee, 2010b, Paffen et al., 2006), and selectively attending a percept prolongs its dominance (Meng & Tong, 2004, van Ee, Noest, Brascamp & van den Berg, 2006). In summary, attentional processes may strongly affect rivalry and interact with the neural representations of the rivaling stimuli.

A key issue that bedevils many studies on rivalry is their reliance on introspection (i.e., subjective report). Although occasional physical changes in the stimulus can verify that observers try to achieve a veridical report ("catch trials"), four fundamental issues persist: First, the motor-act of reporting itself may affect perception (Beets, Hart, Rösler, Henriques, Einhäuser & Fiehler, 2010, Maruya, Yang & Blake, 2007, Wohlschläger, 2000); second, the report mode might restrict response possibilities (e.g., button presses allowing only discrete reports); third, very brief dominance periods of one percept might not suffice to trigger a report; and forth, catch trials might not mimic the entire phenomenology of rivalry. Here we use three strategies to overcome these issues: first, we use two reflexes – pupil response and optokinetic nystagmus – as objective indicators of percept; second, we test different input devices, a discrete (button press) and a continuous (joystick) one; third we simulate discrete and gradual transitions in catch ("simulated") conditions.

While changes in pupil size are typically thought of as a reflex to changes in illumination, there are many studies showing cognitive effects on pupil size (e.g., Beatty & Lucero-Wagoner, 2000, Daniels et al., 2009, Einhäuser et al., 2010, Hakerem, 1967, Harrison, Singer, Rotshtein, Dolan &

Critchley, 2006, Hess, 1975, Kahneman, 1973, Privitera et al., 2010, Simpson & Hale, 1969, Steinhauer et al., 1983). In the context of rivalry, transitions induce pupil dilation (Einhäuser et al., 2008b, Hupé et al., 2009) and the pupil light reflex is diminished during suppressed periods (Brenner, Charles & Flynn, 1969, Báràny & Halidén, 1948, Lowe & Ogle, 1966, Richards, 1966). Here we find that if stimuli of different luminance or contrast are presented to either eye, pupil size follows the percept rather than the physical stimulus allowing us to use pupil size as one objective indicator of rivalry.

When observers are presented a large coherently moving field (such as when looking outside from a moving train), their eyes usually show an optokinetic nystagmus (OKN, Purkinje, 1925): slow phases try to match the stimulus speed to keep the retinal image stable and are interrupted by fast phases that reset the eye in orbit. Here we employ OKN slow phase speed as second objective measure of rivalry. In the present context, this measure is of particular interest, as previous studies have described both rivalry and the resulting OKN as all-or-nothing mechanisms (Enoksson, 1963, Fox, Todd & Bettinger, 1975, Logothetis & Schall, 1990, Watanabe, 1999, Wei & Sun, 1998). Combining OKN with an analog input device allows us to challenge this interpretation. Using both pupil size and OKN allows us to verify that results are general and not restricted to specific methods of measurement or stimuli.

Using OKN and pupil size, using discrete and continuous response modes, and using sharp and piece-meal simulated transitions, we address three questions: is awareness temporally "all-ornone" or gradual, are the results explainable by piece-mealing, and do reflexes have access to different levels of processing than introspection?

4.2 Results

4.2.1 Experiment 1 - Pupil size as measure of rivalry

To robustly induce rivalry, ten observers were presented two stationary gratings that were distinct in color (red/green) and orientation (+60° or -60° relative to the vertical). In a monocular rivalry condition (Breese, 1899), both gratings were overlaid as plaid and presented to both eyes simultaneously (Figure 1A; note that we stick to the term *monocular* rivalry although the stimulus was presented to both eyes); in binocular rivalry, each grating was separately presented to one eye through a stereoscope. In addition, either the green grating's luminance (binocular and monocular condition) or contrast (binocular only) was varied across 4 levels between experimental trials, while the red grating was kept identical at an intermediate level of luminance or contrast. During each 5-minute trial, both gratings were constant, and observers were asked to indicate by pressing a button, which grating they perceived. Despite a constant stimulus, pupil dilation depended on the luminance of the dominant percept (Figure 1B): if the grating of higher luminance or contrast was perceived dominant, the pupil size was smaller than if the other grating was dominant, and significantly so for binocular luminance (t(9)=6.79, p<0.001) and for binocular contrast (t(9)=4.99, p<0.001) conditions. During monocular rivalry, pupil size was significantly smaller during the second half of a dominance duration (i.e., close to the next perceptual transition) if the dominant percept was brighter than the suppressed percept (t(9)=2.34, p<0.05). We align pupil traces to the times when observers reported transitions. The average over these aligned traces shows that the difference in pupil dilation is largest just before and after the transition (Figure 1C-E) and levels off after about 1.5s. Some of the leveling off in the average trace may be attributed to the high variability of time to the subsequent transition (i.e., the high variability in dominance durations). We control this confound by performing the analysis in a normalized time frame: we resample the time between each pair of subsequent perceptual transitions (i.e., a dominance duration) to a single fixed length before averaging. This time-normalized representation still shows a gradual change in pupil from one transition to the next transition (Figure S1). This rules out dominance-duration variability as sole source of the graduality of transitions.

Importantly, the difference in pupil size between percepts increases with increasingly distinct stimuli, while the time course remains rather similar (Figure 1F-H). This pupil response is therefore also distinct from a generic biphasic pupil response associated with the perceptual transition as such, which is independent of the polarity of the transition (low to high or high to low) and degree of dissimilarity between the rivaling stimuli (Figure 1I-K, cf. Einhäuser et al., 2008b, Hupé et al., 2009). In sum, experiment 1 demonstrates that pupil size – both in monocular and binocular rivalry - follows the perceived rather than the physical stimulus. A similar result has recently been found independently and was first reported as abstract (Fahle, Stemmler & Spang, 2010) together with a presentation of the current results (Naber & Einhäuser, 2010). The most important aspect is that pupil dilation seems to indicate a *gradual* transition between the two perceptual states (Figure 1B). Whether these gradual transitions are truly a property of rivalry rather than of the pupillary response itself, shall be addressed in experiment 2.

4.2.2 Experiment 2 – Graduality: a true property of rivalry

Experiment 1 leaves open whether the time course of the pupil around transitions reflects a gradual nature of rivalry or just sluggish pupil dynamics. To distinguish these two alternatives, we simulate abrupt rivalry transitions and compare the speed of pupil size changes around these simulated transitions to real rivalry transitions.

All methodological aspects of experiment 2 were identical to that of experiment 1 with the following exceptions: First, rather than using multiple contrast or luminance levels, we only used the stimulus conditions for which the difference in luminance or contrast between the rivaling stimuli had been maximal in experiment 1; second, we simulated rivalry in half of the trials by switching presentation of the two gratings per dominance duration ("simulated rivalry"). Dominance durations in these trials were based on the preceding rivalrous trial and perceptual transitions consisted of abrupt switches between images of both "rivaling" gratings.

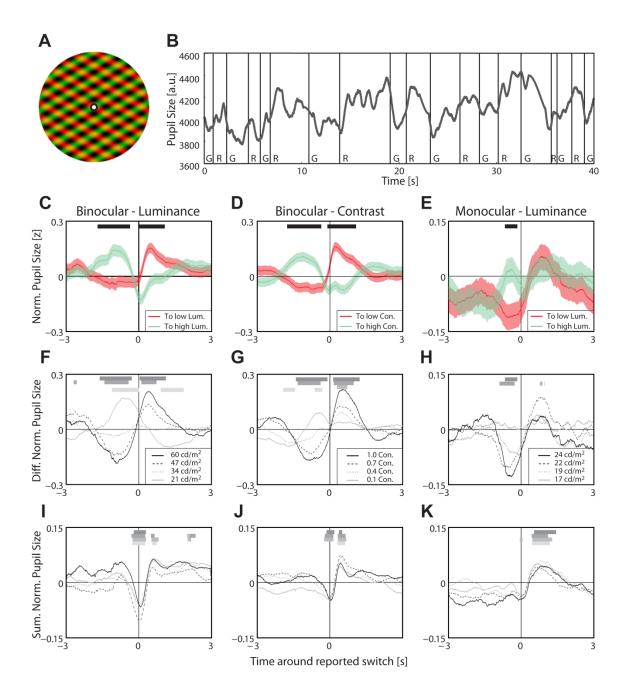


Figure 1. Experiment 1 – Pupil size as a function of rivalry dynamics. (A) Example of a monocular rivalry stimulus presented in experiment 1. Fixate on the center dot to observe rivalry. The perceived luminance of each grating fluctuates over time during which one grating has a more dominant luminance than the other. (B) Example of the pupil size as function of time during a single rivalrous trial of one observer. Letters indicate which grating was dominant (R = low luminance red grating, G = high luminance green grating). Black vertical lines are indications of perceptual transitions by the observer. The pupil adapted to the perceived luminance of the dominant percept during rivalry, while physical stimulation was kept constant. (C-E) Average pupil size as function of time relative to the perceptual transitions; red: transition from high to low luminance or contrast, green: transition from low to high luminance or contrast. Light colored patches indicate s.e.m. over all dominance durations. Bars indicate time points were both traces are significantly different at an uncorrected p < 0.05. (F-H) Differences between pupil size traces for the two switch directions as a function of time around transitions for all tested luminance and contrast conditions (legend provides luminance/contrast of changed grating, other remains constant, see Methods), means across observers (n=8); grey-level coded bars indicate time points at which means are different from 0 at p < 0.05. (I-K) Sum of pupil size traces, notation otherwise as in panels F-H. (C-H) For pupil size as a function of normalized relative time between transitions, see Figure S1.

Visual inspection of the average traces indicates that pupil size changes more abruptly during simulated transitions (Figure 2A-C, dotted traces) than during rivalrous transitions (Figure 2A-C, solid traces) for all conditions. This is particularly evident in the difference plot between the two transition polarities (Figure 2D-F), where effects of the transition itself (i.e., irrespective of polarity) are subtracted out. Although this is already suggestive of rivalrous transitions being more gradual than simulated transitions, such apparently faster transitions in the average trace of simulated trials, may in principle, still be a consequence of decreased variance (jitter) between the times of actual transitions (simulated or real) and their report. We controlled for this potential confound by calculating the steepness (speed of transition) in a 0.2 second window around each change in pupil size tied to a perceptual transition. When using the z-normalized pupil size for computing pupil speeds, pupil speeds around simulated transitions were significantly larger than around rivalrous transitions for all conditions (Binocular luminance: simulated: 4.4 ± 1.2 , rivalrous: 0.9 ± 0.5 , t(7)=7.73, p<0.001; Binocular contrast: simulated: 2.5± 0.8, rivalrous: 1.2± 0.3., t(7)=6.53, p<0.001; Monocular luminance: simulated: 1.5 ± 0.5 , rivalrous: 0.8 ± 0.5 , t(7)=2.95, p<0.05; Figure 2G-I, all values in units of z-normalized pupil size divided by 200ms). Finally, to exclude artifacts of trial-wise normalization, we computed the same analysis for unnormalized pupil sizes and find the same pattern (t(7)=5.95, p<0.001; t(7)=5.02, p<0.01; t(7)=3.53, p<0.01, respectively). These data confirm that transitions in simulated rivalry are indeed significantly steeper than in real rivalry. Hence, the gradual nature of a change in dominance is not a mere consequence of sluggish pupillary dynamics, but it is a true property of perceptual transitions in rivalry.

4.2.3 Experiment 3 – Generality of graduality and limitations of report

Pupil size indicates the gradual nature of rivalry. To address whether this phenomenon is restricted to the effect of perception on pupil dynamics or a general property of rivalry, we use an alternative objective measure. Especially in the context of binocular rivalry and moving stimuli, the velocity of the slow phase component of the optokinetic nystagmus (OKN) provides such an alternative.

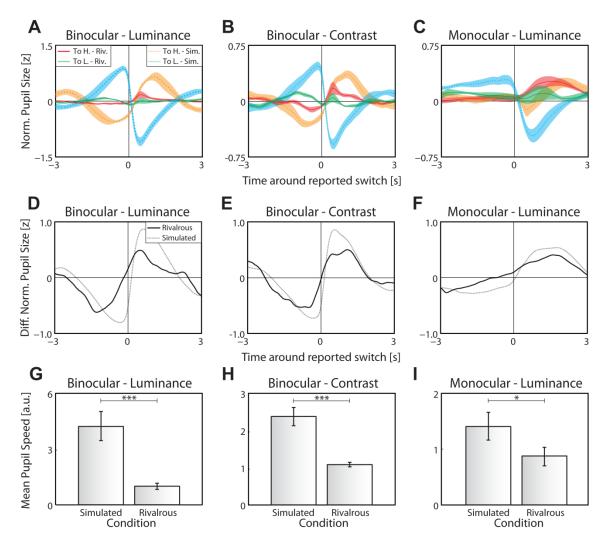


Figure 2. Experiment 2 – Pupil graduality. (A-C) Average pupil size as a function of time relative to the perceptual transitions for rivalry (green and red traces) and physical stimulus changes (simulated rivalry, orange and cyan traces) per condition. **(D-F)** Difference in average pupil size per for rivalrous transitions (black solid traces) and simulated transitions. To compare rivalrous and simulated transitions, average pupil traces were normalized by dividing through the distance between the maximum and minimum of each trace per observer and trial. **(G-I)** Average horizontal pupil speed in a 0.2 time window around the pupil speed's zero crossing, mean and s.e.m. across observers for simulated (*left*) and real (*right*) rivalry. Pupil size was more gradual during rivalrous transitions as compared to simulated transitions.

Eight observers were presented a grating moving to the right to one eye and a grating moving to the left to the other eye, both at a speed of 6.7 deg/s (Figure 3A). Our analysis is based on the horizontal eye velocity during the slow phases of the OKN, whose direction significantly depends on whether the leftward or rightward moving grating is perceived as dominant (horizontal velocity left: -1.15 ± 0.27 deg/s, right: 1.09 ± 0.20 deg/s, t(7)=5.49, p<0.001; Figure 3B). Note that the low gain of about 0.16 (=1.1/6.7) is a consequence of averaging over the whole period, including times around the

transitions: Similar to the pupil signal in experiment 1, the OKN velocity changed smoothly around a perceptual transition (Figure 3C, solid traces) and leveled off to baseline around 2s afterwards. Similar to experiment 2, we excluded the possibility that the smoothness of the transition is a property of the OKN velocity rather than of the rivalry process.

We simulated rivalry by interleaving experimental trials in which both gratings for each eye drifted in the same direction and physically switched their direction with the same temporal statistics as the preceding rivalrous trial (i.e., the same randomized dominance durations). In these cases, transitions in OKN velocity are more abrupt and take less time to follow the change in stimulus direction (Figure 3C, dotted traces). The difference in the steepness of transition is quantified by the average eye acceleration during the transition, which is significantly larger for simulated than for real perceptual transitions (simulated: $36.8\pm 3.7 \text{ deg/s}^2$, rivalrous: $21.7\pm 1.6 \text{ deg/s}^2$, t(7)=4.74, p<0.01; Figure 3D). In line with the pupil data from experiment 2, the gradual nature of transitions indicated by the OKN is therefore a true and general property of rivalry. This raises the question as to whether rivalry is governed by a continuous process that is shadowed by a discrete (binary) response mode.

If fluctuations in visual awareness of percepts are in fact governed by a gradual process, why do its measurements suggest an all-or-none nature (Fox & Check, 1972, Norman, Norman & Bilotta, 2000)? One plausible hypothesis sees the typically discrete response mode (button press) responsible. There are two ways button presses can influence measured dominance durations. First, button-press report may miss very brief dominance durations (van Ee, 2009); second, the act of overtly reporting *per se* may influence perception. For the first issue, it is conceivable that short dominance durations are not reported, because they do not reach awareness or an internal integration criterion for report. To test this, we use pupil size and OKN-slow-phase velocities and their sign changes (i.e., a directional change in pupil size and crossing of the zero-velocity line) as objective indicator of perceptual dominance. While in real rivalry it remains open for principled reasons whether very brief reflex-based dominance durations are noise (i.e., false alarms for transitions by reflexes) or true dominance periods missed by overt report, simulated rivalry provides such ground truth. Since simulated rivalry is based on real-rivalry button-press data, noise related to the reflex itself would show up as transitions in both

conditions, while truly missed short periods of dominance would only be present in real rivalry. In general, pupil-based and especially OKN-based dominance durations are largely consistent with button-press-based dominance durations; for some regime of parameter settings, however, there is an abundance of short dominance durations in the signals for real rivalry as compared to simulated rivalry (Figure 4A-D).

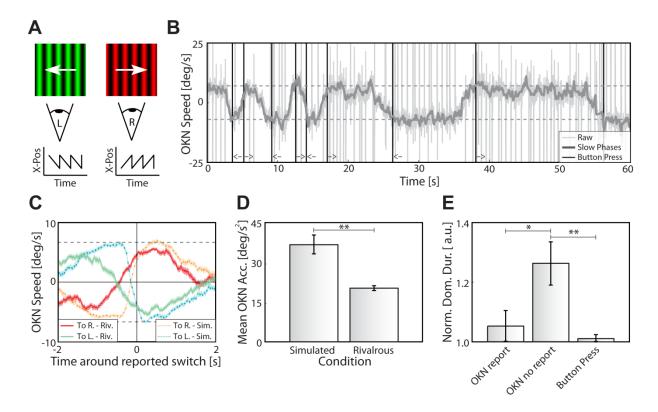


Figure 3. Experiment 3 – OKN as a function of rivalry dynamics. (A) Example of binocular rivalry stimuli and OKN patterns. Rivalry and OKN were induced by presenting dissimilar gratings with opposite movement directions to each eye separately. (B) Example of the derivative of the horizontal eye position (OKN speed) as function of time during a single trial of one observer (dark grey). OKN's fast phases (light gray spikes) were removed and interpolated, and the resulting trace was smoothed. Black vertical lines indicate perceptual transitions; arrows denote movement direction of the dominant percept. Dashed grey horizontal lines at (-)6.67 deg/s indicate speed of the rivaling stimuli. The OKN speed of slow phases gradually increased and decreased as a function of time to transition. (C) Average OKN speed for rivalry transitions (green and red traces) and physical stimulus changes (simulated rivalry, orange and cyan traces), mean and s.e.m. across all dominance durations. OKN speed was more gradual during rivalry transitions as compared to physical changes of stimulus direction. (D) Average horizontal eye acceleration in a 0.2 time window around the OKN speed's zero crossing, mean and s.e.m. across observers for simulated (left) and real (right) rivalry. Acceleration during a perceptual transition, an indication of graduality of the OKN speed signal, was lower for rivalrous trials. (E) Normalized dominance durations per report conditions, mean and s.e.m. across observers. Dominance durations were normalized by dividing by the median dominance duration per observer. OKN-based dominance durations (default parameter settings) differ significantly in a condition when observers in addition report dominance by button press (left bar) as compared to trials without active report (middle bar). In the parameter regime, OKN-based dominance durations in the report condition do not differ from those based on subjective (button press) reports (right bar).

In addition, latencies between physical transitions and button presses are longer (pooled pupil conditions: 0.53s± 0.09s; OKN: 0.66s± 0.03s) than between physical transitions and reflexive sign changes (pupil: $0.41s\pm 0.10s$, t(23)=3.62, p<0.01; OKN: $0.42s\pm 0.05s$; t(7)=5.08, p<0.001). Thus, it is likely that observers are unaware of or fail to report short dominance durations because of these latencies. Furthermore, information on intermediate states of rivalry (Brascamp, van Ee, Noest, Jacobs & van den Berg, 2006, van Ee, 2009) can also be lost when relying solely on button-press data. The second option, a direct effect of overt report on dominance durations is also supported by our data. For parameters that closely match OKN-based to button-based dominance durations, OKN-based dominance durations are shorter if observers actively report their percept than if they merely watch the stimulus passively (t(7) = 3.21, p < 0.05; Figure 3E; Figure 4E-F). This result stresses the effect of report on dominance durations and is in line with earlier observations (Beets et al., 2010, Wohlschläger, 2000). Note that we did not measure no-report conditions for pupil experiments, because pilot data had already indicated that the pupil is less reliable in determining perceptual dominance as compared to OKN, which is confirmed by the data we report here (~65% overlap of report-based dominance with pupil-based dominance versus ~90% overlap with OKN-based dominance, Naber & Einhäuser, 2010). In sum, reflexes show effects of discrete overt report on rivalry: first, a possible miss of brief dominance durations; second, a direct effect of report on perception. Given this strong impact of report, it is likely that the commonly used discrete response mode (button presses) may shadow the gradual nature of rivalry.

4.2.4 Experiment 4 – Continuous input device and piece-meal rivalry

To directly test whether the subjective report has at least some access to the gradual process underlying rivalry, we asked the same eight observers to report their perceptual state, that is the "amount by which one percept is dominant", by a continuous input device (an analog joystick) while being presented the same rivalrous stimulus as in experiment 3. To mimic the perceptual impression more closely, the simulated condition here implemented a wave-like transition rather than the abrupt change of experiment 3 (Figure 5A; details see Materials and Methods). The subjective report through

the joystick was very consistent with the objective OKN measure (Figure 5B), as reflected in the high peak cross-correlation between joystick deflection and OKN slow-phase velocity (simulated: r=0.81s±0.03, rivalrous: r=0.70s±0.03; Figure 5C). Observers even indicate intermediate states in which both percepts dominate equally by centering the joystick for a prolonged period (e.g., Figure 5B at around 15s and 45s). The joystick response lagged, however, considerably behind the OKN response, which is reflected in the time of peak in the cross correlation (simulated: 0.51s±0.10s, rivalrous: 0.86s±0.09s) as well as in the time between zero crossings of OKN velocity and joystick (simulated: 0.54s±0.07s, rivalrous: 0.84s±0.09s).

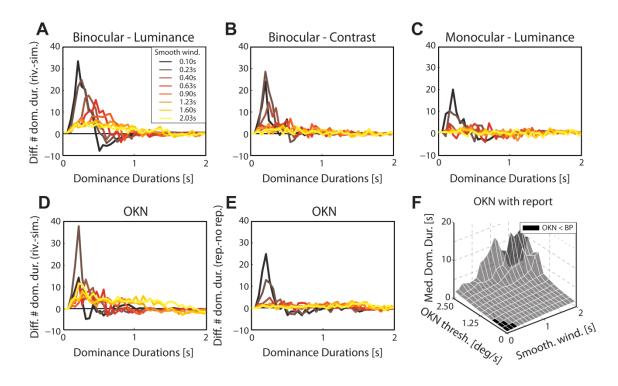


Figure 4. Parameter settings and dominance durations. (A-D) Difference between dominance-duration histograms for real-rivalry and simulated-rivalry based on pupil data (experiment 2, panels A-C) or OKN data (experiment 3, panel D) for different widths of the smoothing window applied to the raw trace. For short smoothing windows an abundance of short dominance durations that go unreported by button-presses is observed. (**E-F)** Difference between dominance-duration histograms between report (active) and no-report (passive) trials based on OKN (experiment 3) and their dependence on the smoothing window (panel E) and sign change threshold (panel F). In real-rivalry trials there is no ground truth as to whether transitions - based on pupil and OKN - are veridically identified. However, for a wide range of smoothing parameters there is only a small or no difference in such pupil and OKN-based dominance durations and those obtained from the button presses. For short time windows on the smoothing filter of the reflexive measurements and low thresholds, however, we observe significantly shorter dominance durations based on reflexes than based on button presses for rivalrous and reported trials as compared to simulated and unreported trials, respectively. This possibly reflects the difficulty for short dominance durations to be reported (see text). These data leave us confident that pupil and OKN sign changes are a reliable indicator of transitions in rivalry and may provide access to short dominance durations that observers cannot consciously report.

This suggests that very brief dominance periods, which are potentially reflected in the reflexes, either do not reach awareness or fail to be reported. This could partially account for the difference between subjective and objective measures described above (Figure 3E; Figure 4E-F). Consistent with the interpretation of a lag between a low-level transition in percept and its availability to introspection, simulated transitions exhibit a significantly shorter lag between OKN and joystick than real transitions (peak cross-correlation: t(7)=3.96, p<0.01; time between OKN and joystick crossing: t(7)=2.54, p<0.05). Similarly, the peak correlation between OKN and joystick is significantly larger for simulated rivalry (t(15)=2.30, p<0.05; separated by switch direction). Unlike in experiment 3, the OKN transitions themselves were comparable between simulated and rivalrous trials (simulated: 31.8± 4.6 deg/s^2 , rivalrous: 29.7± 4.5 deg/s^2 , t(7)=1.07, p>0.25; Figure 5D) as were the speed characteristics of the joystick (simulated: 65.2 ± 9.6 deg/s, rivalrous: 63.3 ± 9.7 deg/s, t(7)=0.64, p>0.50; Figure 5E). Joystick speed and OKN mean acceleration in a 0.2s time window around transitions were also correlated (mean r=0.65± 0.07, p<0.001). As such, there was no difference between simulated and real rivalry in the response measures, indicating that the simulation of the transition between percepts captured the perceptually relevant aspects of the real rivalry transition. Despite possible misses of rapid changes in awareness as shown in experiment 3, experiment 4 demonstrates that the gradual nature of rivalry transitions revealed by the objective measures (reflexes) grossly corresponds to the subjective percept. Hence, the seeming all-or-none nature is likely to be an artifact of the response mode. Interestingly, a wavelike transition between percepts offers a possible explanation for a considerable amount of the observed graduality. If this hypothesis holds true, this would suggest that rivalry is globally gradual, but local differences in perceptual dominance contribute to its graduality. Consequently, visual awareness would be gradual in time because of fragmentation in space. Irrespective of whether piecemeal rivalry is the cause, our data show graduality of rivalry in time, whose accessibility is influenced by response mode.

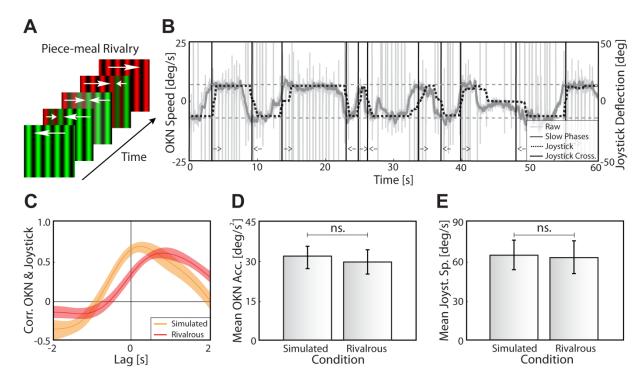


Figure 5. Experiment 4 – Piece-mealing and joystick report. (A) Example of piece-meal rivalry. Piece-meal rivalry consists of gradual transitions between percepts during which parts of both percepts are spatially intermixed. **(B)** OKN speed (notation as in Figure 2B) compared to joystick deflection (*dashed black line*) for a single rivalrous trial of a single observer. Joystick deflection was a good indicator of rivalry dynamics and delineated intermediate states. **(C)** Cross-correlation of OKN speed and joystick deflection (positive lags: OKN leading), mean and s.e.m over dominance durations; *red:* real rivalry, *orange:* simulated rivalry (piece-meal). Observers had longer latencies and lower peak correlations for rivalrous trials as compared to simulated rivalry trials. **(D)** OKN acceleration in a 0.2s time window around OKN zero-crossings, mean and s.e.m. across observers for simulated (*left*) and real rivalry (*right*). Unlike for the abrupt changes in experiment 2, OKN acceleration was not different from real rivalry trials for piece-meal simulation. **(E)** Joystick speed in a 0.2s time window around zero crossings of joystick position, mean and s.e.m. across observers for simulated (*left*) and real (*right*) rivalry. Speed of the joystick during a perceptual transition did not differ across conditions.

4.3 Discussion

The time course of two reflexes – pupil dilation and OKN – points to a continuous process underlying rivalry. Subjective perception has access to this continuous process, though this access is substantially delayed and in turn influences rivalry dynamics. Our results have implications not only for current models of rivalry, but also for the debate as to whether visual awareness is globally all-or-none or a gradual phenomenon (e.g., Overgaard et al., 2006, Sergent & Dehaene, 2004).

Remarkably, OKN and pupil dilation, which are typically thought of as reflexive behaviors to physical changes, depend on the percept rather than on the stimulus. These "reflexes" serve as rapid measures of the perceptual state and thus as an objective indicator of a seemingly subjective state: the awareness of either perceptual interpretation. Previous studies showed that the pupillary reflex is suppressed if contrast increments are presented in the suppressed percept (Brenner et al., 1969, Báràny & Halidén, 1948, Lowe & Ogle, 1966, Richards, 1966). We show, however, that the pupil size is continuously modulated as a function of dominance between incongruent luminance and contrast stimuli. We show that pupil size can be used as novel method to objectively measure both binocular and monocular rivalry. A recent study has suggested that monocular and binocular rivalry share common underlying mechanisms (O'Shea et al., 2009). In the present study, the increased pupil size modulation for binocular rivalry as compared to monocular rivalry could be a consequence of different luminance settings or different perceived luminance. It is, however, possible that both rivalry types generally differ in rivalry strength or exclusivity of dominance (Knapen et al., 2007a). Such differences could be related to the fact that during monocular rivalry only the patterns (color, luminance and orientation) rival, while patterns and eyes rival during binocular rivalry. Despite the quantitative difference in pupil size modulation, its robust occurrence in both rivalry types suggests that monocular and binocular rivalry share a similar mechanism driving pupil size.

We have discovered several additional advantages of the utilization of reflexes during rivalry. Reflexes have a shorter latency than subjective report, and they avoid an influence on perception by the response mode itself. The influence of report on rivalry is consistent with the observation that report mode affects dominance durations (Beets et al., 2010, Wohlschläger, 2000). Here we show that

rivalry is slowed down when observers do not report the percept. Attentional factors may – at least in part – account for this effect as they have been found to strongly relate to rivalry dynamics. In particular, distracting observers with a dual-task during rivalry, slows down the rate of alternations (Alais et al., 2010b, Paffen et al., 2006). This result elegantly concurs to our finding that passive viewing of rivalry similarly slows down the rate of alternations. In agreement with the idea that attention is responsible for alternation rates in rivalry, a recent study demonstrated that the cortical thickness of the superior parietal lobe (SPL), a brain area anatomically close to parietal areas that get activated during both shifts in attention (Corbetta, Shulman, Miezin & Petersen, 1995, Yantis, Schwarzbach, Serences, Carlson, Steinmetz, Pekar & Courtney, 2002) and perceptual transitions in rivalry (Kleinschmidt, Büchel, Zeki & Frackowiak, 1998, Lumer et al., 1998), relates to individual differences in alternation rates in rivalry (Kanai et al., 2010). Furthermore, perceptual transitions are generally initiated at the most salient (Paffen et al., 2008, Stuit, Verstraten & Paffen, 2010b) or attended location (Paffen & Van der Stigchel, 2010). As such, our data suggest that deployment of attentional resources to the stimulus through active report of perception, increases the likelihood of transitions between interpretations of a stimulus, and thus increases switch rates during rivalry.

The notion of rivalry as an "all-or-none" process probably dates back as early as Necker (1832) who described the transitions of his bi-stable cube as "sudden and involuntary" (p. 336). However, for the case of binocular rivalry, Wheatstone (1838) observed that "When complex pictures are employed in the stereoscope, various parts of them alternate differently" (§14). Our results imply that such fractionation of percepts (piece-meal rivalry, also see Leopold, Wilke, Maier & Logothetis, 2005) may – at least in part – be responsible for the gradual transitions indicated by the reflexes. Recent evidence similarly indicated that fluctuations in the visual awareness of percepts during binocular rivalry are gradual because sensitivity to probes presented in the suppressed percept slowly rises as a function of time towards the next transition, and vice versa, sensitivity to probes in the dominant percept slowly declines over time as a perceptual transition gets more likely to occur (Alais et al., 2010a). In one experiment, these authors exclude piece-meal periods from analysis based on observer report. In the light of our present results, the reliability of such introspection-based analysis is

questionable. Specifically, latencies in responses (and awareness) might prevent observers from reporting piece-meal periods veridically. In addition, piece-meal rivalry can manifest itself either as discrete transitions or as different levels of perceptual fading, which challenges the dissociation between an all-or-none experience of rivalry and a gradual underlying adaptation process. Both effects can lead to a globally gradual impression of rivalry, although the former retains discreteness locally. In any case, our data show that rivalry is globally gradual over time and that piece-meal rivalry offers *one* possible explanation that is consistent with the data. We have chosen a sinusoidal simulation of piece-meal rivalry to incorporate graduality of changes in dominance (for details see Methods). We observe similar joystick reports in simulated and real rivalry with these settings, which indicates that the simulation was realistic. Nonetheless, studying which simulation parameters reflect the most "natural" perceptual transitions and how they affect the reflexes could quantify the contribution of piece-mealing to graduality further and remain interesting issues for future research.

Neuronal explanations of rivalry generally describe that distinct pools of neurons encode percepts separately and inhibit each other reciprocally (e.g., Klink, van Ee, Nijs, Brouwer, Noest & van Wezel, 2008a, Lehky, 1988, Sugie, 1982). Adaptation of neurons in the dominant pool eventually leads to a decrease in inhibition and thus to a transition in dominance towards the previously inhibited and rivaling pool. Our data do not directly contradict this notion or constrain the role of inhibitory connections, but they point in the direction that spatiotemporal adaptation, a process also subject to interocular grouping (e.g., Kovács et al., 1996, Lee & Blake, 2004), may play a role in the graduality of rivalry dynamics. The fractionation of percepts has been linked to representations in early visual areas because the size of fractions during piece-meal rivalry changed with eccentricity congruently with the human cortical magnification in these areas (Blake et al., 1992). This relation with cortical magnification in early visual areas has been argued to be at least partially responsible for visual field anisotropies in visual awareness in a variety of phenomena (Naber, Carter & Verstraten, 2009). Recent studies also demonstrated that brain activity in V1 is highly correlated with transitions in visual awareness (Lee et al., 2005, Lee et al., 2007, Lee & Blake, 2002). It is thus not unlikely that the gradual nature of visual awareness has its roots in spatiotemporal mechanisms controlled by early

visual areas. Even if the loci of rivalry representations would be known, a different question remains as to which processes are responsible for the (gradual) transition as such. One study argues that highlevel fronto-parietal areas produce activity related to the initiation of perceptual transitions (Lumer et al., 1998) but does not find evidence for whether this activity precedes and thus triggers changes in awareness. A recent study does find a causal relationship between parietal areas and perceptual alternations by disrupting activity with transcranial magnetic stimulation and measuring alternation rates during rivalry (Kanai et al., 2010). It is still, however, uncertain whether the application of TMS to parietal areas disrupts the ability to report perceptual transitions or disrupts the actual initiation of an alternation. Nonetheless, the initiation of changes in awareness by higher-order areas could be well reflected in the observed pupil dilation around a transition, and may have its roots in processes related to decision making (Einhäuser et al., 2010, Einhäuser et al., 2008b), motor planning (Hupé et al., 2009), or attention allocation (Daniels et al., 2009). On the other hand, activity in later areas might be a net result of activity fluctuations related to dominance in rivalry processed by low-level visual areas. Indeed, we find that – the presumably low-level controlled – reflexes have much shorter latencies than high-level subjective report as a response to perceptual transitions. We now can - with the use of reflexes – objectively examine whether high-level effects are a result of or a cause for changes in awareness during rivalry (Leopold & Logothetis, 1999).

4.4 Conclusions

Reflexes reveal that rivalry is a gradual process, its dynamics are affected by the response mode, and fast changes in dominance can slip away unnoticed (or unreported) by observers. Consequently, reflexes allow access to earlier (subconscious) levels of perception, which are unavailable to awareness, and thus stress the limits of relying on introspection alone.

4.5 Materials and Methods

4.5.1 Observers

Ten observers (age: 19-48, seven female, three male) participated in experiment 1, eight observers (age: 19-48, six female, two male) in experiment 2, and another group of eight observers (age: 19-28, five female, three male) in experiment 3 and 4. All had normal or corrected-to-normal vision, were naïve to the purpose of the studies, and gave informed written consent before each experiment. The experiments conformed to National Guidelines for psychological experiments as laid down in the Ethics Regulations of the German Psychological Society and to the ethical principles laid down in the Declaration of Helsinki.

4.5.2 Apparatus

Binocular stimuli were presented on 21 inch Samsung Syncmaster CRT screens at a viewing distance of 30 cm. Monocular stimuli were presented on a 21 inch EIZO Flexscan CRT screen at a viewing distance of 70 cm. The display refresh rate of all screens was 85 Hz and the resolution was either 1152x864 pixels (experiment 1 and 2) or 1280x1024 (experiments 3 and 4). Screens were gamma corrected, achieving a linear mapping of pixel values to stimulus luminance. Each colored grating used a single gun of the monitor, whose CIE color space coordinates (x,y) were (0.623, 0.344), (0.287, 0.609), and (0.151, 0.065) for the red, green, and blue gun, respectively. Stimuli were generated on an Optiplex 755 DELL computer, using Matlab (Mathworks, Natick, MA) and the Psychophysics toolbox (Brainard, 1997, Pelli, 1997) and EyeLink toolbox (Cornelissen, Peters & Palmer, 2002) extensions. Binocular stimuli were dichoptically presented with two monitors by projecting them with a mirror stereoscope to each eye separately. Mirrors were transparent for infra-red light (i.e., cold mirrors), allowing an infrared sensitive camera (EyeLink 2000, SR Research, Osgoode, ON, Canada), positioned behind the mirrors, to track both pupil sizes and direction of gaze at a rate of 500 Hz. Monocular stimuli were presented with a single screen and observers looked through a transparent mirror that reflected infrared light (i.e., a hot mirror) from the eyes to the eye-tracking camera (Eyelink

"Tower Mount") that recorded at 1000 Hz. In all experiments, the observers' head was supported by a chin- and forehead-rest. In all pupil experiments, observers fixated a fixation dot (0.8° diameter) centered over the stimulus. The eye-tracker was (re)calibrated before each experiment and after each break (see procedure).

4.5.3 Stimuli and Procedure – Experiment 1

Three different stimulus sets were used in four separate sub-experiments, conducted on separate days. The first stimulus set consisted of sinusoidal gratings with a spatial frequency of 2 cycles per degree and opposing orientations (i.e., -60° and +60°), one grating colored red and the other green (Figure 1A). The red grating's luminance ranged from 0.011 cd/m² to 18.5 cd/m². The green grating's luminance varied across trials (21.1, 33.5, 47.0, or 60.4 cd/m²). Binocular rivalry was induced by presenting both red and green grating separately to each eye. Gratings were presented in a gray (33.5 cd/m²) annulus of 10 degree diameter. The whole stimulus was framed by a 2° wide rectangular bar consisting of a high spatial frequency noise pattern, to ensure a steady binocular fusion of the backgrounds. Stimulus' orientation, color, and presentation to the corresponding eyes were randomized during each experiment.

The second stimulus set similarly consisted of sinusoidal gratings but instead of luminance, contrast was varied across trials. The red grating had a Michelson contrast of 0.6 with a maximum luminance of 11.2 cd/m². The green grating's contrast was varied, having either one of four Michelson contrasts of 0.1, 0.4, 0.7, or 1.0, corresponding to a minimum-maximum luminance of 30.2-36.9, 20.1-47.0, 10.1-57.0, or 0-67.1 cd/m², respectively.

The third stimulus set consisted of overlapping sinusoidal gratings with a spatial frequency of 1 cycle per degree. These stimuli induced a form of *monocular* rivalry during which the visibility of each grating fluctuated over time. These fluctuations consisted of one grating being more visible (i.e., a higher perceived luminance) than the other until its perceived luminance decreased while the other grating's luminance increased. Similar to the first stimulus set, luminance of the green grating was varied across trials. The red grating had maximum luminance of 5.7cd/m². The green grating's

luminance was varied across 4 levels, 16.9cd/m², 19.4cd/m², 21.8cd/m², or 24.2cd/m². In contrast to the first and second stimulus set, the overlapping gratings were presented monoptically without the mirror stereoscope.

Each of the four possible grating pairs was presented four times per sub-experiment, resulting in a total of 16 trials (4x4). A single trial lasted 120 seconds and was followed by a 20 second break. During each trial, observers viewed the stimuli and indicated the dominant percept with two buttons. As dominance of each percept fluctuated, intermediate states occurred in which both percepts were equally dominant. Nonetheless, observers were instructed to always indicate one (i.e., the most dominant) percept as dominant. After 8 trials, observers were allowed to take a 5 minute break.

4.5.4 Stimuli and Procedure – Experiment 2

In experiment 2, all stimulus aspects were identical to experiment 1, except that only the stimuli, for which the green grating was most distinct from the red grating, were used: binocular green grating luminance of 60.4 cd/m², binocular green grating contrast of 1.0, and monocular green grating luminance of 24.2cd/m². For each of the 3 conditions (binocular luminance, binocular contrast, monocular), observers conducted 4 trials of 3 minutes each. Two of these trials were real-rivalry trials as in experiment 1, two were simulated-rivarly trials, in which alternations in dominance were simulated by switching the presentation of each stimulus (i.e., the red or green grating) per dominance duration. Distribution of dominance durations in each simulated-rivalry trial was based on the report of the preceding real-rivalry trial.

4.5.5 Stimuli and Procedure – Experiments 3 and 4

In experiment 3 and 4, a large (height: 50.6 deg, width: 37.1 deg) drifting sinusoidal grating (0.15 cycles/deg) was presented to each eye, one dark and red (peak luminance 17.4 cd/m²), the other light and green (68.2 cd/m²) on a dark background (<0.01 cd/m²). Both gratings were moving in opposite lateral directions (left and right) at a speed of 6.7 deg/s.

In experiment 3, we simulated rivalry by presenting the same stimulus to both eyes and physically switched colors and drifting directions simultaneously. Statistics of dominance durations were matched to the preceding real rivalrous trial. In experiment 4, the perceptual transition was simulated as a smooth transition through a state of piece-meal rivalry. The previously invisible stimulus became visible by spatially moving it over the dominant stimulus from one side to the other. During a simulated transition, complementary parts of both stimuli were thus visible simultaneously but divided by a vertical border at which both stimuli transparently overlapped (width: 14 degrees). The transitions followed a sinusoidal movement pattern with half periods (i.e., dominance duration) of either a fraction of 0.8 or 1.2 of the median dominance duration from the preceding rivalrous trial.

Experiments 3 and 4 consisted of 4 conditions, which differed in presentation condition (real rivalrous versus simulated rivalry) and response mode (active versus passive) and were repeated twice (8 trials per experiment). In active report, observers were either instructed to indicate the dominant percept by holding down the arrow key on a keyboard (experiment 3) or by deflecting a joystick (experiment 4). They were told to release buttons or keep the joystick in a middle position when no percept was dominant. During passive trials, observers were instructed to just watch the stimulus. Trials lasted 5 minutes and were followed by short breaks.

4.5.6 Analysis

In all binocular experiments the pupil sizes of both eyes were highly correlated (r>0.99 in all cases) as was the OKN in experiment 3 and 4 (r>0.98), such that only the right eye was used for analysis in all cases. Pupil size was based on its diameter as recorded by the Eyelink tracker system. Eye-position and pupil size were interpolated with a cubic spline fit during periods in which observers blinked their eyes. For analyzing how the pupil size developed around a perceptual transition (Figure 1C-K), pupil size was normalized to z-scores per trials (i.e., trial mean subtracted and divided by standard deviation). Horizontal eye velocity as function of time is given by the derivative of the eye's raw horizontal position. To obtain the slow phase of the OKN, multiple thresholds were applied to the absolute values of convolution filtered (square smoothing window of 0.1s width) velocity traces (>.5

deg/s), acceleration (>.1 deg/s²), and the derivative of acceleration (>.01 deg/s³) of the horizontal eye position signal to remove all fast phases from the OKN speed trace (Figure 3B, slow phases). The zero crossing points of the OKN's slow phase component velocity were assumed to be objectively defined perceptual transitions. The obtained OKN zero crossings points were filtered for random noise in OKN speed. If crossing points were preceded by a relatively low maximum or minimum (i.e., those extremes were between a "sign-change threshold" of 1.6 or -1.6deg/s), they were assumed to be a result of intermediate percepts and removed from the analysis of transition speeds. Mean velocity of the OKN was calculated per slow phase and smoothed using a sliding square window of 0.1 seconds width. Dominance durations were calculated from either the button presses, joystick deflection baseline crossings, or from distance between the unfiltered (i.e., no removals because of low preceding extremes) zero crossing points of the OKN. For rivalrous trials, the latency of responses of both the button presses and joystick deflections as compared to the OKN were based on the median time between a button press or joystick crossing and the preceding OKN crossing that indicated perceptual transitions. For simulated trials, the latency of the button presses, joystick crossing, pupil or OKN sign changes were based on the median time from a simulated transition. If the latency was longer than 2 seconds, it was assumed to be a missed transition and was therefore removed from analysis.

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4.7 References

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4.8 Supporting Information

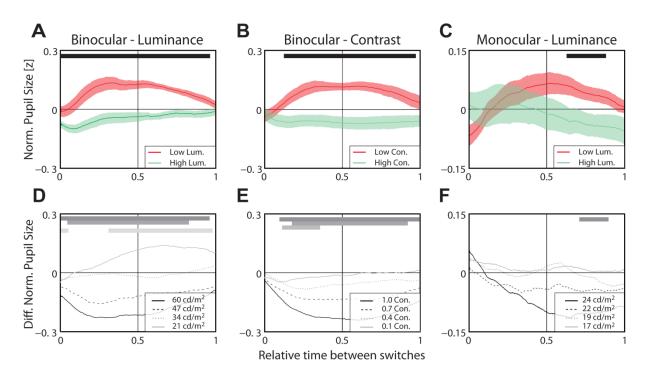


Figure S1. Pupil size during rivalry in a normalized time frame. (A-C) Normalized mean and transparent s.e.m. pupil size (z-score) as a function of relative time between perceptual transitions per dominant percept for each stimulus set. The time axis was normalized to unit length between transitions by re-sampling all pupil traces per dominance duration (3000 samples) before averaging (details see Alais et al., 2010a, Einhäuser et al., 2004). For the red trace the transition from high luminance to low luminance percept thus happens at time 0 and back at time 1, while the reverse holds for the green trace. In this periodic time frame time, 1 for the red trace corresponds to time 0 for the green trace and vice versa. The pupil increased or decreased in size when the dominant percept was low or high in luminance or contrast, respectively. (D-F) Mean differences in pupil size traces between the percepts as a function of relative time between perceptual transitions. Grey values of traces indicate the level of luminance or contrast of one of the gratings (the other rivaling grating had a fixed intermediate level of luminance or contrast). The degree of pupil size modulation to the luminance or contrast of the dominant percept depended on the difference in luminance or contrast between the rivaling percepts. Thick patches at the top indicate when traces are significantly (p<0.05) different from each other (panels A-C) or from 0 (panels D-F).

5. Chapter 5

Perceptual Benefits of Objecthood

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Abstract

Object-based attention facilitates the processing of features that form the object. Two hypotheses are conceivable for how object-based attention is deployed to an object's features: first, the object is attended by selecting its features; alternatively, a configuration of features as such is attended by selecting the object representation they form. Only for the latter alternative, the perception of a feature configuration as entity ("objecthood") is a necessary condition for object-based attention. Disentangling the two alternatives requires the comparison of identical feature configurations that induce the perception of an object in one condition ("bound") and do not do so in another condition ("unbound"). We used an ambiguous stimulus, whose percept spontaneously switches between bound and unbound, while the stimulus itself remains unchanged. We tested discrimination on the boundary of the diamond as well as detection of probes inside and outside the diamond. We found discrimination performance to be increased if features were perceptually bound into an object. Furthermore, detection performance was higher within - and lower outside the bound object as compared to the unbound configuration. Consequently, the facilitation of processing by object-based attention requires objecthood; that is, a unified internal representation of an "object" - not a mere collection of features.

5.1 Introduction

The question: "what is an object?" has attracted widespread interest. Two main views on how objects are formed exist: a "bottom-up" local processing of Gestalt cues and a more traditional Gestalt "topdown" global organization (e.g., Treisman & Gelade, 1980). The bottom-up approach suggests that the brain uses specific Gestalt cues (Brunswik & Kamiva, 1953) to form a holistic object representation from a constellation of parts. From this point of view, the representation of an object is formed if the right combination and lay-out of features is chosen. The top-down approach proposes that something becomes an object after a higher level representation is formed (e.g., Kahneman, Treisman, & Gibbs, 1992). Specific combinations of features may activate such a representation, but the representation itself is needed to bind features into a single object. These views are not mutually exclusive. Indeed, more recent findings suggest that both, early-feature integration and higher stages, play a crucial role in the processing of objects (e.g., Altmann, Bülthoff, & Kourtzi, 2003; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003). Nonetheless, experimental studies have not yet fully disentangled effects of object representations from feature configurations. These disparate views on object integration call for resolution. Does attention manifest itself along feature configurations or is it deployed to objects (e.g., Crundall, Dewhurst, & Underwood, 2008; Houtkamp, Spekreijse, & Roelfsema, 2003; Roelfsema, Houtkamp, & Korjoukov, 2010)?

How can effects of objects be disentangled from the features they are made of? In the realm of attention, the question how objects guide attention allocation has been the topic of many studies (e.g., Duncan, 1984; Kahneman et al., 1992; Watson & Kramer, 1999). Evidence in favor of object-based attention mainly demonstrates a benefit for responses when attention has to switch within a single object opposing to between multiple objects (e.g., Egly, Driver, & Rafal, 1994; Moore, Yantis, & Vaughan, 1998). Several other paradigms, including inattentional blindness (Moore & Egeth, 1997) and visual search (Enns & Rensink, 1991), are similarly affected by object-based effects. In principle such results could still be linked to feature constellations, rather than being specific to "objecthood". Even if features are bound to objects pre-attentively, a subjective impression of objecthood might or might not be required for "object-based" benefits. The notion of object-based attention has therefore

been challenged. In addition the lack of a precise definition of an "object" (Scholl, 2001) makes studying objects independent of the constituting features challenging. This definition problem has thwarted a sequence of studies from making solid statements about how attention is allocated to objects and what underlies object-based attention effect. Studies that evaluated performance facilitation of attending to an "object", have thus experienced difficulty with the disentanglement of features cues that constitute the object and the cognitive concept and representation of an 'object'. Indeed, subjective formations of objects are highly associated with, and arguably defined by, feature cues (i.e., Gestalt) like contour and form. Several attempts have been made to circumvent this problem: studies have avoided crafting objects with stimulus manipulations, but instead control an observers' perceptual interpretation of features as an object (e.g., Baylis & Driver, 1993). However, eventually all reported attentional object-based benefits could be explained by specific features such as contour (Gibson, 1994), closure (Marino & Scholl, 2005), line collinearity (Avrahami, 1999; Crundall, Cole, and Galpin, 2007; Kimchi, Yeshurun, & Cohen-Savransky, 2007), and other Gestalt-like principles (Feldman, 2007). These studies opened up the possibility that cues such as figure-ground organization, closure, and collinearity facilitate performance and underlie the within-object advantage. From this point of view, it may be that a collection of organized stimulus features instead of a unique object representation is what derives "object-based" benefits.

Ambiguous stimuli can disentangle the subjective impression of objecthood from the physical constellation of object features. Using fMRI, Murray, Kersten, Olshausen, Schrater, and Woods (2002) demonstrated that ambiguous stimuli are useful as a tool for studying object processing in the absence of confounding effects related to feature constellations (see also Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002; Fang, Kersten, & Murray, 2008). The stimulus they used was an ambiguously moving diamond which induces two interpretations: either a bound percept of a single object or an unbound percept of multiple objects (Lorenceau & Shiffrar, 1992). The diamond's configuration can lead to the percept (i.e., a subjective impression) of a single diamond moving sideways behind three bars (Figure 1a), or as multiple apertures that independently move up and down (Figure 1b), while the stimulus is kept constant. Independent of physical changes, attention may be

either spatially divided over the four apertures of the ambiguous diamond or allocated to the object as a whole. The ambiguous diamond is an ideal tool to address the issue whether object-based attention effects are still present if the perceptual differentiation between objects is only caused by an internal subjective interpretation. Thus, by using this ambiguous stimulus, the problem of defining an object is removed because the observers' internal percept defines the objects, and, in contrast to Baylis and Driver's design (1993), the attended objects will always constitute of exactly the same physical properties.

In the present study, we use the ambiguous diamond to test whether a single or multi-object percept has an effect on discrimination and detection performance. In other words, we address the question as to whether the perceptual integration (i.e., binding) of the independent moving apertures into a single object (i.e., a diamond) will facilitate its processing. We will show that subjective impression of a single bound object improves observers' performance in both discriminating and detecting physical changes of the object as compared to the situation in which the percept constitutes of multiple unbound (i.e., non-integrated) objects. We further will show that the processing on an object itself gets facilitated while processing on regions outside the object get suppressed. Our experimental results are strong evidence for the notion that gestalt cues are not solely responsible for object-based effects and that the formation of a unique representation of an object is sufficient to enable attention to be allocated to an object.

5.2 Methods

5.2.1 Observers

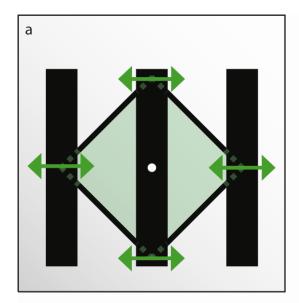
Author M.N. and 9 naïve observers (4 male and 6 female students in the age range of 20-30) participated in each experiment. In each experiment, two observers were excluded from analysis for reasons provided below. Data of both experiments were therefore based on 8 observers. Observers had normal or corrected to normal vision. Each observer gave written informed consent before participation; all procedures adhered to national standards on experiments with human observers and with the Declaration of Helsinki.

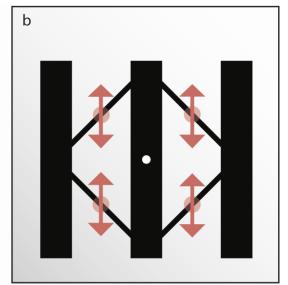
5.2.2 Stimuli

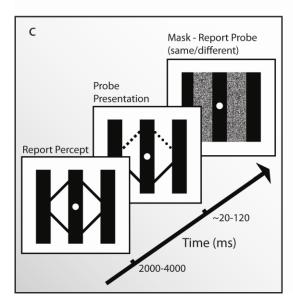
The stimulus used in both experiments was a 10 deg wide square rotated 45 deg (i.e., a diamond) moving sideways behind three vertical bars (see Movie 1 in supplementary materials). The movement of the diamond induces an ambiguous perceptual state consisting of either a percept of a single object oscillating side to side horizontally (Figure 1a) or multiple apertures moving up and down (Figure 1b). As differentiation between the two percepts includes the process of binding features into an object, we will refer to the single-object percept as *bound* and the multi-object percept as *unbound*. The visibility (i.e., dominance) of these percepts alternates over time, each percept being dominant for several seconds until the other percept takes over. To induce ambiguity, the diamond had a 1 deg sinusoidal movement pattern between outer left and right borders of the occluding bars. These bars ensured the invisibility of the diamond's corners, an essential property for the stimulus' ambiguity. A 0.1 deg wide fixation dot was presented on the center of the screen. Mean luminance of the stimulus was 33.9 cd/m².

5.2.3 Apparatus

Stimuli were generated using Matlab (Mathworks. Natick, MA) with Psychophysics toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented by an Optiplex Dell computer and a 21 inch EIZO Flexscan monitor on a black background with 1152 x 864 pixels at 100Hz refresh rate. Head position was stabilized using a chin and forehead rest that assured a steady viewing distance of 73 cm.







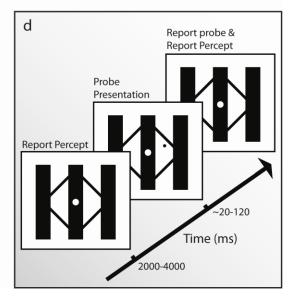


Figure 1. Stimuli. The ambiguous moving diamond induces two distinct percepts (colors and arrows are for visualization only and not present in the actual stimulus): **(a)** a single *bound* object (green surface and arrows) coherently moving sideways or **(b)** multiple *unbound* objects (red arrows) making oscillating movements up and down. To experience the perceptual ambiguity induced by this stimulus, see movies in supplementary materials: movie 1 for the ambiguous stimulus, movie 2 for disambiguation by luminance changes **(c)**. Procedure during discrimination Experiment 1: Observers indicated the dominant percept, 2000-4000 ms later two apertures were briefly changed to either a dashed and/or dotted line, and the probes were masked by random noise pattern after 20-120 ms (the SOA depended on the observers' performance threshold). Probes were either *different* (i.e., one dashed and the other dotted) or the *same* (i.e., both dashed or both dotted). **(d)** Procedure during detection Experiment 2: Observers continuously indicated the dominant percept, and every 2000-4000 ms a small probe was presented for 20-120 ms inside or outside the diamond. Black and white values in this figure are inversed, that is, the background and fixation dot were actually black and the diamond lines were white during the experiment.

5.2.4 Procedure

Observers performed two experiments on separate days. Experiments consisted either of a discrimination (Figure 1c) or detection task (Figure 1d) in which the performance during both the

bound and unbound percept was measured. Observers were familiarized with the stimulus and setup before the actual experiment. During the experiment, observers had to fixate and indicate the dominant percept by holding down one of two buttons.

5.2.5 Experiment 1 - discrimination

The first experiment was designed to test whether perceptual binding of multiple apertures (i.e., the diamond's borders) into a single object facilitated discrimination performance. In each trial of Experiment 1, between 2 and 4 seconds after observers started reporting their percept, two adjacent borders of the diamond were briefly (see below for timing) changed to either a dotted and/or dashed pattern (Figure 1c). This probe was followed by a random noise mask to prevent image after-effects. After mask onset, observers stopped reporting their dominant percept and indicated using two buttons whether both borders were the *same* (i.e., both dotted or both dashed) or *different* (i.e., one dotted and the other dashed). Observers were allowed to take all the time they needed to make their decision. The next trial only started after the observer's response and an experiment consisted of a total of 300 trials.

5.2.6 Experiment 2 - detection

In the second experiment we tested whether detection performance in and around the objects was modulated by perceptual binding. Observers were briefly presented (20ms) with 0.1 deg wide Gabor shaped probes in and around the diamond while they – at the same time – reported their dominant percept (Figure 1d). Every time observers had detected a probe, they reported this with an additional button. A total number of 1200 probes were shown during the experiment. The time between probe onsets was 2 to 4 seconds and probes could be shown anywhere in, and around the stimulus within an annulus shaped region with an inner and outer radius of 5 and 15 deg, respectively. Trials in which reaction times were faster than 200ms or slower than 2000ms were excluded from analysis (0.7% of all trials).

5.2.7 Individual adjustment of perceptual dominance

Since perceptual dominance can vary over the course of the experiment and is influenced by interruptions of stimulus presentation (e.g., Orbach, Ehrlich, & Vainstein, 1963), and biases in

dominance (i.e., one percept is preferred over the other) could in principle be directly related to detection or discrimination performance, we aimed at about equal probability in dominance for both percepts (i.e., bound & unbound). This perceptual balance was created by altering the luminance of the occluding bars: A higher luminance biases dominance towards the bound percept, and a lower luminance towards the unbound percept (see Movie 2 in supplementary materials that demonstrates that dominance of the percept depends on the luminance of the occluding bars). We adjusted this luminance for each observer in a short experiment preceding each of the main experiments. For 5 minutes observers only indicated the dominant percept and a QUEST procedure (Watson & Pelli, 1983) resulted in a luminance value for the occluding bars at which the observer's perceptual dominance between the percepts was balanced. The luminance corresponding to equality spanned a wide range across observers, ranging from 0.11 to 6.77 cd/m² (Median: 0.40 cd/m²). In the test preceding experiment 1, two observers showed a substantial bias in dominance towards the unbound interpretation (73% and 80% dominance) and were thus removed from analysis. In the test preceding experiment 2, one observer failed to balance both percepts (70% dominance for unbound) and was excluded from analysis.

5.2.8 Individual adjustment of performance

We prevented floor and ceiling effects in discrimination and detection performance by having observers perform a 5-minute version of the main experiment in which a QUEST procedure searched for the 75% correct performance threshold. Discrimination performance was adjusted by varying the time between probe and mask onset (Stimulus Onset Asynchrony, SOA): shortening the SOA resulted in a performance decrease. The mean SOA over all observers for a 75% performance was 63ms (SD: 34ms). Detection performance was manipulated by adjusting the probe luminance: lowering luminance resulted in a decrease in performance (Mean: 0.65, SD: 0.08).

To make sure that observers did not exchange response buttons, and stayed actively involved with the task, we added catch trials in each experiment. During these trials the occluding bars suddenly changed to white (luminance: 33.9 cd/m²), where it was expected that the observer would always report the *bound* percept. One observer did not report this *bound* percept in 3 out of 4 cases in

Experiment 2, which indicates that this observer might have accidentally switched buttons. This observer was excluded from the analysis of experiment 2.

5.2.9 Analysis

First we computed *performance* (number of trials in which probes were correctly discriminated or detected divided by the total number of trials) and *dominance* (number of trials in which a percept was dominant at the time of probe onset divided by the total number of trials). For both experiments, trials in which no percept was reported were excluded from analysis. Differences in performance between conditions were evaluated and statistically tested using paired t-tests.

5.3 Results

5.3.1 Experiment 1 – Object Border Discrimination

We first examined how observers' subjective impressions of the ambiguous diamond affected dominance and discrimination performance. The analysis showed that discrimination performance depended significantly on whether the bound or unbound percept was dominant at the moment of probe onset (Figure 2a). Observers performed significantly better at discriminating features across the stimulus for the bound percept as compared to the unbound percept (Difference: 5%; t(7) = 3.98, p < 0.01). Dominance of both percepts was balanced well across observers (mean unbound: 54%, SD: 9%; t(7)=1.20, p > 0.25). Response times were not significantly different between percepts (mean bound: 1.64s, SD: 0.43; mean unbound: 1.59s, SD: 0.38s; t(7) = 1.55, p > 0.10). Although there was an overall selection bias of *same* over *different* probes (t(7)=6.08, p < 0.001), we found no further response biases between the percepts (t(7)=0.58, p > 0.50). In conclusion, the results of Experiment 1 clearly indicate that discrimination performance is better during the bound percept than during the unbound percept.

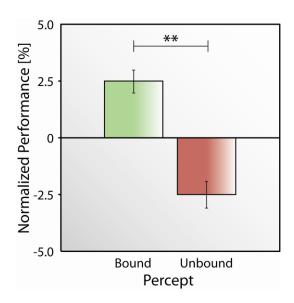


Figure 2. Performance in Experiment 1. Mean and standard errors of discrimination performance per percept. Discrimination performance was significantly better for the bound percept as compared to the unbound percept.

5.3.2 Experiment 2 – Object Area Detection

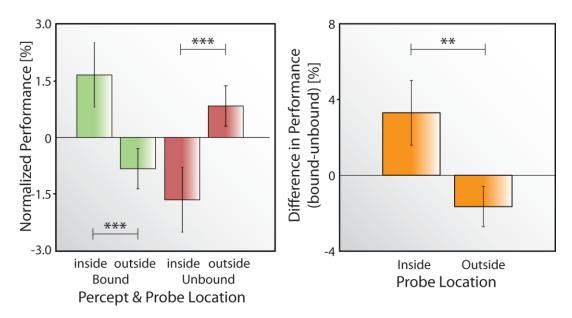


Figure 3. Performance in Experiment 2. (a) Mean and standard errors of normalized performance (mean performance was subtracted per subject) per percept and per presented probe location of either inside or outside the diamond, and (b) difference in detection performance between bound and unbound condition separately for probes presented either inside or outside the diamond. Detection performance was higher inside the diamond as compared to outside the diamond during the bound percept. Detection performance was worse inside the diamond as compared to outside the diamond during the unbound percept.

In the second experiment, we tested how subjective impressions of the stimulus affected detection rather than discrimination performance. Specifically, we examined whether there were differences in detection performance between the bound and unbound percept, and whether this depended on the location of the presented probes (i.e., inside or outside the diamond). Detection performance during the bound percept was higher for probes presented inside the diamond as compared to outside the diamond (Figure 3a; t(7) = 8.98, p < 0.001). Vice versa, detection performance during the unbound percept was lower for probes presented inside the diamond as compared to outside the diamond (t(7) = 7.50, p < 0.001). Compared to the unbound percept, detection performance during the bound percept was higher and lower for probes presented inside and outside the diamond, respectively (Figure 3b; Difference: 5%; t(7) = 3.63, p < 0.01). There was no significant difference in dominance between the bound and unbound percept (t(7) = 2.14, p > 0.05). Independent of the probe location, there was no significant difference in performance between the bound and unbound percept (t(7) = 1.38, p > 0.05). Similarly, there were neither significant differences in reaction times between

percepts (mean bound: 0.49s, SD: 0.05; mean unbound: 0.49s, SD: 0.05s; t(7) = 0.09, p > 0.75), nor between locations (inside-bound versus outside-unbound: t(7) = 0.31, p > 0.75; outside-bound versus inside-unbound: t(7) = 1.03, p > 0.25). In summary, Experiment 2 showed that detection performance increased inside the object as compared to outside the object during the bound percept; and that the opposite pattern was observed for the unbound percept.

5.4 Discussion

We have examined how the subjective impression of binding feature elements into an object influences discrimination and detection performance. With the ambiguous stimulus we could distinguish between an observers' impression of a bound single-object percept and an unbound multi-object percept without change to the physical stimulus. We demonstrate that the bound percept facilitates discrimination and detection performance at and within an object's borders. Our results extend the findings by Baylis and Driver's (1993) by excluding the potential confound of differences in gestalt cues in the physical stimulus. Since our design neither included stimulus manipulations nor differences in cue constellations between the percepts, our findings show strong support for the notion that object-based benefits are a result of a higher-order internal representation of an object. Thus, "objecthood" is not simply a collection of specific rules or features, but a unique representational entity that confers the benefits of object based attention.

The facilitation of processing inside the object relative to the outside in the bound condition finds its straightforward interpretation in the concept of object-based attention: Attentional resources are allocated to the object through the object's borders and inner body, and irrelevant areas around the object are suppressed. Such an interpretation is in line with physiological findings that show that neurons with receptive fields within an object have enhanced activity (Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999). There are several indications that such grouping-related dynamics in activity are controlled by recurrent processes (Lamme & Roelfsema, 2000; Roelfsema, 2006).

Besides the facilitation of the region within the object and suppression outside the object in the bound condition, we observed suppression inside and facilitation outside in the unbound condition. Several explanations are conceivable for this reversal. First, it is possible that during the bound condition the object representation adapts and object-based attention is also subject to adaptation. In this view, poorer processing in the inside during the unbound percept is a consequence of this adaptation. If all the reversals were due to adaptation, both inside and outside performance should approach equality over time, for which we find no robust evidence (data not shown). Nonetheless, as adaptation likely contributes to rivalry as such (Alais, Cass, O'Shea, & Blake, 2010), an effect cannot

be excluded. A second explanation would be a phenomenon related or similar to crowding (Bouma, 1970). In the unbound situation there are more items around the inside probe that could interfere with detection (4 apertures instead of one object). The outside would be affected less, since fewer items (1 or 2) are in the immediate vicinity. A third explanation uses the spatial distribution of attention around an attended item. The localization of attention is often assumed to consist of a facilitatory central region with an inhibitory surround (Tsotsos, Culhane, Wai, Lai, Davis & Nuflo, 1995; Bahcall & Kowler, 1999; Mounts, 2000a, b; Cutzu & Tsotsos, 2003; Carlson, 2007; Scalf & Beck, 2010; Hopf, Boehler, Luck, Tsotsos, Heinze, & Schoenfeld, 2006). Similar to the bound situation, in which the outside of the object is suppressed and the inside facilitated, in the unbound condition, the individual items (apertures) are facilitated and their surround is suppressed. Quantitative predictions will depend on a large set of parameters, including width of center and surround, dynamics of attention and the interaction between suppressive and facilitating regions. Nonetheless, it is conceivable that non-linear interaction between suppressive zones of individually attended apertures inside the diamond yield a net-suppression; while outside the diamond, the suppressive zones are more separated, do interact less, and facilitation remains dominant on average. We consider it likely that all 3 explanations - adaptation, a phenomenon akin to crowding, and the spatial distribution of attention - in part contribute to the observed effect. Disentangling them in future research will foster our understanding of object-based attention.

Desimone and Duncan (1995) have argued that objects compete for limited processing capacity and that competition can be biased by top-down mechanisms that select relevant objects. In the context of the present results it is possible that the competition between independent unbound objects decreases the processing accuracy of these objects in general. When these objects are grouped or "bound", competition disappears and processing for all bound components is facilitated. Another explanation can be extracted from the view that object-based attention is a form of an object-guided spatial attention mechanism (Davis, Driver, Pavani, & Shepherd, 2000; Martínez, Teder-Salejarvi, & Hillyard, 2007; Roelfsema, Stanisor, & Wannig, 2010; Weber, Kramer, & Miller, 1997). The grouping of independent parts or attributes as one object makes attention automatically spread evenly over the

entire object (e.g., Kahneman & Henik, 1981; He & Nakayama, 1995). As many studies have presented evidence for the existence of activity patterns closely tied to such object processing in relatively high cortical areas (e.g., Cusack, 2005; Cusack, Mitchell, & Duncan, 2010; Shafritz, Gore, Marois, 2002), it is tempting to suggest that a top-down cortical mechanisms is required for the perception and recognition of an object (e.g., Grill-Spector, Kourtzi, & Kanwisher, 2001) and subsequent attention allocation (O'Craven, Downing, & Kanwisher, 1999). In the light of our results, such a top-down mechanism does not rely on bottom-up feature constellations, but can operate solely on the basis of high-level representations.

In conclusion, with our stimulus and design we addressed the problems inherent in the definition of an object that have challenged the interpretations of a large body of recent scientific outcomes (e.g., Baylis & Driver, 1993; Gibson, 1994; Houtkamp, Spekreijse, & Roelfsema, 2003; Crundall et al., 2008). We found that the status of being an "object" is generally ambiguous and depends on the experience and interpretation of the observer. Some observers experience multiple elements in a scene as spatially separate and independent components. Others observe the same exact elements as a single object, bound by a previously stored visual representation. Objects do have to contain some specific features, such as borders, to separate them from their background, but a specific composition of features is not sufficient to produce an object. Gestalt rules such as closure and collinearity can ease and facilitate the process of binding multiple elements into a single object, but a high-level object representation is necessary to induce this process.

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6. Chapter 6

Animal detection and identification in natural scenes: Image statistics and emotional valence

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Abstract

Humans process natural scenes rapidly and accurately. Low-level image features and emotional valence affect such processing, but have mostly been studied in isolation. At which processing stage these factors operate and how they interact has remained largely unaddressed. Here, we briefly presented natural images, and asked observers to report presence or absence of an animal (detection), species of the detected animal (identification), and their confidence. In a second experiment, the same observers rated images with respect to their emotional affect and estimated their anxiety when imagining a real-life encounter with the depicted animal. We found that detection and identification improved with increasing image luminance, background contrast, animal saturation, and luminance plus color contrast between target and background. Surprisingly, animals associated with lower anxiety were detected faster and indentified with higher confidence, and emotional affect was a better predictor of performance than anxiety. Pupil size correlated with detection, identification and emotional valence judgments at different time-points after image presentation. Remarkably, images of threatening animals induced smaller pupil sizes, and observers with higher mean anxiety ratings had smaller pupils on average. In sum, rapid visual processing depends on contrasts between target and background features rather than overall visual context, is negatively affected by anxiety, and finds its processing stages differentially reflected in the pupillary response.

6.1 Introduction

Our visual system is optimized to detect, classify, and identify objects that we encounter in everyday life. Without this skill we would not be able to recognize components of our visual field as, for instance, potentially useful or threatening. The well-developed character of this skill is expressed in the accuracy and speed at which we can process objects in natural scenes (Potter & Levy, 1969). For example, the human and monkey brain can accurately distinguish between specific classes of objects within 45ms (Mouchetant-Rostaing, Giard, Delpuech, Echallier & Pernier, 2000) to 150ms (Thorpe, Fize & Marlot, 1996b, VanRullen & Thorpe, 2001b) and instantiate a behavioral reaction to them within about 120ms (Kirchner & Thorpe, 2006). Independent of whether brain signals reflect differences across object categories through low-level features or high-level decision-making (Rousselet, Husk, Bennett & Sekuler, 2008, VanRullen & Thorpe, 2001b), these studies demonstrate how fast information about objects can be extracted, represented and used.

But why can we recognize objects so accurately and fast and what are the mechanisms underlying the rapid processing of objects? Some studies have found evidence suggesting that visual processing of objects consists of two stages: an early perceptual stage (~75ms) that distinguishes between observed features, and a later pathway for decision making (~150ms) (Johnson & Olshausen, 2003, Johnson & Olshausen, 2005, VanRullen & Thorpe, 2001b). While the diagnostic act of recognizing and categorizing objects probably happens at a later stage (Smith, Gosselin & Schyns, 2007, van Rijsbergen & Schyns, 2009), these studies stress that the analysis of features performed by our visual system is highly important for successful detection and identification. In a similar vein, several other studies suggested that the automatic feed-forward analysis of specific image features is mainly responsible for accurate and fast behavioral responses (Kirchner & Thorpe, 2006, Thorpe et al., 1996b, VanRullen & Thorpe, 2001a, VanRullen & Thorpe, 2001b). Results that support this line of thought come from a variety of studies in which a specific set of image statistics, such as color, texture, and shape were varied to study their effect on detection (e.g., Vogels, 1999). Image statistics that have been identified to help object or scene recognition are contrast (Brodie, Wallace & Sharrat, 1991, Macé, Delorme, Richard & Fabre-Thorpe, 2010), color (Brodie et al., 1991, Delorme, Richard

& Fabre-Thorpe, 2010, Elder & Velisavljević, 2009, Gegenfurtner & Rieger, 2000, Goffaux, Jacques, Mouraux, Oliva, Schyns & Rossion, 2005, Humphrey, Goodale, Jakobson & Servos, 1994, Oliva & Schyns, 2000, Wichmann, Sharpe & Gegenfurtner, 2002, Wurm, Legge, Isenberg & Luebker, 1993, Yao & Einhäuser, 2008), background coherence with the object (Biederman, 1972, Biederman, Glass & Stacy, 1973), shape or posture (Delorme et al., 2010, Elder & Velisavljević, 2009), object size (Delorme et al., 2010), texture (Delorme et al., 2010, Elder & Velisavljević, 2009, Renninger & Malik, 2004), Fourier spectra (Gaspar & Rousselet, 2009, Joubert, Rousselet, Fabre-Thorpe & Fize, 2009, McCotter, Gosselin, Sowden & Schyns, 2005), and, though weakly, luminance (Delorme et al., 2010, Elder & Velisavljević, 2009, Macé et al., 2010, Nandakumar & Malik, 2009). Many of these studies used datasets of images that contain objects belonging to an explicit (target) category. Rarely, however, were subcategories or image features controlled for. Depending on the specific choice, categories might be subject to a selection bias and may have distinct visual features that make them especially easy to detect and recognize (Ohman, 1993, Ohman, Flykt & Esteves, 2001, Tipples, Young, Quinlan, Broks & Ellis, 2002). Frequently, animals are chosen as target category, and, indeed, they have very specific characteristics, such as eyes and elongated legs, that are considerably important for their successful identification (Delorme et al., 2010). In addition, images of animals are likely to be pre-segmented by the photographer (Wichmann, Drewes, Rosas & Gegenfurtner, 2010) and animals are therefore often subject to "unnatural" positions and figure-ground separations. Hence, a variety of features and their constellations are important for efficient and rapid processing of objects. It has remained elusive, however, to what extent all these features relatively contribute to recognition performance. Here we integrate a large variety of features and their relations in a model to predict several measures of performance.

There are a few indications that particular features have a significant but weaker influence on recognition performance as compared to other features. For example, some studies argue that luminance or color have less influence on performance than texture, shape, and certain diagnostic parts (e.g., eyes and mouth) of the object (Delorme et al., 2010, Elder & Velisavljević, 2009). However, "texture" is by definition a repetitive pattern with a specific luminance, contrast, color, and orientation,

and thus not independent from these constituting features. Similarly, shape of an object is defined by differences between the object and background. Image statistics such as shape are hence a high-level and more abstract description for constellations of very basic features. If this terminological hierarchy is compared with the hierarchy of the visual system (Felleman & Van Essen, 1991), we see that information about luminance, contrast, orientation, and color is indeed already available in early visual areas while shape is processed at later stages by areas such as the LOC (e.g., Baylis & Driver, 2001, Grill-Spector, Kushnir, Edelman, Itzchak & Malach, 1998, Grill-Spector, Kushnir, Hendler, Edelman, Itzchak & Malach, 1998, Kourtzi & Kanwisher, 2000, Kourtzi & Kanwisher, 2001, Malach, Grill-Spector, Kushnir, Edelman & Itzchak, 1998). Thus, direct relations between performance and basic individual features such as luminance, contrast or color could have been shadowed by seemingly stronger but indirect relations between performance and high-level features. More importantly, indirect and direct effects on performance cannot be disentangled unless the components of which an object constitutes are separately assessed. For example, an object has to be separated from its background in order to study the effects of shape on performance. So far there has been little research on the features of the object itself because virtually all studies (except for Delorme et al., 2010, Elder & Velisavljević, 2009, Wichmann et al., 2010) have only looked into the overall statistics of the entire image. And although the degree and causality of the contribution of such high-level features to performance is debatable, there is still a broad range of other – both low-level and high-level – features for which it is unclear to what extent they affect detection and identification performance. Hence, a thorough test as to how low-level and high-level features affect performance and to what extent these effects depend on whole image, background, or object statistics, is needed.

Besides the aforementioned features, high-level concepts, such as emotions associated with an image or the object depicted therein, may also influence detection or identification. Animals, for example, may provoke a wide-spread set of emotions such as fear or emotional affect. Although it seems reasonable to assume that objects can induce specific emotions only when they are identified, in some cases emotional processing might not require detailed sensory information. Similar to the fast and automatic feed-forward brain mechanism that processes image features (Kirchner & Thorpe, 2006,

Thorpe, Fize & Marlot, 1996a, VanRullen & Thorpe, 2001a, VanRullen & Thorpe, 2001b), it has been suggested that another distinct brain mechanism (i.e., a sub-cortical route to the amygdala) processes fear-inducing stimuli (Adolphs, Gosselin, Buchanan, Tranel, Schyns & Damasio, 2005, Isbell, 2006, LeDoux, 1996, Morris, Ohman & Dolan, 1999) and incorporates an evolutionary innate bias towards threatening animals or objects (Deloache & Lobue, 2009, Lobue & DeLoache, 2008, LoBue & DeLoache, 2010, Ohman et al., 2001, Seligman, 1970). An alternative theory proposes that observers have acquired an attentional bias towards threatening stimuli by learning (Blanchette, 2006, Brosch & Sharma, 2005, Lipp, Derakshan, Waters & Logies, 2004, Mogg & Bradley, 1998, Tipples et al., 2002, Waters, Lipp & Spence, 2004). Nevertheless, the emotional valence tied to an object may accordingly help improve the speed and accuracy at which they are detected and identified. More importantly, we can again question to what degree emotions help to process and behaviorally react to objects. Relating this issue back to image statistics, it is important to control for confounds induced by image statistics when measuring effects of anxiety for objects presented in images. Studies on anxiety so far have only controlled for a small part of the differences in image statistics between non-threatening and threatening categories, and this factor may have caused seemingly conflicting results on anxiety.

Here we try to assess the weighted effects of a variety of both low level and high level image features on performance. As it is important to dissociate between detection and identification performance (Evans & Treisman, 2005), we have designed a rapid "animal"/"no animal" detection task that includes the identification of presented species after detection of an animal. We used images of animals with different levels of threat (e.g., snakes are of high threat and caterpillars are of low threat) to investigate the role of emotional valence and its interaction with image statistics. Besides subjective ratings of anxiety and affect per image, we use pupil size dynamics as an objective measure of emotional valence (e.g., Beatty & Lucero-Wagoner, 2000, Hess, 1975) and as reflection of activity in the (para)sympathetic nervous system (e.g., Steinhauer & Hakerem, 1992). In a separate analysis, animals were dissected from their background for comparison with their background features. With these measures, we will assess the following four questions: (i) Which features correlate with detection, identification, reaction times, and confidence, and which of these relations is strongest? (ii)

How do features of the object itself affect performance as compared to the statistics of the whole image? (iii) How do low- and high-level features correlate and to what extent do these correlations explain differences in performance across object categories? More specifically, does anxiety affect performance after controlling for covariance of image statistics? (iv) Is anxiety or emotional affect reflected in visible physiological signals? Specifically, does the pupil, an outwardly accessible physiological measure of neural function, reflect emotional valences?

6.2 Methods

6.2.1 Observers

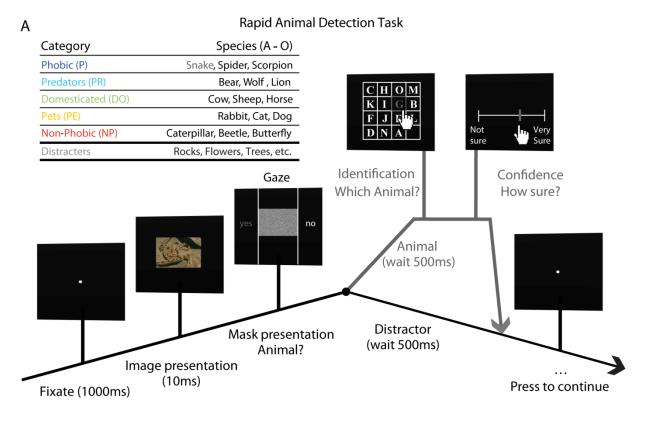
Eight observers (age range: 22-26, 2 female, 6 male) participated in the experiments. All had normal or corrected-to-normal vision, were naïve to the purpose of the studies, and gave informed written consent before the experiments. The experiments conformed to Institutional Guidelines for experiments with human subjects and to the Declaration of Helsinki.

6.2.2 Apparatus

Stimuli were presented on a 21 inch EIZO Flexscan CRT screen at a viewing distance of 70 cm. The display refresh rate of the screen was 100 Hz and the resolution was 1152x864 pixels. CIE color space coordinates (x,y) of the screen were (0.623, 0.344), (0.287, 0.609), and (0.151, 0.065) for the red, green, and blue guns, respectively. Stimuli were generated on an Optiplex 755 DELL computer, using Matlab (Mathworks, Natick, MA) and PsychToolbox (Brainard, 1997, Pelli, 1997) and EyeLink toolbox (Cornelissen et al., 2002) extensions. During the rapid animal detection experiment (see procedure), pupil diameter (size) and direction of gaze were tracked with an infrared sensitive camera (EyeLink 2000, SR Research, Osgoode, ON, Canada) at a sampling rate of 1000 Hz. The eye-tracker was (re-)calibrated before each experiment and after each break. Observers' head was supported by a chin- and forehead-rest to ensure steady viewing.

6.2.3 Stimuli and Procedure

Our study consisted of two separate experiments: a rapid animal detection and identification task (Figure 1A) and an emotional valence rating task (Figure 1B). Both experiments were taken on separate days. To prevent effects of learning due to feedback (the prolonged presentation for rating could give observers feedback about their performance, when done after the rapid presentation) and priming (rapid presentation could affect subsequent ratings and vice versa), substantial time elapsed between the two tasks (mean±sd: 248 ±110 days).



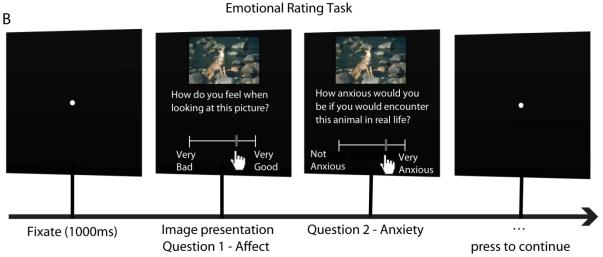


Figure 1. Paradigms and stimuli. (A) In the rapid presentation task observers were shown an image of either an animal or distracter for 10ms that was subsequently masked by a random noise image. Observers decided as fast as possible whether they had seen an animal or not by making an eye movement to the left or right part of the screen (text is here displayed as "yes"/"no" for reasons of legibility, but the actual display text was "no animal"/"animal"). Only for trials in which observers indicated to have seen an animal, they were asked to identify the species from a list (see grey arrow, arrangement of species is here illustrated by letters for reasons of legibility, but in the actual display full species names were shown) and could indicate their confidence on a ruler (0–100). **(B)** In the emotional valence rating task, observers were shown images of animals until response. Observers were asked to indicate their affect (-100–100) for the animal and their level of anxiety (0–100) if they would encounter the animal in a real life.

The first experiment was a rapid "animal"/"no animal" detection and identification task. Observers were presented with a variety of chromatic images of natural scenes that either did or did not contain an animal. Images were chosen from two databases (http://www.photolibrary.uk.com/; http://visionlab.ece.uiuc.edu/datasets.html) with a total of 708 animal pictures that were divided in five object categories (Figure 2A): Phobic animals (P), predators (PR), domesticated animals (DO), pets (PE), and non-phobic animals (NP). Each animal category was divided in three sub-categories of species (Phobic-animals: Snakes, spiders, and scorpions; Predators: Bears, wolves, lions; Domesticated animals: Cows, sheep, horses; Pets: Rabbits, cats, dogs; Non-phobic animals: Caterpillars, beetles, butterflies). The non-phobic category was intended to match phobic animals with respect to their gross visual appearance: in particular, snakes share visual features with caterpillars and have been used as visually similar categories earlier (Lobue & DeLoache, 2008). Based on previous literature, phobic animals and predators were subsumed as "threatening", all other categories as "non-threatening" hereafter (also see second experiment below for the justification of categorization). We further distinguished between the superordinate categories of mammals (predators, domesticated animals, and pets) and non-mammals, (phobic and non-phobic animals). The images containing no animals (distracters, DI) consisted of 383 natural scenes that included natural objects such as flowers, meadows, trees, mushrooms, fruits, vegetables, or stones (Figure 2B). Per observer, a total of 437 (62%) images of animals and 263 (38%) images of distracters were randomly chosen for presentation. Each animal species counted 28-30 images that for each experiment were randomly chosen from a database that contained between 42 and 68 images of each species. All images were 10° of visual angle in width and 7° in height. Pixel values of images were normalized such that the entire range (0-255) of possible luminance value was covered.

A rapid-detection trial (Figure 1A) started with the presentation of a fixation dot (0.8° diameter) for 1000ms, followed by an image for 10ms and a subsequent white-noise mask. Observers were instructed to decide as fast as possible whether the presented image contained an animal or not by making an eye-movement to either one side of the screen. Each side of the screen contained the text animal or no animal. The location of this text (i.e., left or right) was fixed per observer but

counterbalanced across observers. If observers reported having seen an animal – independent of whether their observation was correct – they were asked to identify the species of the animal. Five hundred milliseconds after the animal/no-animal decision, observers could choose the observed species from a 4 by 4 grid of 15 species-names with a computer mouse. The arrangement of species in the grid was randomized across observers. The identification response was followed by an indication of the observers' level of confidence on a ruler that scaled from 0 (not confident) to 100 (very confident about identification). The experiment continued with the next trial after a button press and observers could take a break after each block of 100 trials.

The second experiment consisted of an emotional valence rating task in which observers were asked to rate their level of affect and anxiety for images of animals that were shown in the rapid presentation task (Figure 1B). Observers fixated for 1000ms and were subsequently shown an image of an animal until response. The images were accompanied with a question and a ruler on which the observer could indicate their response with a computer mouse. The first question was designed to measure the observers' level of emotional affect for the animal. To the question "How do you feel when looking at this picture?" observers could indicate how they felt on a scale from -100 (very bad) to 100 (very good). The next question appeared after observers had rated their affect: "How anxious would you be if you would encounter this animal in real life?" Observers could indicate on a scale from 0 (not anxious) to 100 (very anxious) their level of anxiety for the animal. The next trial started after a button press.

6.2.4 Analysis

To separate the effects of the image as a whole, the target animal alone, and the background (non-target image area), author MH and a novel observer independently produced cut-outs of the image areas containing only the animal (Figure 3A). Cut-outs were consistent across both annotators and the overlap (intersect) of both cut-outs was considered the animal for further analysis. The following statistics were computed separately for the entire image, for the animal alone, and for the background alone (for extreme examples, see Figure 3B): mean and median luminance, mean luminance contrast,

mean color and luminance contrast between animal and background, mean radius of animal shape, variance in radius of animal shape (i.e., spikiness and elongation of shape), animal size, horizontal and vertical position of the animal, and distance between centre of gravity of animal and centre of image. Luminance contrast was computed as the standard deviation in luminance.

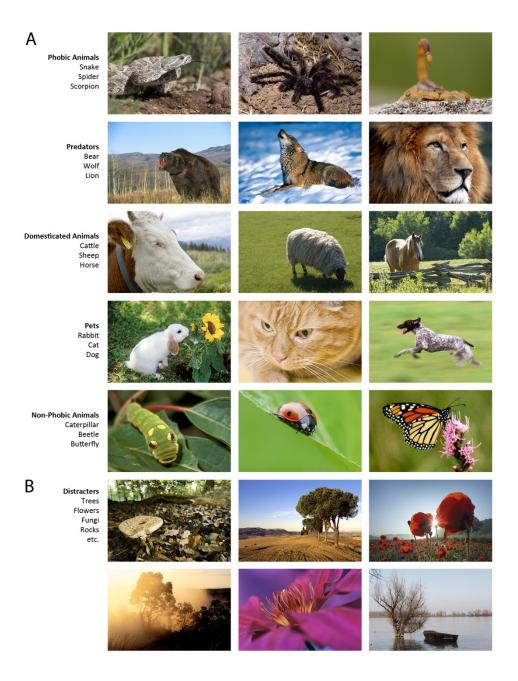


Figure 2. Image examples. (A) Examples of presented images of animal species (columns) per category (rows). **(B)** Examples of several non-animal distracter images from different categories.

We calculated the contrast in color between the animal and its background (hereafter: "color contrast animal-background") in the physiologically defined DKL color space (Derrington, Krauskopf, & Lennie, 1984). DKL space is spanned by three orthogonal axes, luminance, the difference between long (L) and medium (M) wavelenght cone exictations (L-M axis, aka "red-green" or "constant-blue"), and the difference between the short (S) wavelenght cone excitation and the sum of the other two cone excitations (S-(L+M), "blue-yellow" or "tritanopic confusion" axis). Color contrast animal-background then was defined as the distance between the mean position of the animal's pixels and the mean position of the background's pixel in DKL space, projected on the isoluminant plane. The similar measure without the projection on the isoluminant plane encompasses both luminance and color information and will be referred to as "color+luminance contrast animal-background".

6.2.5 Statistics and Notation

When we report multiple post-hoc comparisons across animal categories (e.g., for detection probabilities), we provide only noteworthy t-tests and correlations in the main text. To avoid overloading the main text, we in addition only report the effect that has the highest p-value (i.e., is "least significant" colloquially speaking). That is, a statement like "(t(7) > 1.90, p < 0.05, conf =)" is meant to imply that all *p*-values were below 0.05, all *t*-values above 1.90 and the degree of freedom at least 7. Full tables are given in the appendix. Main effects or interactions of ANOVAs as well as correlation are referred to as "significant", if their *p*-value is below a corrected alpha level that has been adjusted to an expected false-discovery rate (FDR) of 5% using the Benjamini & Hochberg (1995) method. Spearman correlations coefficients between behavioral data sets (i.e., performance and emotional valence) were based on the average per image. A general linear model (GLM) was created with the various image statistics and emotional valence as independent variables and the measures of performance as dependent variables. Another GLM used behavioral statistics and emotional valence as independent variables and pupil size as dependent variable. Input of the GLMs was z-score normalized. For some analyses, pupil size was normalized by subtracting the pupil size at image onset from pupil traces per trial, and subsequently dividing by the same value. This way the normalized

pupil size represented the proportion pupil size change with respect to image onset. Some analyses were based on the "absolute" pupil size (i.e., not normalized). Note that absolute pupil size is somewhat arbitrary as it depends on the settings of the gaze-tracking camera. These settings were set individually for each observer. To enable comparison within observers, settings were kept fixed across trials. To allow comparison of absolute data between observers the variation of settings across observers were kept to a minimum (mean and s.e.m. threshold for detection in the unit of the device were: 120.5 ±4.8 for pupil and; 228.9 ±2.5 for the cornea reflex). Since we are interested in *relative* rather than *absolute* reaction times, we define reaction times as the time between image onset and the moment the center of gaze crossed the 25% or 75% border of the screen (see Figure 1A). This is a more robust measure than saccadic onset because it reduces the probability to miss-categorize decisions based on initial mistake saccades that preceded but was directed to the other direction than the final decision side. This measure further incorporates time delays of such initial erroneous saccades and therefore includes a measure of decisional uncertainty. Trials with reaction times shorter than 50ms (5 trials of 5600) and reaction times longer than 1500ms (123 trials) were removed from analysis (2% of all trials).

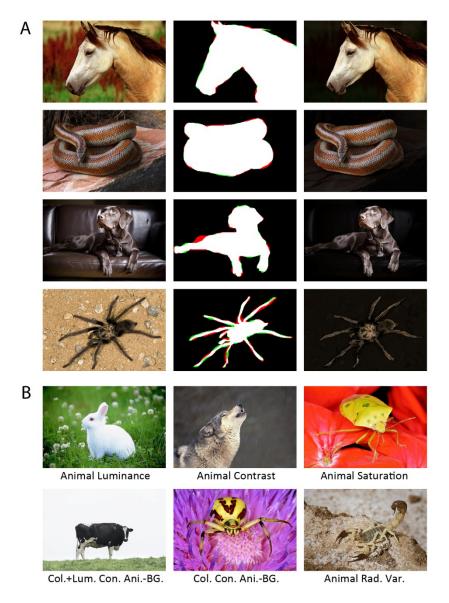


Figure 3. Cutout examples and extreme Image statistics. (A) Four examples (rows) of original animal images (first column) of which the animal was cut out (second column) and analyzed separately from its background (third column). Cutouts were created by two individuals. Green and red areas indicate non-overlapping parts of the individual cut-outs, white areas indicate overlap between the two individual cut-outs (see second column). **(B)** A variety of image statistics were computed for correlation with performance; the panel depicts examples of images with statistical extremes are shown. For example, the Animal Rad. Var. image shows an image in which the animal has a highly variable shape (i.e., not circular or rectangular but complex). Col. Con. Ani.-Bg. shows an image of an animal whose color strongly contrasts with its background.

6.3 Results

6.3.1 Performance, emotional valence, and image statistics per animal category

Threatening animals are generally believed to be detected and identified with high accuracy (Deloache & Lobue, 2009, Lobue & DeLoache, 2008, LoBue & DeLoache, 2010, Ohman et al., 2001, Seligman,

1970). Here we tried to replicate these findings by computing performance and emotional valence ratings per animal category. Of all animal pictures, 70%±15% were correctly detected (i.e., hits) and consequently 30%±15% missed. Of all distracter pictures, 73%±22% were correctly rejected, and consequently 27%±22% mistakenly induced a false alarm of an animal.

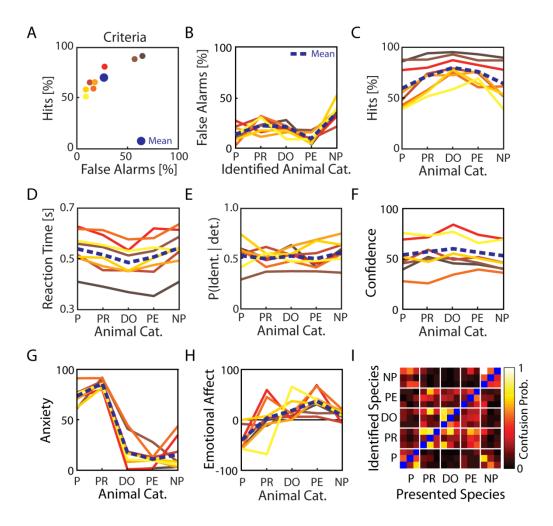


Figure 4. Detection and Identification Performance. (A) Percentage of hits (animal correctly detected) and false alarms (distracter mistaken for animal) for each of the 8 observers (colored points) and the average (blue). Observers clearly perform above chance (diagonal) and show similar performance despite variability in their criteria. (B) Percentage of false alarms by animal category (abbreviations see text); each observer is presented by a line (colors as in panel A). Note the similar pattern across observers. (C) Probability to correctly detect an animal (percentage of hits) by category (notation as panel B). (D) Mean reaction times per category. (E) Probability to correctly identify the animal's category, given it was correctly detected. (F) Mean confidence ratings (G) mean anxiety, (H) mean emotional affect per category. (I) Identification confusion matrix given an animal is detected correctly but incorrectly identified. Brighter patches indicate that species are more likely to be mixed-up with each other during identification. Matrix is normalized per presented species (3 per category) with the main diagonal excluded (blue), such that each entry gives the probability of a presented species (column) being confused with another species (row), excluding correct identifications. White lines delineate animal categories, order of species per category as given in Figure 1A. See Figure 1 for list of abbreviations of categories. Note that the lines in panel B through H are meant for illustration only and do not indicate a functional dependence.

Although observers differed in their subjective criteria (i.e., some observers were more liberal to mistakenly indicate a distracter as animal, Figure 4A), the performance per animal category was generally similar across observers (Figure 4B-F; for box plots, see Appendix). There was a significant main effect of animal categories on detection probabilities (hit rates, Figure 4C; F(4,7) = 12.62, p < 0.001; FDR adjusted alpha-level for all ANOVAs: 0.022). Detection probabilities were higher for predators (PR), domesticated animals (DO), and pets (PE), and were smaller for phobic animals (P) and non-phobic insects (NP). Remarkably, the threatening animals did not differ significantly from the non-threatening animals (t(38) = 1.41, p > 0.10, conf = -0.19-0.03). The mammalian animal categories of predators, domesticated animals, and pets did have higher detection probabilities than phobic animals (t(38) > 2.76, p < 0.01, conf = -0.24-0.04; see Appendix for all post-hoc comparisons). Domesticated animals and pets also had better detection performances than non-phobic animals (t(7) > 2.75, p < 0.05, see Appendix for confidence intervals). A very similar pattern was found for reaction times (Figure 4D; F(4,7) = 15.06, p < 0.001): Mammals were detected faster than phobic animals and non-phobic animals (t(7) > 2.95, p < 0.05). Since reaction times were qualitatively similar to accuracies across categories, data are not affected by a speed accuracy trade-off. Identification performance, calculated only for trials in which animals were correctly detected (i.e., the conditional probability identification given detection), showed no significant differences across animal categories (Figure 4E; F(4,7) = 1.47, p > 0.20). Unconditionally (i.e. without taking detection performance into account), identification showed differences across animal categories (F(4,7) = 3.73, p < 0.05), which also directly follows from the results on detection and identification conditioned on detection. Confidence ratings, however, depicted a pattern analogous to detection probabilities (Figure 4F, F(4,7) = 3.31, p < 0.05; t(7) > 2.64, p < 0.05). In general, data implied that detection was better (higher performance, faster reaction times) for mammals than for non-mammals. Once correctly detected, animal identification did not depend on category, while confidence followed a similar pattern as detection. This suggests a dissociation between detection and identification based on category.

Interestingly, the dependence of detection and confidence on category does not seem to follow an intuitive anxiety or emotional axis. To test whether the a priori categorization indeed matches the subjective experience of our observers, we assessed levels of anxiety and affect per animal category during the second, emotional valence rating experiment. As expected, anxiety ratings were substantially higher for threatening animals (i.e., phobic animals and predators) than for other animal categories (Figure 4G; F(4,7) = 101.39, p < 0.001; t(7) > 8.72, p < 0.001, for all comparisons between threatening and non-threatening animals). Emotional affect also differed significantly across categories (F(4,7) = 10.00, p < 0.001) and was negative for phobic animals (Figure 4H; t(7) = 4.87, p < 0.01, conf = 20.14-39.65), neutral for predators (t(7) = 0.25, p > 0.75, conf = 35.46-67.95) and domesticated animals (t(7) = 2.30, p > 0.05, conf = 49.73-68.73), and positive for pets (t(7) = 4.73, p < 0.01,conf = 59.45-78.36) and non-phobic animals (t(7) = 2.47, p < 0.05, conf = 50.19-58.70). These data indicate that anxiety and affect are distinct concepts and measurements. The overall pattern of anxiety across animal categories did neither seem to overlap with detection nor with identification performance. Surprisingly, no effect of anxiety on performance was seen across categories. This suggests that low-level features rather than higher-order emotional valences may underlie the differences in performance across animal categories. Interestingly, mammals were more easily mixedup with each other during identification, and the same held for phobic and non-phobic animals (Figure 4I; t(5) > 2.21, p < 0.05, for all comparisons of phobic animals and non-phobic animals versus mammals). At least for the species considered here, features or high-level categories (e.g., mammal) other than those defined by emotional valence contribute more strongly to identification errors.

To summarize, detection performance and identification performance were not necessarily determined by the mean level of threat or affection for the depicted animals per category. For instance, although observers had negative affect and high anxiety for phobic animals, these animals were still difficult to detect. Predators were also not easier to detect than non-threatening animals. These findings might indicate that differences in image statistics relate to the differences in performance across animal categories. To test this hypothesis, we next assess the relative contributions of emotional valence and image statistics to performance.

6.3.2 Correlations between performance, emotional valence, and image statistics

To assess how strong emotional valences and image statistics affected performance, we calculated for a subset of dependent variables whether they correlated with image statistics (Figure 5). Correlations with image statistics were only based on images with animals (n=708) and data were based on the average across observers per image. Correlations that include identification or confidence (in identification) were only based on images that at least one observer had correctly detected (n=681). To control for correlations across variables, we performed a partial correlation analysis for correlations between performance and emotional valences treating image statistics as controlling variables (for correlations between image statistics and emotional valences, see Figure 6). We only report the most noteworthy correlations (for scatter plots, see Appendix). We found no significant relations between anxiety and detection probability (r(706) = -0.06, p > 0.10), while correlations with identification probability (r(680) = -0.11, p < 0.01), reaction time (r(706) = 0.12, p < 0.01), and confidence (r(680) = -0.14, p < 0.001) were significant. Emotional affect similarly correlated with identification probability (r(680) = 0.10, p < 0.05), reaction time (r(706) = -0.11, p < 0.01), and confidence (r(680) = 0.12, p < 0.01).

Image statistics that correlated with detection included animal luminance (r(706) = 0.29, p < 0.001), animal contrast (r(706) = 0.21, p < 0.001), background contrast (r(706) = -0.19, p < 0.001), animal color saturation (r(706) = 0.20, p < 0.001), animal size (r(706) = 0.19, p < 0.001), and variance of shape radius (r(706) = 0.11, p < 0.01). Also color contrast animal-background and color+luminance contrast animal-background had significant effects on detection (r(706) = 0.20, p < 0.001; r(706) = 0.27, p < 0.001). All other performance variables (i.e., identification, reaction time, and confidence) had very similar correlations with the image statistics (p < 0.01).

The significant correlations of performance with image statistics were higher than the correlations with emotional valence for detection (t(10) = 3.10, p < 0.05, conf: 0.04-0.22), but not for the other performance variables (t(7) < 2.31, p > 0.05). The absolute correlations of image statistics that related to merely the animal cutouts were also higher than the correlations related to the whole image (t(22) = 5.59, p < 0.001, conf: 0.07-0.16) or only the background (t(22) = 3.55, p < 0.01, conf:

0.04-0.17). Correlations with detection were further higher than correlations with identification (t(14) = 5.39, p < 0.001, conf: 0.03-0.07). Similar to the correlations between performance and emotional valences, we also performed a partial correlation per image statistic with each performance variable while we controlled for correlations across image statistics. After this control, only background contrast, color+luminance contrast animal-background, size of animal, and variance of shape radius of animal correlated significantly with performance. As color+luminance contrast animalbackground incorporates information about luminance and saturation, it also correlates with these statistics (Figure 6). From this point of view, color+luminance contrast animal-background is an intermediate-level statistic and can therefore explain all the variance in performance without the help of the more low-level statistics of luminance and saturation. Indeed, when removing the contrast animal-background factors as covariates from the partial correlation, animal luminance and saturation significantly correlates with all performance variables except for reaction times (r(680) > 0.10,p < 0.01). As a final control, we created a GLM with image statistics and emotional valences as independent variables and performances as dependent variables (Table 1). For reasons of statistical power, we kept the model simple by only selecting the variables that significantly correlated with performance (Figure 5) and were indicated as independent factors by a factor analysis (see Appendix). The standardized beta coefficients were comparable with the correlations reported above (r(46) = 0.55,p < 0.001) but some remarkable deviations were observed. Despite that the GLM was statistically stricter than the correlation analysis, several image statistics and emotional valences that correlated significantly with performance were not significant predictors of performance in the GLM. Absolute beta coefficients of detection were not higher than identification (t(11) = 0.72, p > 0.20), beta coefficients of animal features were smaller instead of larger than background and whole image statistics (t(22) = 2.20, p < 0.05), and beta coefficients of image statistics were not higher than emotional valences (t(10) = 0.53, p > 0.50). It was also remarkable to see that anxiety was not a significant factor in the model to predict any performance variable. When comparing beta coefficients across observers (i.e., we performed another GLM on data per observer), emotional valences was a stronger predictor than anxiety of detection (t(7) = 5.53, p < 0.001) and reaction times (t(7) = 10.12,

p < 0.001). No other remarkable patterns were found across predictors. In sum, the overall pattern that emotional affect and several image statistics can decrease or improve performance remains evident after controlling for covariance across predictors.

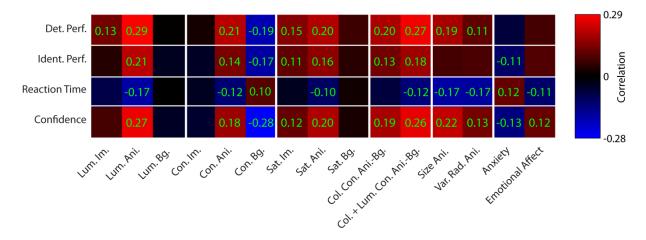


Figure 5. Correlations matrix. Matrix of correlations between performance variables (vertical axis), and image statistics and emotional valences (horizontal axes), r-values given as numbers. Only significant correlations (p smaller than an FDR-adjusted alpha level of 0.014) are presented with numbers. Most noteworthy correlations were those between animal (rather than image) statistics and performance, and absent or weakly negative correlations between anxiety and performance. Animal (i.e., the object of interest or target) statistics have much larger effects on performance than whole image statistics, and anxiety has a weak effect on performance, which is reversed relative to our prior expectation. See Figure 1 for list of abbreviations of categories. Abbreviations of image statistics: Rad. Var. = variance in radius of animal shape outline, Col. = color, Lum. = luminance, Con. = contrast, Ani. = animal, Bg. = background.

In conclusion, both image statistics and emotional valences contribute to the recognition of animals in natural images. Features generally related to the contrast between animal and background rather than the image as a whole contributed significantly to performance. In addition, background contrast decreased performance. Contrast in luminance and color between animal and background also affected performance, and this became particularly evident after controlling for correlations across image statistics. It has been suggested, however, that an animal is more likely to be presented in the center of the image because of pre-segmentation by the photographer that took the actual images (Wichmann et al., 2010). This bias could potentially underlie our finding that a stronger contrast between statistics of the object and background rather than the whole image increased performance because parts of the image that are presented in the fovea could be enhanced as compared to parts in the periphery. However, the animal's position varied and did not have any effect on detection

(r(706) = 0.04, p > 0.25) or identification performance (r(680) = 0.07, p > 0.05). Thus, the effect of low-level features on detection and identification performance was independent of object position. Levels of emotional valences – higher level features that are explicitly tied to the object – also significantly contributed to detection, identification, reaction time, and confidence. The negative effect of anxiety on performance was unexpected as literature generally reports a positive effect (see Introduction). Furthermore, anxiety was not a significant predictor in the GLM, probably because emotional affect co-varied with anxiety (see Figure 6) and explained more variance in performance than anxiety. Taken together, this indicates that anxiety only weakly affects the processing of objects and that emotional affect is a better predictor of performance. To get a better picture of whether anxiety is really involved in physiological processes related to object recognition, we next assess how they the pupil responses to the presentation of animal pictures.

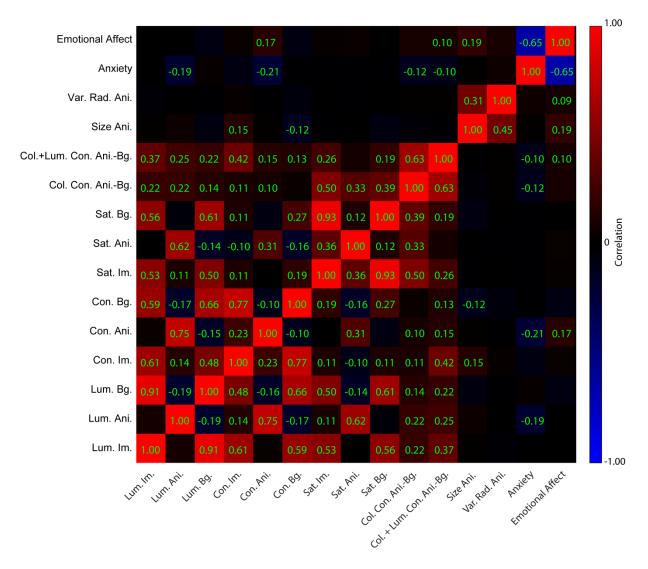


Figure 6. Correlation matrix. Matrix of correlations between image statistics and emotional valences. Only significant correlations (at FDR-adjusted alpha level of 0.020) are depicted.

6.3.3 Pupil size as a window to different stages of object processing and anxiety

To investigate at which stages specific factors have an effect on the neural processing of animal images, a physiological signal is needed that reflects such processing. We here quantify the relations between the time course of pupillary responses and performance, and emotional valences (for effects of image statistics on pupillary responses, see for example Alpern & Campbell, 1962, Gamlin, Zhang, Harlow & Barbur, 1998, Li, Liang & Sun, 2006, Tsujimura, Wolffsohn & Gilmartin, 2001, Young & Alpern, 1980). We computed correlations between pupil size and these dependent variables as a function of time around image onset (Figure 7A). All dependent variables correlated with pupil size

(p < 0.05) at some time point. Correlations with anxiety and identification peaked during intermediate time points (1000-1500ms), detection probability and confidence peaked during both the pupillary response (approximately 600ms; see Figure 7C-G for examples of the pupillary responses) and during later time periods (>1500ms), and correlations with reaction time and confidence peaked during periods the pupil dilation or constriction was fastest (i.e., around the pupillary response, when pupil changes were fast). Remarkably, anxiety, confidence, and reaction times correlated with normalized pupil size already before the onset of the trial (for possible interpretations, see Discussion). As a control for correlations among the behavioral variables, we performed a GLM with these variables as predictors and pupil size as dependent variable (Figure 7B). GLM beta coefficients were very similar to the correlation data (compare Figure 7A with 7B). To summarize, performance and emotional valence tied to the presented objects were reflected in the pupil.

We further checked for relations between average performance or emotional valence, and pupil size throughout the experiment. We calculated the mean of each dependent variable per observer over all trials and computed correlation coefficients between these means. Remarkably, the overall mean pupil size correlated with the mean anxiety rating per observer (r(6) = -0.81, p < 0.05). This negative correlation between mean pupil size and anxiety ratings could imply that the pupil size is an objective indicator of an observer's general anxiety level. Anxiety might not only be reflected in the mean pupil size but also in the amplitude of the pupillary response. However, the correlation between image statistics and anxiety ratings (see Figure 6) could indicate that the reported differences in pupil size are a result of image statistics rather than anxiety. To disentangle the effects of image statistics and emotional states on pupil size, we hypothesize that fear for an animal is a subjective concept that is not necessarily determined by a particular set of image features.

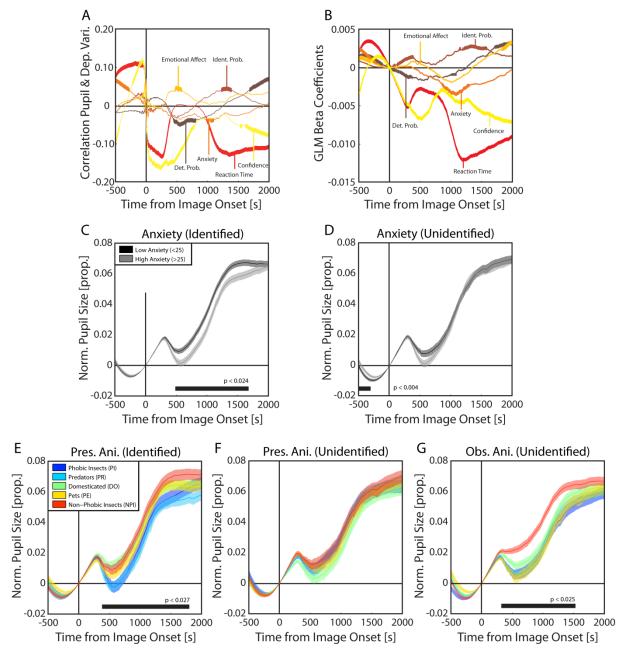


Figure 7. Pupil responses. Change in pupil size relative to image onset as a function of time after image onset. (A) Pupil size was correlated with each dependent variable at some point in time (thick lines represent periods of significant correlations at p < 0.05). (B) Beta coefficients of a GLM indicated how strong behavioral factors predicted pupil size. (C-G) Pupil size plotted per anxiety level for correctly identified animals (C), for unidentified animals (D), per presented animal category for identified animals (E), per presented animal category for unidentified animals (F), and per *observed* (i.e., perceived animal rather than presented) animal category for unidentified animals (G). In sum, anxiety is reflected in the pupil after correct identification of the animal. Significance levels for the plots where pupil size is presented per animal category (panels E-G) were based on comparisons between pooled trials of threatening animals on the one hand and pooled trials of non-threatening animals on the other hand. High and low anxiety levels in panels C and D were based on splitting the respective data at the median, such that each level (high anxiety, low anxiety) contains the same number of trials.

We therefore argue that if the pupil shows a clear response to threat of the presented animal while the animal could not be consciously identified, image statistics may underlie effects of anxiety

on pupil size. On the contrary, if the pupil only shows a response to threatening animals when identification was successful but not when unsuccessful, image statistics do not underlie the effects of anxiety on pupillary responses. To test this hypothesis, we performed several additional analyses of the effects of anxiety on pupil size as a function of time around image onset (Figure 7C-G). First, we computed pupil size for correctly identified animals that were either rated with high or low anxiety (Figure 7C). The pupil responded with a larger amplitude (i.e., more negativity in the signal) and with an overall lower pupil size after ~600ms to images of animals rated with high anxiety. We further computed pupillary responses for unidentified (i.e., correctly detected but incorrectly identified) animals per anxiety level of the presented animal (Figure 7D). If animals were not correctly identified, the pupil did not show a significant difference between low and high threatening animals. The level of threat per animal category also determined the amplitude of pupillary responses and the subsequent overall pupil size for correctly identified animals (Figure 7E). Threatening animals (i.e., phobic animals and predators) induced larger pupillary amplitudes at ~600ms than non-threatening animals. Similar to the anxiety levels, this effect was only pertinent for animals that were correctly identified because unidentified animals induced no such difference in pupil size across animal categories (Figure 7F). In turn, there is a significant effect if pupil traces are sorted per subjectively observed (i.e., perceived animal as indicated by the observer) rather than truly presented animal category (Figure 7G). These results indicate that the effects of anxiety on pupil size only occur after proper identification of the presented animal. This is support for the notion that anxiety is a separate mechanism that operates on object processing independent of image statistics.

We found evidence that anxiety contributes to performance and is reflected in pupillary responses after conscious identification of the animal. The degree of an observer's overall anxiety for depicted animals is also reflected in the average size of the pupil. In other words, both short-term anxiety and long-term anxiety are reflected in the pupil (for details, see Discussion), and short-term anxiety only occurs after the activation of a higher object representation.

6.4 Discussion

6.4.1 Performance relies on contrasts between object and background

Successful detection of animals in images mainly relied on increased levels of image luminance, animal saturation, animal size, animal shape, color and luminance contrast between animal and background, and on decreased levels of background contrast. Except for image luminance and background contrast, features predominantly tied to the target object seem to contribute to performance; a phenomenon that most studies have disregarded because they did not aim at distinguishing between effects of object features and overall image features. It is unlikely that this phenomenon is explained by the overall foveal rather than peripheral position of animals because of lacking effects of position on performance. Although this could be the result of lacking variance in animal position (animal center of gravity was 1.0± 0.6 deg; image size was 10 by 6.7 deg), it has been shown that the categorization of animals that are presented in the near-periphery rather than the fovea is still highly accurate (±90% at 10°; Thorpe, Gegenfurtner, Fabre-Thorpe & Bülthoff, 2001). Hence, we suggest that performance is predominantly affected by object features and their contrast with their backgrounds rather than overall image features. Obviously, the background alone cannot provide definite proof on the presence or absence of an animal for any given image, though – especially when the distracter database is carefully selected and the potential habitat of all species under consideration is visually similar. Nonetheless the background could in principle still be probabilistically informative on the presence or absence of an animal and may even aid identification (say, if the background is predominately green, the animal is probably more likely a cow than a whale), rendering the relative importance of target features a non-trivial. Scene gist and context can be important factors for rapid categorization (Joubert, Fize, Rousselet & Fabre-Thorpe, 2008, Joubert, Rousselet, Fize & Fabre-Thorpe, 2007). In addition, we found that background luminance contrast negatively affected performance. It could well be that the presence of high luminance contrasts in the background "distracts" the visual processing of the object. Nonetheless, image features that were tied to the segmented object or ground depicted correlations with performance. While clearly beyond the scope of the present study, using targeted feature manipulations ('t Hart, Schmidt, Klein-Harmeyer &

Einhäuser, 2011) to address the question as to whether these results are an effect of background per se (e.g., by inducing higher-order contrasts), a general property of natural scenes or merely an effect of the chosen databases will be an interesting issue for further research.

6.4.2 Moderate contributions of all image features to performance

We found that a variety of features had significant effects on performance during the task to detect and identify animals as fast as possible after the rapid presentation of natural images. If our visual system is indeed tuned for processing natural stimuli particular efficiently (Barlow, 1961) and effortlessly (Li, VanRullen, Koch & Perona, 2002), it seems natural that those features represented abundantly early in the visual hierarchy contribute especially to rapid processing. However, each of the features investigated here, explained only a moderate percentage of variance in performance. Despite the considerable number of image features covered, there are of course many other features left untested that might explain the remaining variance. We expect that these will be high-level features that are characteristic or diagnostic for the objects (Delorme et al., 2010) and relate to responses higher up in the visual processing hierarchy. In addition, higher areas may also be involved in rapidly forming initial hypotheses about objects that are only later refined by processing in earlier areas (Hochstein & Ahissar, 2002). In any case, a great deal of the unexplained variance might still be caused by the frequency of feature appearance (expertise), by individual preferences for specific features, and to noise in the visual system. For example, it is proposed that observers are flexible when it comes to learning to use new features for categorization (Schyns, 1998, Schyns, Goldstone & Thibaut, 1998). Such flexibility is necessary because the level as to when a feature is informative depends on the task. When for instance only simple features are attended during a task, higher-order information could go lost despite its usefulness. Attention is another factor that could strongly determine how we process object. Although the detection of objects does not necessarily require attention (Li et al., 2002), attention may still modulate performance, in particular for identification (Evans & Treisman, 2005). Similarly, fluctuations in arousal and alertness are likely contributors to trial-to-trial variability, which will remain largely unexplainable based on image features alone. Although image features alone might not explain image processing in full, our study provides a first quantification of how they interact with each other, with object representations, and with high-level processes for rapid detection and identification of objects.

6.4.3 Relative importance of luminance and luminance contrast to performance

Whereas we find an important role of luminance and contrast features, previous studies reported relatively small effects of luminance and contrast on performance as compared to other features (Elder & Velisavljević, 2009, Macé et al., 2010, Nandakumar & Malik, 2009). These results may look paradoxical to ours but there are three possible explanations for this. (I) Some of the previous studies implied that high-level features such as shape and texture affect performance more strongly than luminance. However, shape and texture are higher-level features that depend on low-level features such as luminance and contrast. Hence, it is difficult to make assumptions about their separate contributions to performance as they were not independently assessed. (II) Other studies found a high object recognition performance even after decreasing image luminance or contrast. We would like to stress that the robustness of such performance after degradation of images does not necessarily have to relate to the impact of image features on performance. Very low levels of luminance or contrast might still be successfully extracted and employed by our visual system and enhance performance. For example, objects in isoluminant images are hard to recognize but only a very small deviation from the equilibrium of isoluminance substantially recovers recognition performance (Liebmann, 1927, Schiller, Logothetis & Charles, 1991, West, Spillmann, Cavanagh, Mollon & Hamlin, 1996). (III) In contrast to previous studies, we accounted for contrast of the object separated from its background. As we find that background contrast rather than image contrast correlated with performance, studies that manipulated contrast of the whole image could possibly have found larger effects on performance if only the object or background would have been manipulated separately. In sum, this suggests that luminance and luminance contrast are not unimportant per se, but their importance may depend on relations to higher order features, on other features available, and on the objects they constitute.

6.4.4 Dissociation between detection and identification

Though many image statistics relate to both detection and identification performance, several other statistics relate to only one of them. In contrast to detection, identification was not significantly affected by animal contrast, object size, and variance of object radius. Several other significant correlations with identification were weaker than with detection. This dissociation, however, is subtle and it is hard to draw conclusions regarding distinct visual processes or stages that could separately establish successful detection and identification of objects. However, it has been proposed that correct detection and classification of animals may rely on the analysis of low-level image features rather than on a high-level object and scene representations (e.g., Evans & Treisman, 2005). Importantly, note that detection is not an equivalent but perhaps a prerequisite of identification. Observers might be able to classify an object into a category without being able to identify and thus report which exact object they have seen (also see our animal species mix-up results in Figure 4I), while successful identification cannot occur unless the object as a whole is correctly detected. As such, it is tempting to suggest that after correct detection and the extraction of the object from its background, image features – especially that of object's shape – might lose their usefulness with respect to object processing. That object and background/scene information is processed by distinct visual areas (Epstein, Graham & Downing, 2003, Epstein & Kanwisher, 1998) elegantly concurs with this idea. In the context of these dissociations, our data therefore stress the importance to distinguish between detection and identification in experimental designs.

6.4.5 Weak and reversed contribution of anxiety to performance

Anxiety induced by the animal depicted in the presented images slightly correlated with performance. A partial correlation – controlling for image statistics – revealed a negative effect of anxiety on reaction times and confidence (i.e., high fear reduced performance). A GLM showed that emotional affect rather than anxiety was a significant predictor of performance. These results appear to conflict with several earlier studies, which found that objects that induce fear or negative feelings facilitated processing. However, there are two possibilities that may explain this apparent discrepancy. First,

stronger effects of image features on performance shadowed effects of anxiety when performance was assessed per animal category. This could explain the contrasting results of recent studies that report significant fear-induced increases in performance for threatening animals in some cases (e.g., Lobue & DeLoache, 2008, Ohman et al., 2001) and none or non-specific increase in other cases (e.g., Lipp et al., 2004, Tipples et al., 2002). When categorizing a small number of images into the categories "fearful" or "non-fearful" it is conceivable that one or more low-level image features are overrepresented in one of these categories and eventually lead to differences in performance across categories. If this confound is not controlled for, a facilitation of processing by low-level features may shadow or even reverse the intended effect of threat. Second, it is possible that the advantage does not arise for threatening animals as such, but rather for them being mammals. An advantage for mammals might be based on our increased expertise with this category, which in turn yields better performance. Mammals also have very large and salient eyes and this may too facilitate detection (Delorme et al., 2010). As such, some of the earlier studies may have confounded threat with expertise. Including expertise as factor in addition to threat and low level features may thus be an interesting line of future research.

The very short presentation times used in the current design may additionally have played an important role for the presence of fear-related effects. Many of the previous studies that report an effect of anxiety used a visual-search paradigm in which there is sufficient time for the deployment of attention to the stimuli. It could be that attention cannot be deployed successfully if images are presented very briefly. There is some evidence that attention is crucial for the processing of fear-relevant stimulus as reported in a recent fMRI study. Alpers et al. (2009) found that attention is important for the activation of the amygdala, a brain structure important for the processing of fear-relevant stimuli, during the presentation of spiders. As such, very brief presentation times might not be sufficient to trigger attention related processes and therefore might not activate the mechanism that enhances the processing of fear-relevant stimuli. Nevertheless, even for brief presentations times, our results depict effects of anxiety on performance and agree with the view that anxiety acts as a separate mechanism by modulating the processing of and responses to threatening objects.

6.4.6 Pupil size changes reflect anxiety

Changes in pupil size have been related to a variety of psychological mechanisms including responses to the onset of novel and/or alerting stimuli (e.g., Andreassi, 2000, Beatty & Lucero-Wagoner, 2000, Hakerem, 1967, Hess, 1975, Janisse, 1977, Kahneman, 1973). Here we have assessed how the pupil responses to onset of images that induced different levels of anxiety and that contained a broad range of image features. We find that two types of how anxiety is reflected in the pupil: (I) short-term anxiety (i.e., temporary state of anxiety) was reflected in the pupil as frightening animals induced larger pupillary responses (i.e., more negativity in the amplitude) to the image, and (II) long-term anxiety (i.e., the overall level of anxiety of an individual) was reflected in the average pupil size throughout the experiment as this correlated with the mean anxiety ratings of observers. These finding agree with a previous study that showed increased pupillary response amplitudes for panic disorder patients (Kojima, Shioiri, Hosoki, Kitamura, Bando & Someya, 2004), but also disagrees with another study that reported decreased amplitudes for normal observers with an increased state-anxiety. As Bitsios et al. (2002) used auditory stimuli that were sometimes paired with unconditioned shocks, it could be that the experimental design underlies these results. Indeed, such aversive unconditioned stimuli may have other effects on pupillary responses than non-aversive stimuli (e.g., Reinhard & Lachnit, 2002a). Furthermore, our results show that mean anxiety ratings were higher for observers with smaller pupil sizes. This is unexpected as it is generally reported that raised levels of anxiety increase the pupil size (Nagai et al., 2002, Simpson & Molloy, 1971). Thus, in contrast to previous reports, our data suggest that an observers' increased level of anxiety is reflected in an overall decrement of pupil size. Unlike these previous studies, which used standardized psychological questionnaires to assess state- and trait-anxiety or audience anxiety (Simpson & Molloy, 1971), we here based the anxiety level on subjective image ratings, as our primary aim was to obtain the relative anxiety on an image-by-image basis. Whether higher general anxiety levels according to standardized test yields a different internal mapping of anxiety to our 0-100 scale or whether image-based anxiety ratings are fundamentally different from other types of anxiety remains an open issue. It is known, however, that both state and trait anxiety affect other physiological signals, such as heart rate (Kantor,

Endler, Heslegrave, Kocovski, 2001). It is therefore not unlikely that the pupil is similarly affected by both mechanisms and that we have at least measured some form of anxiety. As several months elapsed between pupil size and anxiety measurements (see Stimuli and Procedure - Methods), it is likely that we have measured effects of trait rather than state anxiety because the former remains stable over time (e.g., Rule & Traver, 1983). Nonetheless, state anxiety might have changed between these moments. Such changes could potentially increase variance and therefore decrease correlations between anxiety and performance, or anxiety and pupil measurement. Although this hypothesis is interesting of its own right and may merit further investigation, it still cannot account for the seemingly contrary effects of anxiety on pupil size or performance.

Based on the relative image-by-image ratings we can speculate on some of the mechanisms underlying the relation between anxiety and pupillary control. Activation of the parasympathetic nervous system (PSNS) is responsible for contracting the pupil at short intervals (600ms) while an activated sympathetic nervous system (SNS) tends to dilate the pupil over longer time intervals (1100ms) (e.g., Steinhauer & Hakerem, 1992). The increased contraction and larger pupillary response amplitudes could thus be a result of an overall activation of the PSNS through anxiety-related processes. Such a relation between anxiety and the PSNS is not implausible as there are known neuronal connections between amygdala and locus coerules (Bitsios et al., 2002) – both fear mediating nuclei (Charney et al., 1995, Davis, 1992). These have projections to the midbrain Edinger-Westphal nucleus which is a parasympathetic control site for pupillary contraction (e.g., Einhäuser et al., 2008b, Loewenfeld, 1993). Our results do not rule out the possibility that these connections are part of the subcortical "quick and dirty" pathway that has been proposed to be responsible for the processing of conditioned threatening stimuli (LeDoux, 1996).

Also remarkable were the correlations between confidence or reaction time, and pupil size before image onset and around the pupillary response. We suppose this is most likely the result of general vigilance. As people have an increased level of attention and/or arousal, the pupil is subject to more variance and reacts more vigorously to visual changes. This would lead to faster pupillary responses and a faster settling back of the pupil size to its baseline. Indeed, we find that the

correlations were most evident during the phases of dilation or contraction, thus during periods the pupil size was either decreasing or increasing at high speed (0-500ms and 1200-2000ms). It would be interesting to study the neurological basis of such vigilance effects and related pupillary dynamics in more detail.

6.5 Conclusion

To summarize, features that pop-out the object from its background mainly accounted for both detection and identification performance. Furthermore, high image luminance increased and high background contrast decreased performance. Anxiety only weakly and negatively affected performance although it pupil responses to fearful images showed that anxiety is a valid concept that changes neural processing. We further reported a slight dissociation between how particular image features affect detection and identification performance separately. These results indicate that future studies on object processing should strongly control for relative effects of image features, intercorrelations, and their relation to a variety of performance measures.

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6.8 Appendix – Supplementary analyses

Analyzing data separately by observer (Figure 8A-D) or pooling across observers (8E-H) yields qualitatively similar results to the individual data presented in Figure 4. Post-hoc tests including the respective test-statistics and confidence intervals for all statistical analysis are provided in Table 2. Inspecting the raw data underlying the correlations between performance measures and features (image statistics and emotional valences) individually (Figure 9) verifies that the reported correlations are not dominated by outliers (cf. Figure 5). A factor analysis revealed groupings of features (Figure 10). Variables that were largely redundant with other variables - namely background luminance (grouped with background contrast and image luminance, red group in Figure 10) or did by themselves not correlate to any performance measure (image contrast, background saturation) were excluded from subsequent GLM analysis.

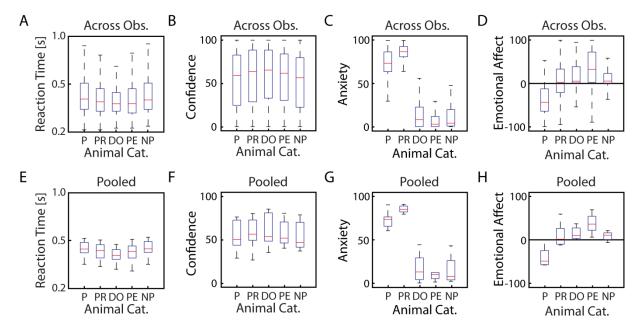


Figure 8. Performance details. Box-plots of the data shown in figure 4: median (red line), 25th and 75th percentiles (blue boxes), and extent of the data without outliers (black dashed lines). (**A-D**) Data across observers, (**E-H**) pooled data. (**A,E**) reaction times, (**B,E**) confidence ratings, (**C,F**) anxiety ratings (**D,G**) emotional affect.

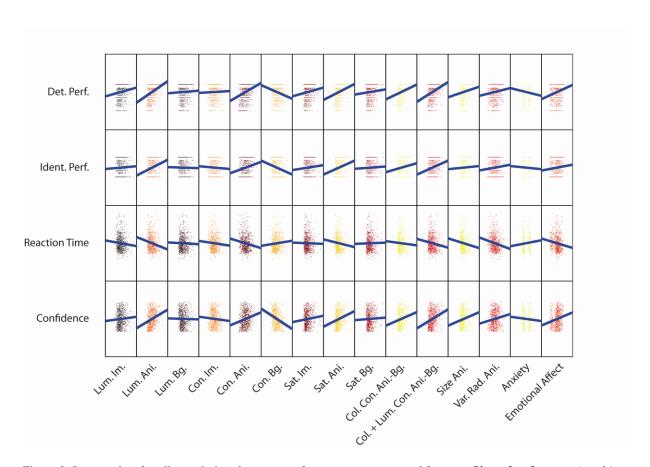


Figure 9. Scatter-plots for all correlations between performance measures and features. Plots of performance (y-axis) as a function of image statistics or emotional valences (x-axis). Each data point indicates the average performance per image. Data was z-score normalized and each line that indicates an axis corresponds to z-score values between -10 and 10. Blue lines are fitted linear regressions. Order of features and performance measures as in Figure 5.

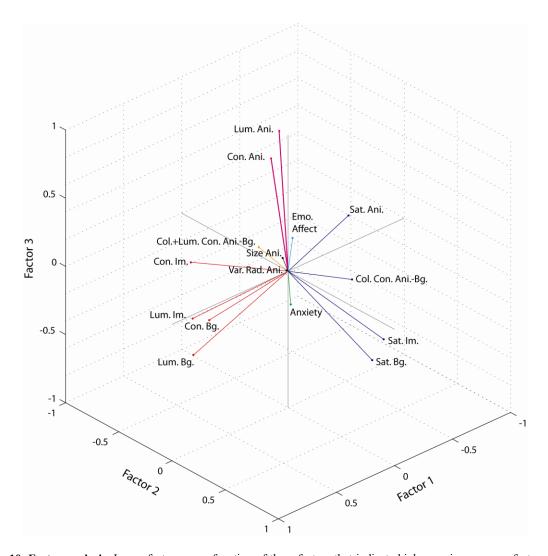


Figure 10. Factor analysis. Image features as a function of three factors that indicate high covariance across features. The colors indicate groups of image features that covariate. Abbreviations as in figure 5.

6.9 Tables

Table 1. GLM – Effects of image statistics and emotional valences on performance (significant predictors are printed in bold).

55	,	8	1 3	(0)	1	1

	Detecti	on	
Variable	Beta	T stat.	P value
Lum. Im.	0.214	3.97	< 0.001
Lum. Ani.	-0.021	0.33	> 0.50
Con. Ani.	0.148	2.92	< 0.01
Con. Bg.	-0.271	6.25	< 0.001
Sat. Im.	-0.044	0.86	> 0.20
Sat. Ani.	0.126	2.55	< 0.05
Col. Con. Ani	0.020	0.34	> 0.50
Bg.	0.020	0.54	> 0.50
Col.+Lum.	0.163	2.87	< 0.01
Con. AniBg.	0.103	2.07	~ 0.01
Size Ani.	0.082	2.22	< 0.05
Var. Rad. Ani.	0.059	1.63	> 0.10
Anxiety	0.030	0.66	> 0.50
Emotional	0.131	2.89	< 0.01
Affect	0.131	2.07	~ 0.01

I	dentifica	tion	
Variable	Beta	T stat.	P value
Lum. Im.	0.122	2.11	< 0.05
Lum. Ani.	-0.020	0.29	> 0.75
Con. Ani.	0.077	1.42	> 0.10
Con. Bg.	-0.248	5.27	< 0.001
Sat. Im.	-0.029	0.53	> 0.50
Sat. Ani.	0.152	2.89	< 0.01
Col. Con. Ani	-0.064	1.02	> 0.20
Bg. Col.+Lum. Con.			
	0.176	2.90	< 0.01
AniBg.			
Size Ani.	-0.003	0.08	> 0.75
Var. Rad. Ani.	0.070	1.81	> 0.05
Anxiety	-0.005	0.10	> 0.75
Emotional Affect	0.025	0.51	> 0.50

Reaction	Times
Rata	Тс

Variable	Beta	T stat.	P value
Lum. Im.	-0.145	2.49	< 0.05
Lum. Ani.	-0.034	0.50	> 0.50
Con. Ani.	-0.043	0.79	> 0.20
Con. Bg.	0.112	2.38	< 0.05
Sat. Im.	0.065	1.18	> 0.20
Sat. Ani.	-0.086	1.62	> 0.10
Col. Con. Ani Bg.	0.024	0.37	> 0.50
Col.+Lum. Con. AniBg.	-0.060	0.98	> 0.20
Size Ani.	-0.069	1.78	> 0.05
Var. Rad. Ani.	-0.126	3.26	< 0.01
Anxiety	-0.030	0.61	> 0.50
Emotional Affect	-0.061	1.24	> 0.20

Confidence

	001111001		
Variable	Beta	T stat.	P value
Lum. Im.	0.202	3.78	< 0.001
Lum. Ani.	-0.047	0.75	> 0.20
Con. Ani.	0.092	1.83	> 0.05
Con. Bg.	-0.358	8.21	< 0.001
Sat. Im.	-0.062	1.22	> 0.20
Sat. Ani.	0.150	3.05	< 0.01
Col. Con. Ani	-0.007	0.12	> 0.75
Bg.	-0.007	0.12	× 0.73
Col.+Lum. Con.	0.210 3.71	3.71	< 0.001
AniBg.	0.210	3.71	
Size Ani.	0.108	2.95	< 0.01
Var. Rad. Ani.	0.068	1.88	> 0.05
Anxiety	0.053	1.15	> 0.20
Emotional	0.133	2.90	< 0.01
Affect	0.133	2.90	~ 0.01

Table 2. Post-hoc comparisons across animal categories. Only the post-hoc tests for significant differences as indicated by an ANOVA are depicted. Significant differences (p<0.05) are highlighted in **BOLD** text.

Detection	Probability
Detection	1 1 0 0 d 0 111t y

<i>p</i> -values	Phobic	Predators	Domesticated	Pets
Predators	0.0046			
Domesticated	0.0022	0.0194		
Pets	0.0045	0.0933	0.2245	
Non-phobic	0.1409	0.0599	0.0011	0.0285
t-statistic	Phobic	Predators	Domesticated	Pets
Predators	4.0910			
Domesticated	4.6858	3.0180		
Pets	4.1098	1.9414	-1.3321	
phobic	1.6598	-2.2419	-5.3225	-2.7500
confidence				
intervals	Phobic	Predators	Domesticated	Pets
Predators	0,0510/0.1909			
Domesticated	0.1003/0.3045	0.0176/0.1453		
Pets	0.0692/0.2568	-0.0092/0.0933	-0.1093/0.0305	
phobic	-0.0191/0.1089	-0.1562/0.0042	-0.2274/-0.0875	-0.2197/-0.0166
Reaction times	(all)			
<i>p</i> -values	Phobic	Predators	Domesticated	Pets
Predators	0.0105			
Domesticated	0.0001	0.0025		
Pets	0.0042	0.2656	0.0955	
phobic	0.6386	0.0215	0.0007	0.0159
t-statistic	Phobic	Predators	Domesticated	Pets
Predators	-3.4605			
Domesticated	-8.5654	-4.6003		
Pets	-4.1774	-1.2099	1.9260	
phobic	0.4907	2.9485	5.8047	3.1620
confidence				
intervals	Phobic	Predators	Domesticated	Pets
Predators Predators	-0.0389/-0.0073			
Domesticated	-0.0687/-0.0390	-0.0465/-0.0149		
Pets	-0.0496/-0.0137	-0.0253/0.0082	-0.0050/0.0494	
phobic	-0.0158/0.0241	0.0054/0.0491	0.0343/0.0816	0.0090/0.0625
1	0.0120/0.0211	3.000 1/0.01/1	3.00 10/0.0010	0.0020/0.00 0

<i>p</i> -values	Phobic	Predators	Domesticated	Pets
Predators	0.0136			
Domesticated	0.0006	0.0028		
Pets	0.0002	0.5411	0.0885	
phobic	0.9107	0.0146	0.0003	0.0220
t-statistic	Phobic	Predators	Domesticated	Pets
Predators	-3.2719			
Domesticated	-5.9072	-4.4919		
Pets	-7.3335	-0.6423	1.9774	
phobic	-0.1163	3.2241	6.6696	2.9295
confidence				
intervals	Phobic	Predators	Domesticated	Pets
Predators	-0.0571/-0.0092			
Domesticated	-0.0944/-0.0404	-0.0523/-0.0162		
Pets	-0.0545/-0.0279	-0.0379/0.0217	-0.0051/0.0575	
phobic	-0.0257/0.0233	0.0085/0.0553	0.0427/0.0896	0.0077/0.0723
Confidence				
<i>p</i> -values	Phobic	Predators	Domesticated	Pets
Predators	0.0059			
Domesticated	0.0001	0.0838		
Pets				

confidence				
intervals	Phobic	Predators	Domesticated	Pets
Predators	-2.1860/8.6082			
Domesticated	2.2756/9.9036	-3.5802/9.3371		
Pets	-2.8243/7.7106	-6.9180/5.3821	-8.3628/1.0700	
phobic	-5.2042/3.5173	-10.3915/2.2824	-11.0435/-2.8225	-5.8813/-0.6919

0.0336

2.0149

0.7739

-2.6358

Predators

0.0003

-2.4636

-6.6331

Domesticated

0.0043

Pets

-4.1559

phobic

t-statistic

Predators

Pets

phobic

Domesticated

0.4892

Phobic

3.9023

8.2335

5.1675

0.7298

Anxiety				
<i>p</i> -values	Phobic	Predators	Domesticated	Pets
Predators	0.0060			
Domesticated	0.0001	0.0000		
Pets	0.0000	0.0000	0.1430	
phobic	0.0000	0.0000	0.7555	0.5044
t-statistic	Phobic	Predators	Domesticated	Pets
Predators	3.8816			
Domesticated	-8.7288	-14.2350		
Pets	-12.1246	-37.7291	-1.6498	
phobic	-13.0446	-12.8014	-0.3238	0.7036
confidence	 .			_
intervals	Phobic	Predators	Domesticated	Pets
Predators	4.9700/20.4646			
Domesticated	-71.020/-40.743	-79.994/-57.203		
Pets	-74.762/-50.360	-79.996/-70.560	-16.253/2.894	
phobic	-68.482/-47.464	-83.748/-57.633	-17.366/13.182	-10.830/20.005
Emotional affec	.+			
	Dhohio	Dradatora	Domosticated	Data
p-values	Phobic	Predators	Domesticated	Pets
Predators	0.0259		Domesticated	Pets
Predators Domesticated	0.0259 0.0009	0.4824		Pets
Predators Domesticated Pets	0.0259 0.0009 0.0007	0.4824 0.0225	0.1478	
Predators Domesticated	0.0259 0.0009	0.4824		Pets 0.0101
Predators Domesticated Pets	0.0259 0.0009 0.0007	0.4824 0.0225	0.1478	
Predators Domesticated Pets phobic	0.0259 0.0009 0.0007 0.0008	0.4824 0.0225 0.7212	0.1478 0.2749	0.0101
Predators Domesticated Pets phobic t-statistic	0.0259 0.0009 0.0007 0.0008 Phobic	0.4824 0.0225 0.7212	0.1478 0.2749	0.0101
Predators Domesticated Pets phobic t-statistic Predators	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155	0.4824 0.0225 0.7212 Predators	0.1478 0.2749	0.0101
Predators Domesticated Pets phobic t-statistic Predators Domesticated	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024	0.4824 0.0225 0.7212 Predators	0.1478 0.2749 Domesticated	0.0101
Predators Domesticated Pets phobic t-statistic Predators Domesticated Pets	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024 5.7372	0.4824 0.0225 0.7212 <i>Predators</i> 0.7417 2.9147	0.1478 0.2749 Domesticated	0.0101 Pets
Predators Domesticated Pets phobic t-statistic Predators Domesticated Pets	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024 5.7372	0.4824 0.0225 0.7212 Predators 0.7417 2.9147 0.3716	0.1478 0.2749 Domesticated	0.0101 Pets
Predators Domesticated Pets phobic t-statistic Predators Domesticated Pets phobic	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024 5.7372	0.4824 0.0225 0.7212 <i>Predators</i> 0.7417 2.9147	0.1478 0.2749 Domesticated	0.0101 Pets
Predators Domesticated Pets phobic t-statistic Predators Domesticated Pets phobic confidence	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024 5.7372 5.6226	0.4824 0.0225 0.7212 Predators 0.7417 2.9147 0.3716	0.1478 0.2749 Domesticated 1.6270 -1.1845	0.0101 Pets
Predators Domesticated Pets phobic t-statistic Predators Domesticated Pets phobic confidence intervals	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024 5.7372 5.6226	0.4824 0.0225 0.7212 Predators 0.7417 2.9147 0.3716	0.1478 0.2749 Domesticated 1.6270 -1.1845	0.0101 Pets
Predators Domesticated Pets phobic t-statistic Predators Domesticated Pets phobic confidence intervals Predators	0.0259 0.0009 0.0007 0.0008 Phobic 2.8155 5.5024 5.7372 5.6226 Phobic 3.4930/40.1280	0.4824 0.0225 0.7212 Predators 0.7417 2.9147 0.3716 Predators	0.1478 0.2749 Domesticated 1.6270 -1.1845	0.0101 Pets

7. Chapter 7

Pupil size reflects familiarity and predicts later retrieval success during encoding of declarative memories

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Abstract

Declarative memories of personally experienced episodes are a key factor in defining oneself as an individual, which becomes particularly evident when this capability is impaired. Assessing the physiological mechanisms of human declarative memory is typically restricted to patients with specific lesions, requires invasive brain access, or functional imaging. We investigated whether the pupil, an accessible physiological measure, can be utilized to probe memories for complex natural scenes. During memory encoding, scenes that were later remembered elicited a stronger pupil constriction compared to scenes that were later forgotten. Thus, the pupil reflects the success or failure of memory formation. During retrieval, unfamiliar scenes elicited stronger pupil constriction than familiar scenes. The pupil responses for familiar scenes during retrieval were similar to the responses to later forgotten scenes during encoding, suggesting that insufficient novelty detection contributes to encoding failures. Pupil responses during retrieval related more strongly to the subjective belief of familiarity than to the objective truth. Nonetheless, the difference between old and novel persisted when memory encoding and retrieval were incidental. All our results were robust across observers, images, and task difficulty, and could not be attributed to image features or the observer's confidence.

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One interpretation of our findings suggests that a cholinergic novelty signal triggered a stronger memory encoding and subsequent pupil constriction for scenes perceived as subjectively novel. In sum, we show that pupil size, long known to be related to working memory, is also a robust correlate of the encoding and retrieval of declarative memories.

7.1 Introduction

Distinguishing novel from familiar items is a key function of the nervous system with immediate relevance for survival (Sokolov, 1963). Consequently, many parts of the human brain react differently to novel as compared to familiar items. For instance, several processes of memory encoding are only triggered if the item is considered novel (Knight, 1996), while familiar items trigger memory retrieval processes (Gonsalves, Kahn, Curran, Norman & Wagner, 2005, Squire, Wixted & Clark, 2007). Various brain areas are involved in distinguishing familiar from unfamiliar stimuli, including the medial temporal lobe (MTL) (Gonsalves et al., 2005, Knight, 1996, Rutishauser, Mamelak & Schuman, 2006, Rutishauser, Schuman & Mamelak, 2008, Viskontas, Knowlton, Steinmetz & Fried, 2006, Xiang & Brown, 1998), Ventrolateral prefrontal cortex, and dorsal posterior parietal cortex (Desimone, 1996, Grill-Spector, Henson & Martin, 2006, Kumaran & Maguire, 2009, Montaldi, Spencer, Roberts & Mayes, 2006, Ranganath & Rainer, 2003, Yonelinas, Otten, Shaw & Rugg, 2005). While some memories are implicit and only expressed in changed behavior, others are explicit such that observers can declare and assess the quality of their own memories (Tulving, 2002). The formation and retrieval of such declarative memories requires the MTL (Squire, Stark & Clark, 2004). This differential engagement of particular structures such as the MTL has been used successfully to predict whether novel items will later be remembered (Chadwick, Hassabis, Weiskopf & Maguire, 2010, Hassabis, Chu, Rees, Weiskopf, Molyneux & Maguire, 2009, Johnson, McDuff, Rugg & Norman, 2009, McDuff, Frankel & Norman, 2009, Polyn, Natu, Cohen & Norman, 2005, Rutishauser et al., 2006) and whether, during retrieval, an item will be recognized correctly and with which confidence (Paller & Wagner, 2002, Rissman, Greely & Wagner, 2010). These measurements require either invasive access to the brain or sophisticated machinery to infer brain activity (e.g., functional magnetic resonance imaging), severely limiting their applicability outside the laboratory and in clinical practice. Here we ask whether the pupil size, a simple and outwardly accessible physiological measure, can similarly serve as probe of declarative memory processes.

Besides its rapid constriction in response to bright stimuli (Loewenfeld & Lowenstein, 1993), the pupil reacts to a variety of cognitive processes, such as attention (Daniels et al., 2009, Kahneman,

1973, Karatekin, 2004, Karatekin et al., 2004), emotions (Bitsios et al., 2002, Charney et al., 1995, Nagai et al., 2002, Simpson & Molloy, 1971, Steinhauer et al., 1983), arousal (Bradshaw, 1967, Yoss et al., 1970), decisions (Simpson & Hale, 1969), or cognitive load (Hess & Polt, 1964). Cognitive processes can enhance or inhibit pupil constriction via several, mostly noradrenergic and cholinergic, pathways (Samuels & Szabadi, 2008). This results in the pupil size exhibiting complex temporal response patterns. In the context of memory, pupil size has long been known to increase with working memory load (Granholm et al., 1996, Kahneman & Beatty, 1966). Since the neural mechanisms of short- and long-term memory are largely distinct and interact in complex ways (Ranganath & Blumenfeld, 2005), it is unclear whether a similarly clear relationship between long-term memory performance and pupil size exists. Only very recently, several studies have started to address the relation between pupil size and forms of memory other than working memory (Heaver & Hutton, 2011, Otero, Weekes & Hutton, 2011, Sterpenich, D'Argembeau, Desseilles, Balteau, Albouy, Vandewalle, Degueldre, Luxen, Collette & Maquet, 2006, Võ, Jacobs, Kuchinke, Hofmann, Conrad, Schacht & Hutzler, 2008). During memory retrieval of words presented visually or auditory, the pupil dilates more for words that have been shown in a preceding study session (Otero et al., 2011, Võ et al., 2008). While only familiar words were used, such that no word itself was novel, this previous study showed that the pupil can distinguish items based on their recency during retrieval. Similarly, the pupil shows a transient increase for famous as compared to non-famous faces (Maw & Pomplun, 2004). In both studies, stimuli (words or faces) were previously known, and whether such a relationship exists for novel stimuli such as previously unseen natural scenes or unknown faces remains open. Small words presented on an otherwise unchanged screen cause little overall luminance change and thus allow to easily isolate a memory-related pupil response. However, in a more realistic situation, a memory-driven pupil response is intermixed with a stimulus-driven component. Whether such a putative memory-component of the pupil response can be isolated is unknown. The presentation of novel stimuli initiates learning processes and the extent to which these processes succeed determines whether a memory will be established or not. The pupil responds to novel items, but whether a significant relationship between the extent of dilation in response to novel items and later memory for

those items is not known. Previously, no such relationship could be identified for words (Võ et al., 2008). To the best of our knowledge, no study so far has addressed the relation of pupil dilation to the formation of declarative memories for truly novel items, their later retrieval among novel distracters, nor used used complex natural stimuli to probe the relation between pupil dilation and memory. In a series of four experiments, we monitored pupil dilation during presentation of novel natural scenes, which we either asked participants to explicitly memorize (exps. 1-3) or to merely use for performing a mock task (exp. 4). We continued by measuring pupil dilation during retrieval, when participants were either asked to distinguish the previously presented scenes from novel ones (exps. 1-3) or during incidental retrieval (exp. 4). This allows us – for the first time - to rigorously evaluate the potential usefulness of pupil dilation for both the prediction of memory formation during encoding as well as recognition during retrieval for declarative memories of complex natural stimuli. We conclude by discussing the neural pathways that drive the different components of the pupil response and their overlap with different components of memory formation, which can be accessed conveniently by monitoring the pupil.

7.2 Methods

7.2.1 Procedure

In four experiments, we measured pupil responses of 8 observers during memorization and during retrieval of natural images. Experiments 1, 2 and 3 each consisted of a sequence of three phases. First, observers were asked to memorize 100 different images, each of which was presented for 1s and followed by a 8s blank period (Figure 1A). This memorization phase was followed by a distraction phase, during which observers performed a Stroop-task (Figure 1B). This task was merely to prevent active rehearsal and is not considered further. During the retrieval phase the 100 "memorized" old images were presented randomly intermixed with 100 different novel images for 1s each. Each image was followed by a blank period, during which observers simultaneously indicated by pressing one of six buttons, whether the image had been presented during the memorization phase ("old image") or not ("novel image") and how confident they were of their decision (3 levels of confidence: "Confident", "Probable", or "Guess", Figure 1C). After a further 1.5s of blank the next image was shown. In retrieval, observers could indicate their response any time after stimulus onset and the next trial only started after a response was given during retrieval (on average there was one trial about every 4s). Thus, images were presented every 9 seconds during memorization and about every 4 seconds during retrieval The distraction phase either lasted for 5 minutes (experiment 1 and 2) or 20 minutes (experiment 3). Observers were instructed to fixate before and after image presentation. The fixation point (1° radius) was green before image onset and red after image offset, indicating that observers were allowed or not allowed to blink, respectively. Observers were allowed to scan the image (i.e., make eye movements) during presentation.

In experiment 4, we tested whether pupilometric effects related to memory require explicit memorization. Therefore we asked a new group of 8 observers to imagine participation as judges in a photo contest and rate the aesthetic quality of several images instead of categorizing images as novel/familiar. During an exposure phase, which matched the memorization phase of experiments 1, 2 and 3 except for the instruction, observers were instructed "to become an expert for a particular set of

images such that we could investigate the effect of expertise on inter-observer rating reliability". To ensure that observers did not explicitly recognize the images during the "retrieval" phase, observers were only asked to rate the aesthetic quality ("how beautiful do you rate this image?") on a scale from 0 to 100 rather than indicating whether they had previously seen the image (Figure 1D). In all other aspects the procedure of experiment 4 was identical to that of experiment 1-3 except that it did not contain a distraction phase.

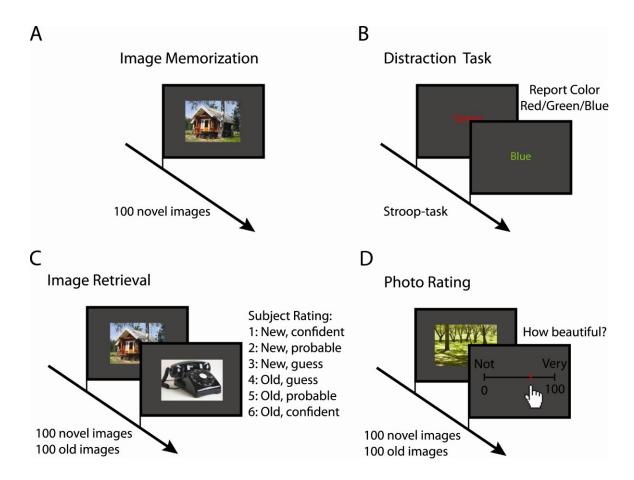


Figure 1. Tasks. (A) *Memorization phase* for experiments 1 through 3, *exposure phase* for experiment 4. Observers were asked to memorize 100 images (Exp.1-3) or had to watch images without explicit instruction for memorization (exp. 4). Image examples are from experiment 1. **(B)** *Distraction phase* for experiments 1 through 3, observers performed a Strooptask to prevent active rehearsal (5mins in Exp. 1,2; 20mins in Exp. 3). **(C)** During the *retrieval phase* of experiments 1-3, observers were presented 200 images, of which 100 had been shown during memorization, and had to report whether the image was old or novel and the confidence in their decision by a single button press (levels in the order of assigned buttons: "1: novel, confident", "2: novel, probably", "3: novel, guess", "4: old, guess", "5: old, probably", "6: old, confident"). **(D)** In experiment 4, observers watched 100 novel images (as shown in panel A) and were then asked to rate the aesthetic quality of 100 novel and 100 old images on a scale from 0 (not beautiful) to 100 (very beautiful) rather than explicitly reporting recognition.

7.2.2 Stimuli

Three different image databases consisting of 200 images each were used (see Figure 2). In experiment 1 and 3, images belonged to the following five object categories: Houses, general landscapes, vehicles, phones, and animals. In experiment 2, images were divided in five natural scene categories: Bushes, mountains, mushrooms, forests, water. Images in experiment 4 similarly belonged to five natural categories: Flowers, general landscapes, mushrooms, forests, meadows. Images in experiment 2 and 4 were more alike per category than images in experiment 1 and 3, and thus more difficult to memorize as reflected in memory performance (see Results). Images were 10° wide and 7° high in visual angle.

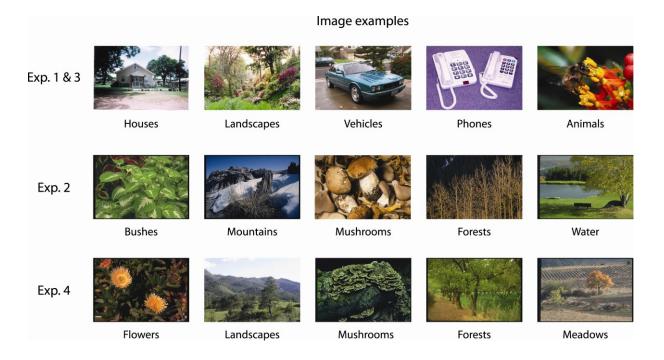


Figure 2. Example images shown to observers. Common objects and diverging landscapes were presented in experiments 1 and 3 and natural images were presented in experiment 2 and 4. Image database was the same for experiment 1 and 3, but different between experiment 2 and 4. Each image database was divided into five categories (see x-labels).

7.2.3 Observers

Thirty-two observers participated (age range: 21-28, 21 female, 11 male), 8 for each of the 4 experiments. One observer was removed from the analysis of experiment 3 because of a combination

of extreme performance (>95% correct), leaving very few miss and false alarm trials, and a largely reduced inter-trial variability in pupil response as compared to all other observers. All observers had normal or corrected-to-normal vision, were naïve to the purpose of the studies, and gave informed written consent before each experiment. The experiments conformed to the ethical principles of the Declaration of Helsinki and were approved by the local ethics commission (Ethikkommission FB04 Philipps-University Marburg).

7.2.4 Apparatus

Stimuli were presented on a 21" Samsung Syncmaster CRT screen at a viewing distance of 70cm. The refresh rate of the screen was 85Hz and the resolution was 1280x1024 pixels. Monitor beams CIE color space coordinates (x,y) were (0.623, 0.344), (0.287, 0.609), and (0.151, 0.065) for the red, green, and blue gun, respectively. Stimuli were generated on an Optiplex 755 DELL computer, using Matlab (Mathworks, Natick, MA), the Psychophysics toolbox (Brainard, 1997), and EyeLink toolbox (Cornelissen et al., 2002) extensions. Pupil size was tracked with an infrared sensitive camera (EyeLink 2000, SR Research, Osgoode, ON, Canada) at a rate of 500Hz. Observers' head was supported by a chin- and forehead-rest. The eye-tracker was (re)calibrated before each experimental phase using a 13-point calibration grid.

7.2.5 Analysis

Pupil size was based on the pupil's diameter as recorded by the Eyelink eye-tracking system. During blink periods (as detected by the eyelink software), pupil size was interpolated with a cubic-spline fit. To compare across observers and to measure the effect of pupillary responses to image onset, pupil size was first trial-wise normalized to z-scores (subtracting mean and dividing by the standard deviation of pupil size). To align pupil size traces at image onset, from each trial's pupil trace the pupil size at t=0 was subtracted.

To quantify retrieval performance, measures from signal-detection theory (SDT) were employed. Two kinds of correct decisions were distinguished (Figure 3A, green and cyan squares):

correctly identifying an image as old (a "Hit") or correctly identifying it as new (a "Correct Rejection", CR). Similarly, we distinguished between two types of errors (Figure 3A, magenta and red squares): incorrectly identifying an image as old (a "False Alarm", FA, i.e. a false memory) and incorrectly identifying an image as new (a "Miss", i.e. a forgotten item). Retrieval performance was then quantified by the receiver operating characteristic (ROC) (Macmillan & Creelman, 2005). Each point of the ROC (cf. Figure 3B) is the cumulative average proportion of correctly remembered items (hit rate, y-axis) and the proportion of falsely remembered items (false-alarm rate, x-axis) at a given confidence level across observers per experiment. A point in the lower left corner (lowest FA and Hit rate) corresponds to the highest confidence level (old, confident). The degree of asymmetry of the ROC was assessed by fitting the z-transformed ROC with a linear regression for each experiment (Macmillan & Creelman, 2005). The slope of this line is 1 if the ROC is symmetric and less than 1 if it is asymmetric (Squire et al., 2007, Wixted, 2007). We further utilized the area under the curve (AUC) of the ROC to quantify how strong the pupil can dissociate between familiar and unfamiliar images (50% is chance, 100% is perfect dissociation). For the AUC calculations, average pupil size between 1500 and 3000ms after stimulus onset were used.

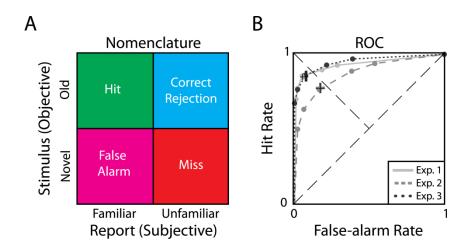


Figure 3 SDT-Nomenclature and behavioral data. (A) Nomenclature used throughout the paper: Trials are classified into one of four categories as a function of stimulus presentation (objective, i.e. ground truth) and subjective report of observers. The terms familiar/unfamiliar denote subjective report, old/novel objective truth; the term "familiarity" is used for both, but explicitly qualified as "subjective" and "objective", where not clear from context; the terms hit, false alarm, miss and correct rejection follow SDT conventions. The color coding indicated is re-used in the following figures. (B) Average hit rate as a function of false-alarm rate (crosses), and average receiver operating characteristic (ROC) across observers as a function of confidence level (1-6) starting with the highest (6: old, confident) in the lower left quadrant for each experiment.

7.3 Results

7.3.1 Behavior

In experiments 1-3 we asked observers to memorize a set of 100 images and later tested their retrieval performance for these against a novel set of 100 images. Observers had good memory for the easy image set in experiment 1 (average Hit: $84.2 \pm 4.6\%$, FA: $6.0 \pm 4.0\%$) and exp. 3 (average Hit: $84.6 \pm 10.0\%$, FA: $8.4 \pm 4.0\%$) while – as intended by the choice of stimulus material - performance was significantly lower for the more difficult image set in experiment 2 (average Hit: $76.8 \pm 9.6\%$, FA: 17.8 ± 8.2 ; performance exp. 1 vs. exp. 2: t(14) = 3.07, p < 0.01; exp. 2 vs. exp. 3: t(14) = 2.43, p < 0.05; exp. 1 vs. exp. 3: t(14) = 0.35, p > 0.50). Using the 6 confidence levels, we computed the receiver operating characteristic (ROC) for each experiment (Figure 3B) (Macmillan & Creelman, 2005). The areas under the ROC curves (AUC) were 0.93, 0.87, and 0.95 respectively, confirming high performance for all experiments. The slopes of the z-transformed ROCs were 0.87, 0.75, 0.74 for experiment 1, 2, and 3, respectively, and were significantly smaller than 1 (t(2) = 5.15, p = 0.036). This ROC asymmetry is a hallmark of declarative memories (for review see Squire et al., 2007, Wixted, 2007), and confirms the validity of our task as a test of declarative memory.

7.3.2 Pupil responses during memorization predict later recognition

In experiments 1 through 3 we obtained usable pupil data from 23 observers. During memorization, the pupil response to image onset consisted of two components: a fast contraction of the pupil approximately 500ms after image onset, followed by a slow dilation of the pupil back to baseline after approximately 1000ms (Figure 4A). Pupil responses to images that were later successfully remembered (hits) were stronger (Figure 4A; green) compared to images that were later forgotten (misses, Figure 4A; red). This difference was significant for the average pupil size in the second after image offset across all experiments (t(22) = 2.21, p = 0.038), and for each individual experiment (Figure 4B). As a function of time, the difference was significant (p<0.05, uncorrected) for each individual time point starting 511ms after image onset (Figure 4A, gray bar). There was no significant

correlation between the luminance of an image and its probability of being remembered (Exp. 1-3: r(299) = 0.09, p = 0.139; Exp. 1: r(99) = 0.032, p = 0.75; Exp. 2: r(99) = -0.029, p = 0.78; Exp. 3: r(99) = 0.008, p = 0.94), verifying that this difference is not caused by luminance impacting memorization and pupil alike, but by one or more cognitive factors. Hence, the pupil response during memorization robustly predicts whether or not an image will later be remembered during retrieval.

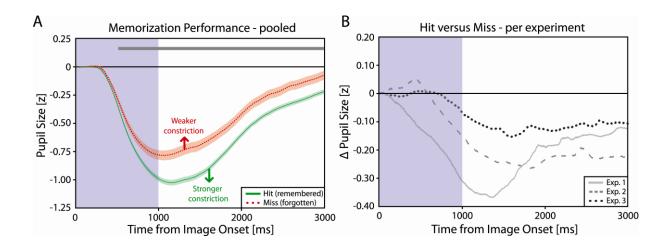


Figure 4. Pupil response during memorization predicts whether an image will later be remembered or forgotten. (A) Average pupil size as a function of time and memorization success. Z-scores were calculated per trial, and subsequently traces were normalized to image onset. Throughout the text, the terms "weaker constriction" and "stronger constriction" are used, irrespective of whether the physiological origin is a stronger/weaker constriction or a weaker/stronger dilation signal. Later remembered stimuli (hits) are green, later forgotten (misses) red. Image onset is at t = 0. Shading around average pupil size indicates s.e.m. across all trials of experiments 1-3. Grey patch at the top of the panel indicates time points of significant (p < 0.05) differences. (B) Difference (Δ) in average pupil size between hits and misses (hits minus misses) as a function of time for each experiment. Shaded areas indicate when the image was on the screen (1s total). Trials were pooled across all observers, and across all experiments (panel A) or per experiment (panel B).

7.3.3 Pupil responses during retrieval distinguishes familiar from novel images

During retrieval, images judged as unfamiliar (Misses and CRs) resulted in stronger pupil constrictions compared to subjectively familiar images (Hits and FAs). This main effect of subjective memory was significant starting approximately half a second after image onset (Figure 5A, see grey patches; F(1,4797) > 3.98, p < 0.05 for each time point after 615ms), well before observers typically responded (mean±sd response times for Exps. 1-3: 2193 ±499ms, 2214 ±424ms, 2229 ±354ms). The pupil response for Hits (Figure 5A, green) started to transition from the correct rejection and miss trace to

the false-alarm trace after approximately one second. On average, the false-alarm pupil response was attenuated earlier than the hit response, indicating that some additional factors, such as reduced alertness or vigilance, may make an early contribution to false alarms. The fact that the difference between hits and misses has the opposite sign during retrieval as compared to the memorization phase provides compelling evidence against any confound by low-level image features that could have potentially influenced pupil and memory alike. Instead, the pupil response that robustly predicts whether or not an image will be recognized or has been recognized must be related to higher-level, cognitive factors.

7.3.4 Subjective and objective familiarity

Unlike subjective familiarity (Hits+FA vs. misses+CR), which shows a significant effect till the end of the trial, objectively novel stimuli (FA+CR) resulted in an stronger pupil constriction compared to objectively old stimuli (Hits+Misses) only between 552ms and 990ms after stimulus onset (Figure 5A, F(1,4797) > 3.88, p < 0.05). The interaction between subjective report and objective stimulus also showed a significant difference in this period (between 621ms and 1027ms, F(1,4797) > 3.87, p < 0.05). The time-course of the latter main effect and the interaction statistically confirms the "cross-over" of the "hit" trace evident in Figure 5A: up to about 1s from matching the objectively similar (CR, actually an old image) to the subjectively similar (miss, report unfamiliar). As expected from the ANOVA data, a post-hoc t-test showed that pupil responses were significantly stronger for unfamiliar compared to familiar images from about stimulus offset (Figure 5B, p < 0.05 for all time-points after 1008ms). This difference between familiar and unfamiliar iages has a similar time course for all experiments (Figure 5C) and is thus independent of task or image-set difficulty. Since the discrimination "objectively old" compared to "objectively novel" showed similar behavior (Figure 5D), this difference cannot be explained by a putative dominance of error trials.

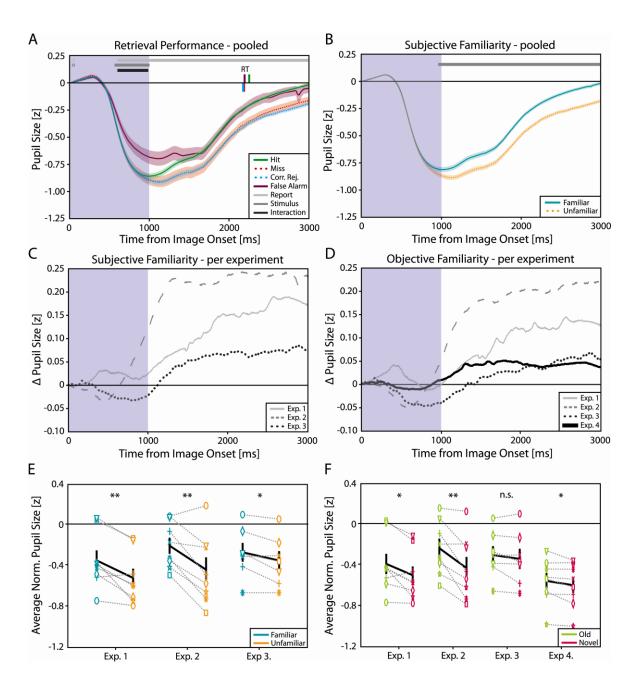


Figure 5. Pupil responses during memory retrieval. (A) Average pupil size as a function of time after image onset for the conditions Hit (green), Miss (red), CR (cyan), and FA (magenta) pooled across observers and experiments 1-3. Shading around average pupil size indicate s.e.m. over all trials and gray patches at the top indicate points of time when pupil size differed significantly (p < 0.05) between familiar (Hit+FA) and unfamiliar (Miss+CR) images (subjective report, familiarity; light grey), old (Hit+Miss) and novel (CR+ FA) images (objective, stimulus presentation; grey), and when there was a significant interaction between report and stimulus (interaction; dark grey). Misses and CRs trials resulted in stronger pupil constriction than Hits and FAs. The small colored vertical bars indicate the mean reaction time for each condition, which were not significantly different across conditions (F(3,4596) = 1.35, p = 0.26). (B) Comparison of average pupil size according to subjective report regardless of correctness, pooled across observers and experiments 1-3. Unfamiliar trials (subjectively new; orange) resulted in a significantly stronger pupil constriction compared to familiar trials (subjectively old; aqua). (C-D) Difference in average pooled pupil size between familiar-unfamiliar (subjective, panel C), and between old-novel (objective, panel D) conditions, as a function of time after image onset for each experiment. (E-F) Average normalized pupil size for each experiment for familiar (aqua, panel E) and unfamiliar (orange, panel E), and old (yellow-green, panel F) and novel images (pink, panel F). Unfamiliar and novel images induced significantly stronger pupil constriction compared to familiar and old images, respectively. Average across observers and s.e.m. are indicated in black.

7.3.5 Trial-by-trial Robustness

All effects during retrieval exhibit a high inter-individual consistency. Considering the time 1.5s-3s after stimulus onset (i.e., right after the cross-over of the HIT trace), of the 23 observers used, 20 showed a decreased average pupil size (i.e. a stronger constriction) for unfamiliar as compared to familiar images (Figure 5E), and similar for novel as compared to old stimuli (Figure 5F). These differences were significant in each individual experiment, with the exception of the objective data in Exp. 3, which, however, included one less observer (subjective: Exp. 1: t(7) = 3.96, p = 0.006; Exp. 2: t(7) = 3.66, p = 0.08; Exp. 3: t(6) = 2.84, p = 0.030; objective: Exp. 1: t(7) = 2.95, p = 0.021; Exp. 2: t(7) = 3.72, p = 0.007; Exp. 3: t(6) = 1.44, p = 0.199). Trial-by-trial analysis showed that the pupil can dissociate novel from familiar stimuli above chance (AUC of 50%, see Methods) for subjective familiarity (Exp. 1-3: t(22) = 5.47, p < 0.001; Exp. 1: 57 ±5%, t(7) = 4.00, p = 0.005; Exp. 2: 58 ±7%, t(7) = 2.99, p = 0.020; Exp. 3: 54 ±4%, t(6) = 2.79, p = 0.032) and – with the exception of experiment 3 – also for objective familiarity (Exp. 1-4: t(30) = 5.68, p < 0.001; Exp. 1: 55 ±5%, t(7) = 3.15, p = 0.016; Exp. 2: 57 ±4%, t(7) = 4.65, p = 0.002; Exp. 3: 52 ±4%, t(6) = 1.29, p = 0.244; Exp. 4: $53 \pm 3\%$, t(6) = 2.75, p = 0.028). These data show that the relation between pupil response and recognition is robust both across and within observers, task design and stimulus set. Importantly, the pupil response can be used trial-by-trial within a single observer to distinguish familiar from novel images.

7.3.6 The pupil response is primarily driven by subjective familiarity

Next we tested whether the pupil is dominated by subjective or objective familiarity (i.e., by subjective report or objective ground truth). We computed for each observer in experiments 1-3 the effect of subjective familiarity as the difference in mean pupil response for images judged as familiar minus images judged as unfamiliar (i.e., the difference between left and right data point in Figure 5E). Similarly, we computed the effect of objective familiarity as the difference in pupil between actually old and novel stimuli (Figure 5F). Comparing these measures, we found that the effect size for subjective familiarity was significantly larger than for objective familiarity (difference in pupil size

was significantly weaker for the objective condition compared to the subjective, t(22) = 3.17, p = 0.004). This confirms the observation (cf. Figure 5A-B) that the pupil – at least after some time after image offset has elapsed – is driven more strongly by subjective than by objective familiarity.

7.3.7 Pupil difference between novel and familiar items does not require explicit memorization

The effects observed during retrieval can potentially be explained by – for example arousal-related – processes that are triggered by successfully recognized target images (i.e., an explicit decision). To test this, we assessed in experiment 4 whether the pupil size still distinguishes familiar from novel images in the absence of explicit recognition (i.e., when no decision related to memory is required). Despite the absence of an explicit recognition component in the task, pupil size still distinguished between novel and old images (Figure 5D, solid black line). The average pupil size differed significantly between objectively novel and old images (Figure 5F, Exp. 4; t(7) = 2.44, p = 0.048). Aesthetic ratings for novel and old stimuli did not differ significantly across observers (t(7) = 0.15, p = 0.884; pooled: t(1598) = 0.17, p = 0.865), and the correlation between pupil size and aesthetics was weak and negative (t(1599) = -0.09, t(1599) = -0.09,

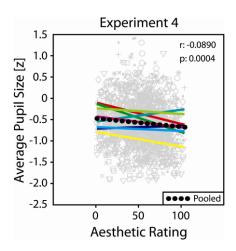


Figure 6. Average pupil size for each trial as a function of aesthetic ratings for images. Average pupil size negatively correlated with aesthetic ratings as the most beautiful images (rating 100) induced smaller pupil sizes. Grey markers indicate data of a single trial per subject, colored line indicates the fitted regression per observer, and the black dotted line is based on pooled data across observers.

This verifies that the observed relation between objective familiarity and pupil size cannot be explained by a putative confound with perceived aesthetics. Experiment 4 therefore demonstrates that the difference in pupil size between old and novel items depends neither on explicit retrieval nor on explicit memorization.

7.3.8 Confidence

Pupil size during retrieval was systematically related to confidence (Figure 7). To statistically assess this relation, we performed 2-factor ANOVAs, each with factors confidence (guess, probable, confident) and familiarity for data pooled over experiments 1 through 3, separately for subjective and objective familiarity. For subjective familiarity, we observed a main effect of confidence (Figure 7A, F(2,4594)=12.57, p<0.001). A consistent pattern emerged for both levels of subjective familiarity (familiar/unfamiliar): the weakest pupil constriction was elicited at the intermediate level of confidence. This inverse U-shape was preserved when objective familiarity (novel vs. old, Figure 7B, F(2,4594)=13.13, p<0.001) or only correct trials (Figure 7C, F(2,3910)=10.33, p<0.001) were considered. For each level of confidence, subjectively unfamiliar images elicited a stronger pupil constriction than familiar ones (Figure 7A, F(1,4594)=26.58, p<0.001), and there was no significant interaction between confidence and subjective familiarity (F(2,4594)=1.23, p=0.29). Objective familiarity also showed a significant main effect (F(1,4594)=7.95, p=0.005), and – with the exception of the "guess" condition - the same consistent pattern: novel images elicited a stronger pupil constriction for confidence levels "probable" and "confident". The deviation of the "guess" condition is not surprising, as it contains an abundance of incorrect judgments, and there was a significant interaction between objective familiarity and confidence (F(2,4594)=6.08, p=0.002). Indeed, considering only correct trials (Figure 7C), the difference between hits (novel and unfamiliar) and correct rejects (old and familiar) was again evident for each level of confidence (F(1,3910)=17.20,p < 0.001) and there was no significant interaction between familiarity and confidence (F(2, 3910)= 1.60, p=0.20). In sum, this analysis shows that intermediate levels of confidence elicit the weakest pupil constriction, effects are more robust for subjective than objective familiarity and - most

importantly – the effect of familiarity on the pupil persists for all levels of confidence. The effect of confidence, however, independently adds variance to the pupil response: if there were only an effect of memory, the weakest pupil constrictions would be expected to be for high-confidence familiar trials, contrary to the inverse U-shape actually observed. With pupil size inversely related to uncertainty (Preuschoff, 't Hart & Einhäuser, 2011), the inverse U-shape may suggest that on top of the memory signal, the pupil signals the uncertainty about one's confidence judgment rather than confidence (i.e., the uncertainty about the correctness of one's memory) per se.

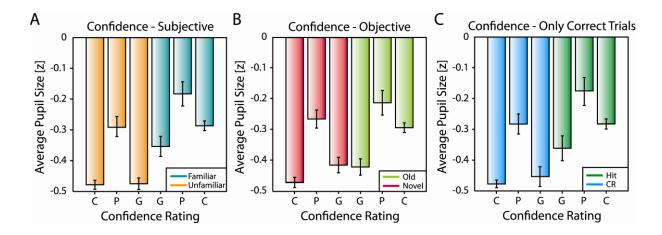


Figure 7. Subjective confidence is reflected in pupil size. (A) Average pupil size after image offset for all trials as a function of confidence ratings per subjective familiarity condition (regardless of objective ruth). Trials for which observers reported high confidence (*Confident*, C) and low confidence (*Guess*, G) resulted in stronger pupil constriction compared to intermediate confident (*Probable*, P) trials for both familiar (aqua) and unfamiliar images (orange). Trials were pooled across observers and experiments 1-3, error bars are s.e.m. across trials. **(B)** Average pupil size as a function of confidence, sorted by objective familiarity - old (light green) and novel (pink). **(C)** Average pupil size as a function of confidence only for hit (green) and correct-rejection (cyan) trials (i.e., subjective=objective). Trials for which observers had high confidence (*Confident*, C) and low confidence (*Guess*, G) resulted in stronger pupil constriction compared to intermediate confidence (*Probable*, P), independent of the subjective or objective state.

7.3.9 Does the pupil reflect a novelty signal that triggers memorization?

The stimuli that elicited stronger pupil constriction (or less dilation) during memorization were the ones later remembered correctly; during retrieval, novel images elicited stronger constriction than the familiar ones. Under the hypothesis that a novelty signal is required to trigger memorization, the pupil might reflect this signal: during retrieval the novelty signal is related to novelty directly, during

memorization those images correctly tagged as novel are later remembered and thus become hits. If true, the pupil response during memorization to images that later become hit should be similar to the pupil response for novel images during retrieval. When aligned to the time when constriction started in both conditions (t=300ms), later hits indeed elicited similar pupil traces during memorization as novel items did during retrieval (Figure 8). The two traces are statistically indistinguishable (p>0.05) from 0.61s to 2.86s (and, by definition, at 0.3s); that is from well before image offset to well after the typical response time. For comparison, we also contrasted the response of later remember stimuli during memorization with the response to correctly remembered stimuli during retrieval (green trace here vs. aqua trace in Figure 5B) and found a significant difference (from about image offset at 1.02s till the end). Note that this significant difference is the result of single-trial learning, since in both conditions the same images are shown but once they are novel and the second time familiar. Similarly, the response to images later forgotten was significantly different from the response to unfamiliar images during retrieval (from 0.65s to the end; misses in Figure 4A vs. orange trace in Figure 8). We thus confirmed that we have sufficient statistical power to compare the pupil response between memorization and retrieval and the lack of such difference (see above) is thus not due to statistical power. Our finding of close similarity between later hits during memorization to novel items during retrieval is in line with the hypothesis that stimuli which were subjectively novel were preferentially encoded and thus later remembered. In contrast, stimuli which were subjectively less novel (note that objectively all stimuli were novel during memorization) were less likely to be remembered. Hence, the notion that the pupil response reflects a generic novelty signal provides a possible unifying explanation for our results during memorization and retrieval.

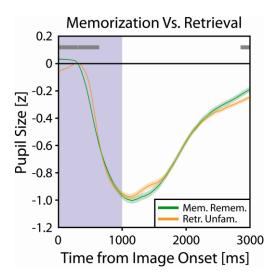


Figure 8. Comparison of the novelty response during memorization and retrieval. Pupil size during memorization of novel images that were later correctly remembered (*green*) compared to pupil size during retrieval of novel images that were reported as unfamiliar (*orange*). Data are the same as depicted in figures 4A (green trace) and 5B (orange trace), but normalized to t=300ms (the time of constriction onset in both conditions to account for the initial unspecific dilation that is present in retrieval but not during memorization).

7.4 Discussion

Our data showed robust relations of pupil constriction to declarative long-term memory processes – both during memorization and retrieval – for a variety of natural stimulus sets and difficulty levels. During memorization, pupil constriction was stronger for images that will later be remembered correctly. During retrieval, unfamiliar items trigger stronger constrictions than familiar ones. The natural stimuli we used varied in mean luminance, but none of our results could be explained by image features or image aesthetics. The pupil size difference during retrieval was observed for both explicit as well as implicit (incidental) retrieval. Also, pupil size was more tightly coupled to the subjective judgment of familiarity rather than to the objective truth.

In learning, the subjective judgment of novelty is hypothesized to be a strong driver of memory formation (Knight, 1996). In our data, items later correctly remembered (i.e., items for which a memory is successfully formed) showed a stronger constriction during memorization than later forgotten items, and the constriction was very similar to the response observed for novel items during retrieval. This suggests that the subjective novelty of a stimulus was a primary driver of the pupil response. While during memorization all images are objectively equally novel, one determinant of later memory strength is the subjective novelty of a stimulus for an individual. In line with the novelty-triggers-encoding hypothesis, the similarity of the response for later remembered novel items and distractors during retrieval suggests that the later remembered items were subjectively novel to the participants and that this in turn facilitated memory formation.

Whereas relations between working memory load and pupil dilation have long been established (Gardner, Beltramo & Krinsky, 1975, Gardner, Philp & Radacy, 1978, Granholm et al., 1996, Kahneman & Beatty, 1966), no study has yet addressed pupil dilation in the context of long-term declarative memory for novel natural scenes. We used a 6-point confidence scale during retrieval combined with analysis of ROC slopes to verify that our participants had established declarative memories. Confidence judgments can be used to distinguish between different models of memory according to whether an effect is observed at certain or all levels of confidence. The dual process model of declarative memory retrieval assumes there are two different mechanisms involved during

familiarity processes (for details, see Wixted, 2007) and predicts that signatures of recollection and familiarity judgments should only be visible for high-and low confidence judgments, respectively. In contrast, we found that the extent of pupil dilation distinguishes between novel and familiar stimuli for all confidence levels. This suggests that the driver of the pupil-response component attributed to memory cannot be explained by the dual process model and is driven by other type of mechanisms (e.g., the unequal variance signal-detection model; for details, see Wixted, 2007). Our findings indicate that the stronger constriction that follows novel stimuli can be utilized successfully to assess components of both memory formation as well as retrieval. We deliberately used natural scenes of varying luminance and aesthetic value to demonstrate that this effect can be observed in relatively realistic situations. This is in contrast to some of the few previous studies that addressed familiarity effects in the pupil with words (Heaver & Hutton, 2011, Otero et al., 2011, Võ et al., 2008). Participants were asked to study a list of words and were later asked to indicate for another list of words whether the word was present on the previously studied list (Heaver & Hutton, 2011, Otero et al., 2011, Võ et al., 2008). Importantly, none of the words were novel as such. Hence, rather than testing the formation of memory for novel items these studies queried a form of recency and no significant relationship between pupil dilation and later memory performance could be found (Võ et al., 2008). In contrast, we demonstrate that pupil dilation during memory formation for novel natural scenes is predictive of later memory strength, i.e. it exhibits a difference-due-to memory effect (Paller & Wagner, 2002) similar to what has previously been found using either invasive recordings or imaging (Johnson et al., 2009, Rutishauser, Ross, Mamelak & Schuman, 2010). Note that in our tasks stimuli were seen only once by participants before the memory test, indicating that the old-novel pupil difference can develop rapidly after single-trial exposure. This suggests that pupil response is a valuable tool to assess memory formation. We consider it likely that simultaneous recordings of pupil diameter with other measures, such as invasive electrophysiology or brain imaging, will provide a powerful combination of signals that operate on different spatial and temporal scales and may thus enable deeper insights into the neural mechanisms of memory formation.

Since the pupil is an outwardly accessible signal that is under little to no volitional control, it has been suggested that the pupil may betray covert thoughts in the context of decision making (Einhäuser et al., 2010), economic gambling (Wang et al., 2006) or valence judgments in social interactions (Harrison et al., 2006), bringing the possibility of lie detection based on the pupil response from mere fiction to within reach of reality. Considering the present results, could the pupil also serve as a reliable indicator of having seen a stimulus previously? This question becomes of particular interest if pupil measurements are combined with brain activity measurements such as fMRI BOLD multi-voxel pattern analysis (Rissman et al., 2010), which are also frequently combined with claims of "mindreading". We found that the pupil difference persists if retrieval is only implicit rather explicit and a previous study indicated that the pupil difference persists also if participants actively try to simulate amnesia for the stimuli presented (Heaver & Hutton, 2011). While we - based on the difference in temporal resolution – consider it likely that the pupil may provide additional information as compared to current fMRI data, this question will only find a definite answer by simultaneous imaging and pupillometry. In the context of "lie detection", it is furthermore important to note that our findings indicate that the pupil response is more closely related to the subjective judgment of familiarity rather than to whether the stimuli are truly familiar. This is in agreement with a previous fMRI BOLD decoding study that similarly indicated that primarily the subjective familiarity of faces could be decoded (Rissman et al., 2010). This thus indicates that neither the fMRI signal nor the pupil response itself could serve as a lie detector in the sense of telling whether or not a person has actually been exposed to the stimulus previously. Rather, both measures would serve as a detector of whether a person subjectively thinks that a particular stimulus is familiar or novel. Further research, with for example truly amnesic patients, will, however, be necessary to confirm or falsify this hypothesis.

7.4.1 A possible neural account of pupil dynamics

Cognitive processes affect pupil dynamics through both the sympathetic and parasympathetic pathways (e.g., Bradshaw, 1967, Einhäuser et al., 2010, Einhäuser et al., 2008b, Friedman et al., 1973, Gilzenrat et al., 2010, Granholm et al., 1996, Hess & Polt, 1964, Jepma & Nieuwenhuis, 2011,

Kahneman & Beatty, 1966, Naber, Frässle & Einhäuser, 2011, Raisig et al., 2010, Simpson & Hale, 1969, Yoss et al., 1970). Pupil dilation via the sympathetic pathway by cognitive processes is assumed to be carried mainly by noradrenergic (NA) projections originating in the locus coeruleus (LC) (Berridge & Foote, 1991, Jepma, Deinum, Asplund, Rombouts, Tamsma, Tjeerdema, Spapé, Garland, Robertson, Lenders & Nieuwenhuis, 2011, Koss, 1986, Nieuwenhuis, de Geus & Aston-Jones, 2011, Phillips, Szabadi & Bradshaw, 2000, Rajkowski, Kubiak & Aston-Jones, 1994, Samuels & Szabadi, 2008, Sterpenich et al., 2006, Vankov, Hervé-Minvielle & Sara, 1995), although direct electrophysiological evidence in humans is still lacking. Only rarely, however, has NA been related to memory processes, and if so, in particular in the context of processing emotional items (Sterpenich et al., 2006). Interestingly, LC neurons respond vigorously to novel objects (Vankov et al., 1995), which in humans would result in more dilation, rather than in the stronger constriction observed here. In contrast to NA, acetylcholine (ACh), which leads to pupil constriction through the parasympathetic nervous system (Hasselmo & Giocomo, 2006) and is best known for mediating the pupil light reflex (Loewenfeld & Lowenstein, 1993), seems to play an important role in memory processes: i) ACh modulates memory encoding in rats (Hasselmo, 2006, Hasselmo & Giocomo, 2006, Warburton, Koder, Cho, Massey, Duguid, Barker, Aggleton, Bashir & Brown, 2003), which has also been shown in humans (Kukolja, Thiel & Fink, 2009, Silver, Shenhav & D'Esposito, 2008) with pharmacological manipulations. ii) Patients with Alzheimer's disease show attenuated pupillary constrictions (Fountoulakis et al., 2004, Prettyman et al., 1997) and reduced levels of ACh (Francis et al., 1999), iii) ACh release has been related to neural plasticity (Bakin & Weinberger, 1996, Kilgard & Merzenich, 1998) and memory consolidation during REM sleep (Power, 2004). The complex interplay between dilation and constriction renders it difficult to conclude from our data alone, whether "sympathetic dilation" or "parasympathetic constriction" is at the foundation of the dilation we observe for forgotten and familiar items or the stronger constriction we observe for remembered and unfamiliar items, respectively. Nonetheless, our data together with the aforementioned evidence allows us to hypothesize that a cholinergic novelty signal both underlies the observed pupil constriction and participates in memory formation. Irrespective of the neural origin, however, the finding that pupil

size predicts as to whether an item will later be remembered provides an immediately available signal that can potentially be used for online monitoring of memory formation. Such online monitoring potentially paves the way for interfering with memory formation, which then – in combination with imaging and electrophysiology – may provide a useful tool both for studying and eventually improving declarative memory formation.

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8. Chapter 8

Mind-reading: Using pupil dilation to defeat your opponent

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8.1 Short Report

The possibility of "mind-reading" is a common theme within popular culture, with the idea that subtle facial signals may provide clues into one's private thoughts. While facial expressions and gaze direction are known to reveal some information about an emotional state or intention (Baron-Cohen, Wheelwright, Hill, Raste & Plumb, 2001; Frith & Frith, 2008), it is less clear whether pupil dilation can be used to gain strategic insights into another's mind. Although pupil dilation accompanies a wide range of behaviors and mental processes including decisions (Bradshaw, 1967; Hess & Polt, 1964; Beatty, & Wagoner, 1978; Einhäuser, Koch, & Carter, 2010; Gilzenrat, Nieuwenhuis, Jepma, & Cohen, 2010), evidence that humans can exploit pupil dilation to infer another individual's decisions is lacking. Here we adapted the popular childhood game "rock-paper-scissors" and show that humans can actually use this signal in a competitive game scenario to increase their wins by approximately 50%.

In rock-paper-scissors, two competitors each choose "rock", "paper" or "scissors", with the winner determined by their respective choices (Fig.S1A, supplemental material online). Here, 3 individuals ("opponents") first played 25 rock-paper-scissors games against a computer while video of their left eye was recorded and pupil size was tracked (Fig.1A). Opponents were instructed to select their choice as the words were read-out by the computer in random order at 4s intervals. After each

game, opponents were given feedback about the computer's (random) choice and rewarded accordingly. Maximal pupil dilation followed the selected word in 45/75 games (upper dashed line Fig.1B; chance: 25/75), confirming that pupil dilation accompanies choices (Einhäuser et al., 2010). A separate group of participants ("players") played against the previously recorded opponents' games. For each game, players were provided the same auditory "rock-paper-scissors" sequence presented to their opponent. Players then made their own selection and were rewarded depending on whether they won, lost or drew against the opponent's real choices. Order of games was randomized for each player to ensure that the sequence of previous choices was uninformative.

Players were presented four different versions of the recorded games: 1) Naïve-eye condition: Ten players were presented video of their opponent's eye (Movie S1A; Fig.S1B) and instructed to look for any behavioral signs that could reveal their opponent's decision. 2) Informed-eye condition: The same players were presented the videos, but were now informed that the largest pupil dilation should follow the presentation of the word selected by their opponent. 3) Informed-reconstructed-pupil condition: To exclude any potential effects of facial features other than pupil dilation, a fresh group of 10 players were only presented a centred black disk that represented the opponents' pupil size over time (Movie S1B; Fig.S1B) with instructions identical to the informed-eye-condition. 4) no-video condition: Only the audio sequence, but no visual information was presented to 5 players from each group (10 total). In all conditions, videos were scaled such that size of the pupil corresponded to a real-life conversation distance of approximately 50cm (Hall, 1959).

Average player performance was indistinguishable from chance if no video was shown (t(9)=0.46, p=0.66, Fig.1B) or if videos were presented but players were naïve to the usefulness of pupil-based cues (t(9)=0.73, p=0.48). However, players performed significantly above chance, after they were advised to use maximum pupil dilation to identify their opponents selection when viewing either unedited footage (t(9)=4.56, p=0.001) or the reconstructed pupil (t(9)=7.71, p=3.02x10-5).

In the naïve-eye condition all players reported a range of strategies (including blinks, small movements of the eye/head/brow in addition to pupil dilations and/or constrictions). Post-hoc testing of individual's performance showed that one player performed significantly above chance (37 wins,

p=0.003, Binomial test) with clear signs of learning (Supplementary Methods and Fig.S2). One additional naïve player learned to choose the option signaled by the pupil significantly above chance (p=0.003). Since the pupil correctly indicated the opponents' choice in only 45/75 trials ("60% validity"), this individual's win frequency remained below significance till the end. To test whether increased validity speeds up learning, we selected 30 trials (10 from each response interval) for which maximum pupil accompanied correct choice ("100% validity"). A fresh set of 10 naïve players played 4 randomized blocks of the 30 trials. On average they performed above chance (t(9)=2.77, p=0.022) and 5 players performed significantly above chance individually (p<0.0005 for each, Binomial test, Fig.1B).

These results provide the first demonstration that people can use pupil dilation to gain an advantage in a competitive game scenario without the use of any fancy equipment or brain-imaging technology. It is possible that other facial features, like individual twitches or blinks, may provide some useful information about a person's decision in this context. However, the fact that the best performance was seen in the reconstructed-pupil condition shows that pupil size alone is at least as informative as pupil size plus untrained use of other facial cues. Remarkably, a few observers implicitly learned to use the pupil despite its relatively low validity in the original condition and half did so when the pupil's validity was increased. While we chose rock-paper-scissors for the present study because its intuitive rule structure allowed naïve participants to play without training, the game shares key elements with more elaborate social exchanges and competitive situations. Hence, our findings are in line with a recent suggestion that the human brain is capable of monitoring pupillary dynamics in social contexts (Harrison, Gray, & Critchley, 2009). Pupil dilation is clearly sufficiently salient to be detected and could potentially be used in a range of social contexts such as reading out a client's preference during financial negotiations or detecting hidden decisions during strategic games such as poker.

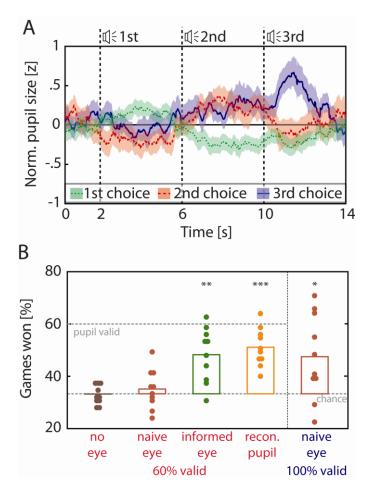


Figure 1. Opponents' pupillary responses and players' performance. **(A)** Average z-normalized pupil size (shading: s.e.m) for games in which opponents selected the first, second or third option; pupil dilation peaks shortly after the presentation of the selected word (dashed vertical lines). **(B)** Percentage of trials won on average (bar) and by individual players (circles). For the 60%-validity conditions upper dashed line indicates maximum performance if a player always selected the interval signaled by the pupil.

8.2 References

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8.3 Supplementary Material

Group performance was tested against chance level (1/3) by a two-sided t-test. Individual performance was tested by a Binomial test. The Binomial test was used as it is an exact statistical test that provides the probability (p) that for a certain total number of trials (n), a certain amount of wins (k) or more are to be expected by chance. For the present case of 1/3 chance, the p-value is thereby given to

$$p = \sum_{k \le i \le n} \binom{n}{i} \left(\frac{1}{3}\right)^i \left(\frac{2}{3}\right)^{(n-i)} = \sum_{k \le i \le n} \binom{n}{i} 2^{(n-i)} 3^{-n}$$

where denotes the binomial coefficient "n choose i". Since learning a successful strategy can be expected to have positive effects, numbers provided in the main text refer to the one-sided version of the test as described here. Using a two-sided version does not change the results qualitatively.

Supplementary Movie S1. Videos depicting three trials (games) as the players viewed it in the informed and naive pupil conditions (A) and in the informed-reconstructed-pupil condition (B).

If you want to try the experiment yourself, watch the movies and pick the best option to beat your opponent. You can use the instructions provided in the informed eye condition, "look for pupil dilations following each of the three auditory word options. The auditory presentation of the word selected by the opponent will be followed by the largest pupil dilation". The answers are provided at the end of this caption.

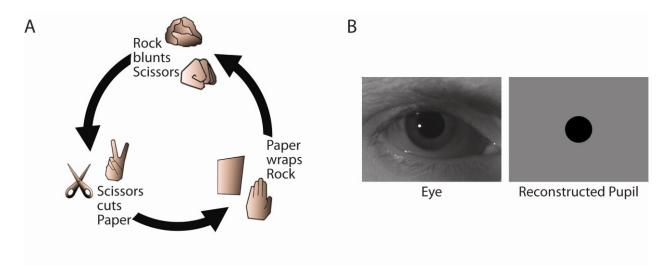
The audio track consists of the words "rock", "paper", and "scissors", presented in 4-s intervals in the identical (randomly ordered) sequence the opponent heard when the video of their left pupil was recorded with a an infra-red camera. To match the real-life conversation distance of about 50cm, videos (640x480pixels) were presented on a 52x32.5cm TFT-screen with a resolution of

1920x1200, a frame rate of 60Hz, and a grey background on which the videos subtended approximately $4^{\circ}x$ 3° degrees of visual angle and the average radius of the pupil was $\sim 0.25^{\circ}$.

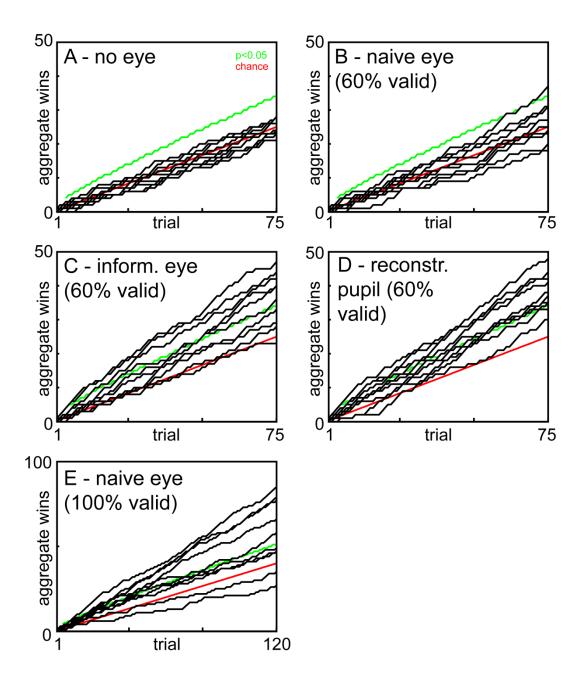
In absolute terms, opponents' pupil size varied on average by 3.75mm (SD: 0.97mm) in each trial (maximum-minimum diameter). Maximum dilation followed the choice in 45 out of 75 trials (1st interval chosen: 28/75, 2nd interval chosen: 25/75, 3rd interval chosen: 22/75).

The 3 trials show 1 game from each of the 3 opponents recorded. In the main experiment the 25 trials recorded from each opponent were shown in a single block with the game order randomised within the block. After each individual game, players received feedback and financial reward for games won (maximum financial reward) and drawn (reduced reward) against the opponent's real choices (totaling approximately \$10-\$20 depending on performance).

[Correct answers for both movies: Opponent 1 selected "Rock" (3rd option). Opponent 2 selected "Paper" (1st option). Opponent 3 selected "Scissors" (2nd option). So you are a winner if you chose "Paper" in the first game, "Scissors" in the second and "Rock" in the last game.]



Supplementary Figure S1. (A) During a game of rock-paper-scissors, two opponents choose one of three options of which rock beats scissors, scissors beats paper, and paper beats rock; if both players choose the same option the game is drawn. Unlike in the original version, here choices were not made simultaneously, but the opponent's choice was concealed till the trial's end; observers were given feedback on the outcome and rewarded depending on whether they had won, drawn or lost. **(B)** Snapshots of a recorded opponents' eye (left) and reconstructed pupil (right).



Supplementary Figure S2. Learning curves for the 5 different experimental conditions (Black lines: aggregate number of wins for each individual; red line: chance level; green line: 5% significance level for Binomial test at the given number of trials). Note that all preceding trials are considered in this computation, such that learned information has to persist longer if learning starts later. A) No-eye control condition: no signs of learning are evident. B) "Naïve-eye" condition (60% validity): one individual shows signs of learning and reaches significant performance (p=0.003) on aggregate. C) Informed-eye condition and D) informed-reconstructed-pupil condition: all but one player performs above chance, but – unlike the "learner" in panel B, most deviate from chance early, reflecting the use of explicit information rather than learning. E) Naïve-eye (100% validity): 5 out of 10 players learn to use the information contained in the pupil signal to perform significantly above chance on aggregate. While 1 player deviates from chance early (signaling an initial intuition about the optimal strategy), the 4 others deviate from chance only later during the session, suggesting that they are learning to use the pupil to their advantage over the course of trials.

9. Chapter 9

9.1 Discussion of dissertation

The experimental results presented in this dissertation have provided several insights into how the visual system handles and resolves ambiguous information. As visual input is generally incomplete, vague, or impoverished, the human mind highly demands on its skill to infer a coherent interpretation from only few available pieces of information. Here we have investigated how this is accomplished, how this affects human behavior, and which cognitive processes are involved. The following paragraphs discuss the findings of this dissertation in the context of cognitive interpretations of ambiguous visual stimuli.

9.1.1 Dominance sequences, durations, and piecemeal dynamics in rivalry

Perceptual rivalry is the process of changes in visual awareness driven by ambiguity. These dynamical changes have very specific properties and depend on a range of cognitive processes. By using ambiguous rivalry stimuli, several novel characteristics of perceptual dynamics were found. First, change sequences and durations of dominance periods of percepts in rivalry were not independent but biased by history (Chapter 2). By showing stimuli to observers that allowed three percepts (tri-stable stimulus), it could be examined whether percept sequences and durations were affected by history. Perceptual reports by observers showed that sequences of serial percepts were not random ("non-Markovian (dependent on history)") but highly depended on which percepts preceded the subsequent percepts. Preceding sequences also determined the dominance duration of subsequent percepts and, vice versa, the dominance duration of a preceding percept affected the sequence order of subsequent percepts. Second, the speed of a perceptual transition during rivalry relied on its direction and the physical properties of the stimulus that triggered the transition (Chapter 3). By careful manipulation of the direction and initiation of alternations between percepts, it was found that the spread of dominance decelerated when it moved towards to fove but not when it moved towards the periphery. In addition, the spread of perceptual dominance in space from one percept to the other was faster when

initiated with a stimulus that consisted of a grating with higher contrast. The latter finding is a clear demonstration of the effect of feature saliency on dynamics in rivalry. The former finding, however, is puzzling and could not be explained by the cortical magnification factor. A solid neuroscientific explanation remains to be found and it can only be speculated that the deceleration of travelling suppression waves are probably related to the connectivity properties of horizontal (lateral) interactions between neurons in the primary visual cortex. Nonetheless, these novel observations enable more refined comparisons across multiple phenomena: The more characteristics of a process are revealed, the better it can be estimated which phenomena share the same underlying mechanism. All the reported novel properties were evident in a variety of phenomena, independent of stimulus design. This suggests that changes in visual awareness might be governed by the same process that is responsible for all kinds of ambiguous stimuli, optical illusions, and other phenomena in which cognition renders stimuli invisible although their appearance remains physically present and unchanged.

9.1.2 A neural explanation of perceptual rivalry

Which brain mechanisms are responsible for rivalry and changes in awareness, and how do these interact? There are multiple theories on consciousness available, each with their own implications and predictions (e.g., Baars, 1993, Crick & Koch, 2003, Dehaene & Naccache, 2001, Eccles, 1992, Lamme, 2006, Llinás, Ribary, Contreras & Pedroarena, 1998). For example, it has been suggested that our nervous system consists of a "Global Workspace" with multiple parallel input processors that compete for dominance to eventually win and "broadcast" the information throughout the brains other processing units (e.g., Baars, 1993, Dehaene & Naccache, 2001). Such theories are plausible and worth investigating more thoroughly to see how they are in accord with behavioral and neurological data. But the question remains whether rivalry is a general process that is instantiated at a single location in the brain. Although it is not unlikely that many different instantiations of ambiguity and illusory disappearances of objects from awareness can be generalized to a single process, there is no meta-study that has compared all possible phenomena and probed their neural locus. Some studies

have, for example, examined rivalry in detail and it was suggested that the representation of perceptual transitions in rivalry may take place at small anatomical levels distributed across several sites in the brain (Hupé, Joffo & Pressnitzer, 2008, Pressnitzer & Hupé, 2006). Indeed, as perceptual rivalry occurs in many sensory modalities (Blake & Logothetis, 2002, Carter et al., 2008, Van Noorden, 1975, Warren & Gregory, 1958, Zhou & Chen, 2009), it is not far-fetched to hypothesize that cognitive ambiguity within a specific feature domain may occur at any site in the brain. A recent fMRI study that applied pattern classification methods to the BOLD responses during perceptual rivalry, showed that the neural locus of the process underlying rivalry between the eyes is in the lateral geniculate nucleus (LGN) while rivalry between features such as color correlates with activity in the early visual areas V1-V3 (Haynes, Deichmann & Rees, 2005, Haynes & Rees, 2005). In addition, several other studies showed that changes during perceptual rivalry depend on activity in designated brain areas that are responsible for the processing of the features or objects in the rivaling stimuli (Castelo-Branco, Formisano, Backes, Zanella, Neuenschwander, Singer & Goebel, 2002, Leopold & Logothetis, 1996, Muckli, Kriegeskorte, Lanfermann, Zanella, Singer & Goebel, 2002, Polonsky et al., 2000, Sterzer, Eger & Kleinschmidt, 2003, Tong et al., 1998). These findings strongly support the view that rivalry and the related changes in visual awareness take place at very local levels in brain areas that are responsible for the processing of the rivaling features. Thus, each part of the brain may incorporate its own process of rivalry through, for example, mutual inhibition and adaptation of pools of neurons that each process a feature or percept (Alais et al., 2010a, Blake, 1989, Blake & Bravo, 1985, Klink et al., 2008a, Lehky, 1988, Matsuoka, 1984, Mueller, 1990, Sugie, 1982). It is still to be discovered how the process of inhibition and adaptation is cortically organized. In particular, how is perceptual dominance represented by neurons, how do attentional processes affect the activity of these neurons, and what is the role of piecemealing and traveling dominance waves in this process? As shown in Chapter 4, simulating rivalry in both temporal and spatial dimensions, and using a continuous measure can specifically address these issues. Looking at perceptual rivalry as a process with predictable patterns (Chapter 2) may further flourish rivalry research in the near future. Especially research that use other methods to measure or simulate rivalry and its underlying neural activities at high temporal and spatial

resolutions with electrophysiology (Bai, Huang, Yang & Wu, 2006, Wilke, Logothetis & Leopold, 2006) and neural models (Knapen, van Ee & Blake, 2007b, Wilson, 2003, Wilson et al., 2001), may reveal the true neural mechanisms of changes in awareness.

Perceptual rivalry may thus occur at any site in the brain where multiple streams of information rival for neurological resources and processing. There are, however, several studies that found evidence of the general involvement of frontoparietal brain areas in perceptual rivalry (Britz et al., 2009, Lumer et al., 1998, Sterzer et al., 2002). Activity in these areas was related to the timing of switches in perceptual dominance. Perceptual switch rates of individuals further correlated with the size of their parietal cortex (Kanai et al., 2010). Thus, activity in these areas do not specifically indicate which percept was dominant at which time point but they might induce and determine the timing of perceptual changes in dominance. Importantly, frontoparietal areas are also involved in the deployment of (spatial) attention. Hence, these areas might be responsible for the allocation of attention to detect the changes in dominance rather than for the initiation of changes. These frontoparietal activity patterns during rivalry might have been correlates of the amount of attention that was employed to the rivalry stimulus. Thus it cannot be concluded that frontoparietal areas are necessary for rivalry and changes in visual awareness. As attention affects the rate of rivalry switches (Alais et al., 2010b, Paffen et al., 2006), it is not unlikely that attention is strongly involved during perceptual dominance and may affect perceptual switches. Furthermore, it has recently been opted that attention rather than awareness is largely responsible for changes in activity in the early visual areas that, however, were initially indicated as crucial brain parts for visual awareness (Watanabe, Cheng, Murayama, Ueno, Asamizuya, Tanaka & Logothetis, 2011). In sum, frontoparietal areas may not necessarily be responsible for the initiation of perceptual switches but could affect the balance of reciprocal inhibition between the neural pools devoted to the processing of each rivaling percept. To test this, activity reflecting attentional deployment needs to be somehow extracted and filtered out from the activity patterns related to the actual rivalry process. In a similar vein, introspection – the subjective report and attendance – of perceptual dominance during rivalry by observers, needs to be circumvented. This is where objective measures of rivalry come into play (Chapter 4). This dissertation reported a novel and successful technique to apply a reflex – pupil size – to objectively measure changes in visual awareness during perceptual rivalry. When two rivaling percepts have dissimilar luminance or contrast levels, the pupil will adapt to the amount of luminance or contrast of the dominant percept. If a percept with a low luminance is dominant, the pupil increases in size, and if perception switches to a percept with a high luminance, the pupil will react by decreasing its size. As shown in this dissertation, the changes in pupil size serve as relatively reliable indicators of perceptual dominance. It is hypothesized that the combination of two objective measures (e.g., pupil and OKN) and a conjunction analysis might be a promising method to pinpoint the neural locus of the processes that handle ambiguous input, initiate rivalry, and induce changes in visual awareness.

9.1.3 The formation of object representations

When ambiguity is resolved and a clear and single interpretation of an item, object, or entire visual surrounding is instantiated, the visual system tends to store its representation for immediate or later use. To attend and recognize previously encountered items, the human brain has a highly organized network that deals with the formation, maintenance, and retrieval of object representations (Knight, 1996, Squire et al., 2007). It is suggested that this network relies on sparse coding, that is, complex visual objects can be efficiently encoded and represented by just a few neurons (Gross, 2000, Logothetis & Sheinberg, 1996, Quian Quiroga, Reddy, Kreiman, Koch & Fried, 2005). If true, only few neurons and their synapses are necessary to store a new memory item. However, before such higher-order representations and cells are activated, visual information streams through a series of hierarchical stages that separately assess the occurrence of and connections between multiple features depicted by the stimulus (Felleman & Van Essen, 1991, Zeki et al., 1991). The resulting pattern of brain activation may eventually activate just a few "grandmother" cells that could be responsible for the detection or recognition of a single object. However, when visual information is ambiguous, incomplete, or noisy, the activation pattern by neurons might be unspecific and may activate multiple grandmother cells. In this case, several object interpretations would be possible. The visual system could then either be forced to choose the most likely interpretation (decision-making) or to switch between them over time (rivalry). Moreover, it may also happen that no object representation is activated. For example, if the stimulus is too noisy, the visual system is simply unable to detect structure, maybe because the code is either too sparse or too distributed. Additionally, presented objects may also be novel to the observer and its sensory activation pattern has not yet been stored as a higher-order neural trace. In the latter case, the new object can be, when required, encoded and stored in the visual system for future purposes. Here it was tested how formed representations deploy attention to objects (Chapter 5), how features can help to minimize ambiguity (Chapter 6), and how the encoding and formation of novel object representations is reflected in the pupil (Chapter 7). These three experiments reported several novel results which are supporting evidence for particular theories on ambiguity and the formation and retrieval of object representations.

Data showed that the deployment of attention to an object is guided by a unique higher-order representation (Chapter 5). An ambiguous stimulus was used to create two separate percepts of either a bound and coherent single object state (i.e., interpretation) and an unbound incoherent multiple object state. Note that the physical appearance of the stimulus remained unchanged while our cognition created multiple interpretations of the stimulus that switches dominance over time. With this stimulus, we tested for differences in target detection and discrimination performance between the single object and multiple object percepts. The dominance of the single object percept resulted in better detection and discrimination performance for areas inside and at the borders of the object compared to outside the object. Vice versa, the dominance of the multiple object percept resulted in better performance outside the object. Thus independent of features and physical appearance of the ambiguous stimulus, attention was only accurately allocated to an object if it was cognitively interpreted as an object. Besides that these findings demonstrate that ambiguous stimuli can provide useful insights into how we process objects and allocate attention, they also support the view that features are not sufficient to explain object-based attention effects and that higher-order object representations are necessary to guide attention. Salient features, such as luminance, luminance contrast, color contrast, shape and collinearity, can, however, facilitate the activation of object representations and resolve ambiguity. It makes sense that an object cannot be recognized as an object if it isn't constituted of features that separate it from its background. Nonetheless, features are not sufficient to allocate attention to objects. We have to be aware of the existence of an object (i.e., objecthood) before the features can be bound together and facilitated as a whole by attentional processes.

The detection of objects and the allocation of attention to them are often followed by recognition or the consolidation of its representation. Object and scene representations are, however, not always effectively stored (**Chapter 7**). Objects are often forgotten (Miss) or they are recognized as familiar while actually being novel (False Alarm). The successful encoding of novel stimuli could therefore be a process that is limited by ambiguity because stimuli are sometimes impoverished and hard to distinguish from others. For instance, when an observer has to encode objects that are similar,

recall performance is typically lower than if objects are highly dissimilar (e.g., Conrad & Hull, 1964). Thus, weak differences in feature modalities across objects may increase ambiguity and consequently impair successful encoding and retrieval. A strong factor that may resolve ambiguity and facilitate object processing is the potential pop-out effect of an object. Here we have demonstrated that the object must contrast with its background along a variety of features to become most salient and easy to recognize (i.e., successfully retrieved) (Chapter 6). The strength of certain object and background features were quantified and luminance, luminance contrast, color contrast, and object size were found to be key features for successful object processing. It was also shown that pupil constrictions reflected novelty of the presented object (Chapter 7). This is termed the pupil old/new effect because new stimuli induce stronger pupillary constrictions as compared to old and familiar stimuli. Besides object retrieval, it was also found that the pupil responded to novelty during the encoding of objects and scenes. If the pupil strongly constricted as a reaction to the presentation of a novel stimulus, there was a larger probability that the stimulus was correctly encoded by the visual system. Taken all together, these results demonstrated that (1) ambiguous conditions can be helpful to learn about object representations in the visual system, (2) ambiguity and resulting multiple neurological object representations can be narrowed down to a coherent and single interpretation by strengthening particular object features, and (3) successful encoding of novel and unambiguous objects was reflected in pupillary constrictions. The next paragraph discusses these three findings from a neuroscientific perspective.

9.1.4 A neural hierarchy for object representations

From the moment light, coming directly from a luminous source or reflected by a visual stimulus, falls on an eye's retina, a stream of neuronal processes is activated that distribute the stimulus' attributes (i.e., features) in multiple components. Luminance, contrast, and colors, and a variety of other features are assessed by functionally separate areas of the visual cortex (Zeki et al., 1991, Zeki, 1978). These functional brain areas project to higher-level areas such as the lateral occipital cortex (LOC) and the temporal lobe to process more abstract representations of objects that consist of the previously

analyzed features (e.g., Aguirre, Zarahn & D'Esposito, 1998, Ishai, Ungerleider, Martin, Schouten & Haxby, 1999, Kourtzi & Kanwisher, 2000, Kourtzi & Kanwisher, 2001, Ostwald et al., 2008). The supposition that there are multiple distinct hierarchical stages that are sequentially activated is not new (e.g., Felleman & Van Essen, 1991, VanRullen & Thorpe, 2001b), but the elucidation of the exact nature of each stage and the behavioral consequences of their mechanisms are challenging and unresolved issues. Here it was investigated how features are extracted and how this process progresses to the activation of higher-order abstract object representations. This hierarchical process seems to be a general mechanism for the detection and identification of objects in natural scenes (Chapter 6) and eventually determines the subsequent allocation of attention to these objects (Chapter 5). Based on recent literature (Roelfsema, 2006), it is tempting to suggest that the allocation of attention is a recurrent (i.e., feedback) process that strengthens the signals of the neurons that are responsible for the processing of the object's features. It was further shown that novel objects and scenes are paired with stronger pupillary constrictions (Chapter 7), an indication that acetylcholine (ACh) - a neurotransmitter that is responsible for the regulation of the constrictory sphincter muscle of the pupil - is likely involved during the successful encoding of novel stimuli into memory. ACh has been indicated as an important neuromodulator of learning (e.g., Roelfsema, van Ooyen & Watanabe, 2010, Seol, Ziburkus, Huang, Song, Kim, Takamiya, Huganir, Lee & Kirkwood, 2007) and the formation of new memories (Hasselmo, 2006, Hasselmo & Giocomo, 2006). It is therefore not unlikely that the pupil reflects the release of ACh through increased constriction as a result of successful memory encoding. The pupil is therefore deemed as a promising tool for future research on the release of ACh (and other neurotransmitters) and its relation to cognition. To conclude, this dissertation has presented evidence that suggests that object processing consists of the extraction of specific low-level features to separate the object from its background. It is further suggested that higher-order features such as anxiety have very limited influence at this initial stage (Chapter 6). This process is followed by the activation of a unique higher-order object representations, and, in case of successful activation, the allocation of attention to the object (Chapter 5), or, in case of unsuccessful matching (i.e., no hit of a stored representation), the encoding of the novel object paired with the release of acetylcholine as

reflected in the pupil (**Chapter 7**). In contrast to previous literature that suggests object-based attention is merely bottom-up driven through features (e.g., Crundall, Cole & Galpin, 2007), it is here shown that the allocation of attention to objects can be guided by higher order object representations as well. Stimulus features are thus essential at early processing stages as they differentiate between multiple interpretations and resolve ambiguity, and object representations are important for further steps related to attention and memory processes.

9.1.5 Pupil dynamics and their implications

The size of the pupil is an extraordinary property of the eye because it reflects a multitude of neural processes and can easily be observed, measured, and utilized for a variety of purposes. Despite the pupil's prone appearance, it is not necessarily a signal that is actively used by others during social interaction. On the contrary, it has recently been proposed that humans have neuronal mechanisms that are engaged with the continuous monitoring of other's pupils (Harrison et al., 2006). This dissertation has shown that observers can indeed detect changes in pupil size and relate it to very obvious mental states of other persons during a competitive game (Chapter 8). It was demonstrated that some observers could use the opponent's pupil to gain the upper hand during a game. The opponent's pupil, however, did not always clearly dilate as a reaction to a decision and was therefore not always informative. After controlling for the pupil's validity, half of the observers were able to successfully extract information from their opponent's pupil, but did not report to have looked for pupil dilations specifically. Thus, although observers have the visual acuity to use the pupil as a visual marker and "read" a person's mind, they were not fully aware of the specific pupil dynamics that contain most information. It would be interesting to test in forthcoming studies whether other cognitive states can be read-out from the pupil in real-life situations and to what extent the reading out of bodily signals is an implicit and evolutionary developed social skill. The exact timing of pupil dilations or constrictions might provide information about the underlying nervous system that is responsible for its dynamics (Steinhauer & Hakerem, 1992), or about the temporal properties and stages along the hierarchical stream of visual processing for a variety of cognitive states (Chapter 6).

Yet it remains considerably vague which cognitive processes underlie changes in pupil size. Although this dissertation presented several correlations of cognitive concepts and behaviors with pupillary dynamics (Chapter 4-8), it is difficult to interpret these findings in the context of a unified framework or single process. For example, it was here reported that pupil size correlates with anxiety, target detection and identification performance, response latencies, confidence, successful memory encoding, and decision-making. A gross part of studies on pupil size as an indicator of cognitive processes have tried to interpret their findings in the context of arousal or mental effort (Andreassi, 2000, Beatty & Lucero-Wagoner, 2000, Janisse, 1977, Loewenfeld & Lowenstein, 1993, for review). Arousal is, however, not sufficient to explain the findings of this dissertation because several results did not fit its properties. For instance, it was shown that observers with increased average anxiety for threatening animals, had smaller pupil sizes (Chapter 6). Assuming that an increased level of anxiety leads to an increased level of arousal, more anxious observers are expected to have an over-all larger pupil size. In a similar vein, observers that had to memorize images had increased constrictions of pupil responses as a reaction to the onset of images that were later correctly remember compared to images that were forgotten (Chapter 7). Again, it makes most sense that images, that are easily remembered, increase arousal and therefore increase pupil size rather than constrict it. Then which processes are responsible for the differences in pupil size during the visual processing of images? As mentioned before, many cognitive processes affect the pupil. For example, surprise (Preuschoff et al., 2011) and anticipation of upcoming events (Reinhard & Lachnit, 2002a) can also dilate the pupil. To address how all these cognitive concepts may relate to changes in pupil size, a fresh look is taken at the neural processes underlying pupil dynamics in the next paragraph.

9.1.6 A neural account of pupil dynamics

The size of an eye's pupil is controlled by two muscles: A radial and sphincter muscle that dilate and constrict the pupil respectively. The radial muscle is activated by the release of norepinephrine (NOR), a noradrenergic hormone and neurotransmitter. Dilation of the pupil is a consequence of the activation of adrenergic related processes such as arousal (Hall, Uhrich & Ebert, 2001), stress (Tanaka, Yoshida,

Emoto & Ishii, 2000), attention (Aston-Jones, Rajkowski & Cohen, 1999, Coull, Jones, Egan, Frith & Maze, 2004), behavioural orienting (Aston-Jones et al., 1999, Beatty & Lucero-Wagoner, 2000), and decision-making (Einhäuser et al., 2010). The sphincter muscle is activated by the release of the neurotransmitter acetylcholine (ACh). Constriction of the pupil is a result of the cholinergic related responses that relate to neural plasticity (Bakin & Weinberger, 1996, Easton, Ridley, Baker & Gaffan, 2002, Juliano, Ma & Eslin, 1991, Kilgard & Merzenich, 1998, Seol et al., 2007, Winkler, Suhr, Gage, Thal & Fisher, 1995), behavioural reward (e.g., Mark, Shabani, Dobbs & Hansen, 2011), sustained attention (Himmelheber, Sarter & Bruno, 2000), and learning (Roelfsema et al., 2010). Note that both the increase and decrease of the release of these neurotransmitters can dilate and constrict the pupil. Furthermore, their effects are not independent as the release of ACh can inhibit the release of NOR (Steinhauer et al., 2004). In sum, pupil size depends on a subtle balance between the amount of ACh and NOR in the nervous system. Although studies on how cognition is reflected in the pupil generally report only effects of dilations, the neural systems driving pupil size depend on both types of neurotransmitters and thus both can also contribute to constrictions of the pupil. For example, it was demonstrated that the increased levels of anxiety might relate to increased levels of attention or focus on the stimulus mediated through ACh which consequences in a smaller rather than larger pupil size (Chapter 6). Additionally, the learning of tasks or encoding of novel stimuli may also be accompanied by the release of ACh and therefore the constriction of the pupil (Chapter 7). The role of both ACh and NOR in cognitive functioning has often been neglected in neuroscientific studies and it is here proposed that pupillometry is an easy and informative method to measure the effects of these neurotransmitters on cognition. With the current knowledge about the pupil, pupillometry is a comparatively simple and effective research paradigm and future studies may uncover a wide range of cognitive functions that are controlled by ACh and NOR. Through the inhibition of either the dilator or constrictor muscles of the pupil with drugs, the separate effects of ACh and NOR can be assessed during cognitive tasks. Drugs that affect one of the muscles in isolation have effectively been administered in earlier studies on pupil dynamics (Steinhauer et al., 2004) and seems to be a promising

test-bed for further research on the separate contributions of either ACh and NOR to attention, arousal, memory, and other cognitive mechanisms.

9.2 Conclusion

This dissertation assessed how visual ambiguity arises, what its properties are, how it affects cognition, and which factors can resolve it. By using a variety of tools, including perceptual rivalry, rapid object detection paradigms, memory encoding tasks, pupil dynamics, and introspection, it was studied (1) which factors underlie the rate and speed of changes in perceptual interpretations induced by ambiguity, (2) the reflection of ambiguity in reflexes and cognitive awareness, (3) the spatial allocation of attention to resolve ambiguity in objects, (4) recognition performance of ambiguous object representations, (5) the ambiguity tied to the encoding of object representations, and (6) the successful and implicit search for cognitive markers in seemingly ambiguous pupil dynamics. In conclusion, this dissertation has outlined how our visual system handles sensory signals from noisy surroundings that inevitably lead to ambiguous situations in which multiple percepts, representations, decisions, and locations have to rival for attention and processing resources. Ambiguity is a core property of sensory systems and provides several advantages to cope with signals from our every day surroundings.

10. Summary

10.1 English summary of dissertation

Brains can sense and distinguish signals from background noise in physical environments, and recognize and classify them as distinct entities. Ambiguity is an inherent part of this process. It is a cognitive property that is generated by the noisy character of the signals, and by the design of the sensory systems that process them. Stimuli can be ambiguous if they are noisy, incomplete, or only briefly sensed. Such conditions may make stimuli indistinguishable from others and thereby difficult to classify as single entities by our sensory systems. In these cases, stimuli fail to activate a representation that may have been previously stored in the system. Deduction, through context and experience, is consequently needed to reach a decision on what is exactly sensed. Deduction can, however, also be subject to ambiguity as stimuli and their properties may receive multiple representations in the sensory system. In such cases, these multiple representations compete for perceptual dominance, that is, for becoming the single entity taken by the system as a reference point for subsequent behavior. These types of ambiguity and several phenomena that relate to them are at the center of this dissertation.

Perceptual rivalry, the phenomenal experience of alternating percepts over time, is an example of how the brain may give multiple interpretations to a stimulus that is physically constant. Rivalry is a very typical and general sensory process and this thesis demonstrates some newly discovered properties of its dynamics. It was found that alternations between three perceptual interpretations – a relatively rare condition as rivalry generally occurs between two percepts – follow predictable courses (Chapter 2). Furthermore, such alternations had several properties that determine their speed and direction of spatial spread (suppression waves) in the visual field (Chapter 3). These properties of ambiguity were further strongly affected by attention and other introspective processes. To demarcate the true underlying process of perceptual rivalry and the accompanied changes in awareness, these subjective processes need to be either circumvented or controlled for. An objective measure of perceptual rivalry was proposed that resolved this issue and provided a good alternative for

introspective report of ambiguous states (Chapter 4). Changes in percepts occur along a specific feature domain such as depth orientation for the famous Necker cube. Alternatively, luminance may also be a rivalry feature and one percept may appear brighter as the other rivaling percept. It was demonstrated that the pupil gets smaller when a percept with high luminance becomes dominant, and vice versa, gets bigger when a percept with low luminance gets dominant during perceptual rivalry. As such, the pupil can serve as a reliable objective indicator of changes in visual awareness. By using such reflexes during rivalry, several new properties of alternations were discovered and it was again confirmed that introspection can confound the true processes involved in ambiguity.

Next, the usefulness of ambiguous stimuli was explored in the context of objects as entities (Chapter 5). Some ambiguous stimuli can induce two percepts that alternate along the feature domain of object coherency, that is, whether a single coherent object or multiple incoherent objects are seen. In other words, an ambiguous stimulus can induce two cognitive interpretations of either seeing an entity or not. It was reported that being aware of a single coherent object results in the increase in visual sensitivity for the areas that constitute the object. These results are evidence of how the activation of a representation of a single and unique object can guide and allocate attentional resources to relevant areas in the visual field in a top-down way. It was further explored which features help to bottom-up access such object representations (Chapter 6). Ambiguity of objects can be successfully resolved by adding strong contrasts between the object and its background in luminance and color. The size and variability of the object's shape was also found to be an important factor for its successful detection and identification. Furthermore, the characteristics of objects do not only determine the rate of success in a recognition task, but are equally important for the storage of their representations in memory if, for instance, the object is novel to the observer. The subjective experience of a novel object is also subject to ambiguity and objects may appear novel to the observer although they are familiar (i.e., previously shown to the observer), or vice versa, they appear familiar to the observer although they are actually novel. It was here shown that such subjective effects are reflected in the pupil (Chapter 7). In addition, if novel images were presented to observers, their pupils constricted stronger as compared to if familiar images were presented. Similarly, if novel stimuli were shown to observers, pupillary constrictions were stronger if these stimuli were successfully stored in memory as compared to those later forgotten. As such, the pupil reflected the cognitive process of novelty encoding. Finally, it was tested whether other cognitive processes, such as decision-making – an important process when multiple options are available and ambiguity has to be resolved with a conscious decision – were also reflected in changes of pupil size (Chapter 8). It was confirmed that the pupil tends to dilate after an observer has made a decision. These dilations can successfully be detected between individuals and further used to gain the upper hand during an interactive game.

In sum, this thesis has explored how ambiguous signals affect perception and how ambiguity inside perceptual systems can be used to study processes of the brain. It is found that ambiguity follows predictable courses, can be objectively assessed with reflexes, and can provide insights into other neuronal mechanisms such as attention, object representations, and decision-making. These findings demonstrate that ambiguity is a core property of the sensory systems that enable living beings to interact with their surroundings. Ambiguity adds variation to behavior, allows the brain to flexibly interact with the world, and lies at the bottom of the dynamics of sense, interpretations, and behavioral decisions.

10.2 Deutsche Zusammenfassung der Dissertation

Unser Gehirn muss zu jeder Zeit relevante Signale von irrelevanten Informationen trennen. Dazu müssen diese als spezifische Einheiten erkannt und klassifiziert werden. Mehrdeutigkeit ist ein wesentlicher Aspekt dieses Verarbeitungsprozesses und kann durch verrauschte Eingangssignale und durch den Aufbau unserer sensorischer Systeme entstehen. Beispielsweise können Reize mehrdeutig sein, wenn sie verrauscht oder unvollständig sind oder nur kurzzeitig wahrgenommen werden. Unter solchen Bedingungen werden Wahrnehmung und Klassifikation eines Reizes deutlich erschwert. Bereits vorhandene kognitive Repräsentationen werden somit möglicherweise nicht aktiviert. Folglich müssen Rückschlüsse über die Reize aufgrund von Kontext und Erfahrung gezogen werden. Ein und derselbe Reiz kann jedoch unterschiedlich repräsentiert und im sensorischen System kodiert werden. Da nur eine Repräsentation die Basis zukünftigen Handelns bilden kann, entsteht eine Art Konkurrenz

innerhalb der Wahrnehmung. Derartige Wahrnehmungsphänomene, die mit der Mehrdeutigkeit von Reizen in Verbindung stehen, bilden den Mittelpunkt der vorliegenden Dissertation.

Wenn einem physikalisch konstanten Reiz mehrere Interpretationen zugeordnet werden, entsteht ein Wechsel zwischen diesen Einordnungen, den man wahrnimmt und Rivalität ("rivalry") nennt. In dieser Dissertation werden diverse neue Erkenntnisse zu diesem grundlegenden Phänomen der sensorischen Verarbeitung beschrieben. So wird gezeigt, dass Übergänge zwischen drei wahrgenommenen Interpretationen – ein vergleichsweise selten untersuchtes Phänomen, da Rivalität meist mit zweideutigen Reizen untersucht wird - vorhersehbaren Mustern folgen (Kapitel 2). Darüber hinaus zeigt sich, dass derartige Übergänge spezifische Eigenschaften aufweisen, welche die Geschwindigkeit und die Richtung ihrer räumlichen Ausbreitung im visuellen Feld bestimmen (Kapitel 3). Diese Eigenschaften der Mehrdeutigkeit werden weiterhin stark von Aufmerksamkeit und anderen, introspektiven Prozessen beeinflusst. Um die der Rivalität in der Wahrnehmung tatsächlich zugrundeliegenden Prozesse und die damit verbundenen Änderungen des Bewusstseins von derartigen subjektiven Prozessen abzugrenzen, müssen letztere kontrolliert oder sogar vollständig umgangen werden. Ein objektives Maß der Rivalität in der Wahrnehmung wird zur Lösung dieser Aufgabe vorgeschlagen und bietet eine wertvolle Alternative zu introspektivem Berichten über den Wahrnehmungszustand (Kapitel 4). Übergänge in der Wahrnehmung entstehen entlang einer bestimmten Merkmalsdimension des Reizes, wie beispielsweise der Orientierung des berühmten Neckerwürfels. Zudem kann auch eine Änderung in der Merkmalsdimension der Luminanz eine unterschiedliche Interpretation des Reizes hervorrufen. Es wird gezeigt, dass die Pupille kleiner wird, wenn eine Interpretation mit hoher Luminanz die Wahrnehmung übernimmt, und umgekehrt, dass die Pupille größer wird, wenn eine Interpretation mit niedriger Luminanz die Wahrnehmung übernimmt. Folglich kann die Pupille als ein zuverlässiges und objektives Maß für Änderungen in der Wahrnehmung verwendet werden. Durch die Verwendung solcher objektiven Maße konnten neue Eigenschaften der Übergänge in der Wahrnehmung aufgezeigt werden, welche die Theorie unterstützen, dass Introspektion die der Verarbeitung mehrdeutiger Situationen zugrundeliegenden Prozesse merklich beeinflussen kann.

Als Nächstes wurden mehrdeutiger Reize im Zusammenhang mit der Wahrnehmung von Objekten eingesetzt (Kapitel 5). Am Beispiel der Kippfigur des "bewegten Diamanten" wird dabei die Bedeutung von mehrdeutigen Reizen veranschaulicht. Beim bewegten Diamanten werden zwei Interpretationen wahrgenommen, die sich entlang der Dimension der Objektkohärenz abwechseln. Das bedeutet, dass die Wahrnehmung zwischen einem einzelnen zusammenhängenden Objekt (Diamant) und mehreren unzusammenhängenden Komponenten kippt. Es wird gezeigt, dass die Interpretation des Reizes als ein einziges kohärentes Objekt, verglichen mit der Interpretation als mehrere Komponenten, zu einer Erhöhung der visuellen Empfindlichkeit innerhalb des Objektes führt. Diese Ergebnisse sind ein Beleg dafür, wie die Aktivierung einer Interpretation eines Reizes als Einzelobjekt (im Vergleich zur Komponentenwahrnehmung) dazu führt, dass die Aufmerksamkeit top-down zu den relevanten Bereichen des Gesichtsfeldes gelenkt wird. Es wird weiter untersucht, welche Eigenschaften des Reizes zu einer bottom-up Aktivierung der Interpretation solcher Objekte beitragen (Kapitel 6). Die Mehrdeutigkeit von Objekten kann erfolgreich aufgehoben werden, indem man einen starken Kontrast in Luminanz oder Farbe zwischen dem Objekt und dem Hintergrund erzeugt. Auch die Größe und die Form haben einen großen Einfluss auf die Detektion und Identifikation von Objekten. Des Weiteren sind die Eigenschaften eines Objektes nicht nur bestimmend für die Erfolgsquote bei der Objekterkennung, sondern ebenso bedeutend für die Speicherung der Repräsentation im Gedächtnis, beispielsweise von neu wahrgenommenen Objekten. Das Klassifizieren von Objekten durch die Versuchsperson wird ebenfalls durch Mehrdeutigkeit beeinflusst. So kann ein Objekt der Versuchsperson einerseits als neu erscheinen, obwohl es bereits bekannt war, weil es beispielsweise der Versuchsperson schon einmal gezeigt worden ist. Andererseits kann auch ein eigentlich unbekanntes Objekt der Versuchsperson dennoch vertraut vorkommen. In dieser Arbeit wird gezeigt, dass solche subjektiven Effekte einen Einfluss auf die Pupillengröße haben (Kapitel 7). Außerdem verkleinert sich die Pupille der Versuchspersonen beim Betrachten neuer Bilder stärker als bei bekannten. Ein ähnlicher Effekt wird gefunden, wenn das Bild vorher erfolgreich im Gedächtnis gespeichert wurde. Daher ist es wahrscheinlich, dass die Pupille die Verfestigung von neuen Objekten im Gedächtnis widerspiegelt. Abschließend wird untersucht, ob sich kognitive Prozesse, wie Entscheidungsfindung – ein wichtiger Prozess, falls mehreren Optionen zur Verfügung stehen und Mehrdeutigkeit aufgehoben werden soll – auch in der Pupille widerspiegeln (Kapitel 8). Es wird zunächst bestätigt, dass die Pupillen sich erweitern, nachdem man eine Entscheidung getroffen hat. Neu wird gezeigt, dass diese Pupillenausdehnungen erfolgreich von anderen Personen erkannt und verwendet werden können, um ein interaktives Spiel gegen die erste Person (den "Gegner") zu gewinnen.

Insgesamt wird in dieser Dissertation untersucht, wie mehrdeutige Reize die Wahrnehmung beeinflussen und wie Mehrdeutigkeit verwendet werden kann, um Prozesse des Gehirns zu studieren. Es hat sich gezeigt, dass Mehrdeutigkeit vorhersehbaren Mustern folgt, sie objektiv mit Reflexen gemessen werden kann, und Einblicke in neuronale Prozesse wie Aufmerksamkeit, Objektwahrnehmung und Entscheidungsmechanismen liefern kann. Diese Ergebnisse zeigen, dass Mehrdeutigkeit eine zentrale Eigenschaft sensorischer Systeme ist, und Lebewesen in die Lage versetzt, mit ihrer Umwelt flexibel zu interagieren. Mehrdeutigkeit macht das Verhalten vielfältiger, ermöglicht es dem Gehirn, mit der Welt auf verschiedenen Wegen zu interagieren, und ist die Basis der Dynamik von Wahrnehmung, Interpretation und Entscheidung.

11.References

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	Naber, M., Rutishauser, Einhäuser, W. (2010). Pupil size predicts image recognition. Visual Neuroscience Summer School Rauischholzhausen
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14. Declaration of Sovereignty

Erklärung

Ich versichere, dass ich meine Dissertation

Cognitive Interpretations of Ambiguous Visual Stimuli

selbständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, Deutschland