Illusions in vision and other modalities are captivating displays of the virtual nature of our subjective world. For this reason, illusions have been an important subject of scientific and artistic endeavors. In his target article, Heiko Hecht discusses the utility of the illusion concept and arrives at the negative conclusion that the traditional understanding of illusions as a discrepancy between world and perception is misguided. In his opinion, the more interesting and revealing cases are when the discrepancy is noticed and accompanies the perceptual state, or when, in the cognitive domain, the discrepancies become exceedingly large, but go unnoticed nonetheless. In this commentary, I argue that Hecht’s criticism of the illusion concept is interesting and deserves further study. But at the current stage, I don’t see that the model captures the essential features of illusory states. The processes on which Hecht focuses can be considered metacognitive appraisals of the respective sensory events, an interesting topic by itself. In the second part and as an overview, I review how research on the classical apparent-motion illusion has shaped our understanding of the neural underpinnings of motion perception and consciousness in general.

Keywords
Apparent motion | Bistability | Cognition | Illusion | Motion quartet | Multistability | Naïve realism | Perception | Phenomenal opacity | Phenomenal transparency | Sensation | Vection

1 Illusions in science and culture

A main staple of research in cognitive science and especially vision science has been, and still is, the investigation of illusions. For one, it is just an amazing fact that although we think that our experience of the world is direct, we live by a subjective model of our environment. We feel that we perceive the world as it is, a naïve realism as we might call it, but we are just not aware that the world is only presented to us as a (re-)construction of our nervous system. In more philosophical terms, this fundamental property of our experience has been referred to as “phenomenal transparency” (Metzinger 2003a), the inability to recognize that our mental states are representations. This is probably the reason why we are baffled in cases when the subjective character of our perception becomes evident, although this rarely occurs under natural conditions.

At least in the context of our modern culture, many people will have had the experience that their train is leaving the station when in fact they have just watched the train on the opposite side of the platform taking off. This phe-
nomenon is termed vection, and everybody who has had this experience will remember the moment of insight when a cue destroys the illusion of self-motion and we realize that our train hasn’t budged. A more historical example of illusions under natural conditions is the waterfall illusion,—, a type of motion aftereffect. After looking at a waterfall or flowing water for a long time, static objects, e.g., the river bank or trees, seem to move in the direction opposite to the previously perceived water flow, probably due to adaptation effects in brain regions processing motion (Anstis et al. 1998). Early descriptions of the effect have been attributed to Aristotle (384–322 BCE) and Lucretius (99–55 BCE; Wade 1998). But apart from these few examples, it’s rarely the case that the constructive nature of our perception is noticeable in everyday life.

Illusions have become a part of our popular culture and have had a strong impact on art. A whole art movement in painting, Op Art, is based on using known and discovering new visual illusions. It is a cultural version of vision research, presenting the fascinating nature of illusions to the public in aesthetically appealing ways. Illusions also feature prominently in the work of surrealist painter Salvador Dalí and other modern artists. For such artists, the medium presented a way of expressing the constructive nature of perception and signalled a departure from realism. For painters in general, knowledge about optics and the basis of visual perception has always been important for guiding the construction process of paintings and the refinement of techniques in order to achieve certain effects in the eye of the beholder. The entwinement of science and art is scrutinized in recent work looking at the interaction between fields (Zeki 1999). Two other forms of art that were more or less invented in close interaction with science are photography and film-making. The very basis of TV and movie presentations is rooted in the fact that we are able to fuse a rapid sequence of static images to construct a natural impression of moving objects. TV displays, projectors, and computer screens work with a certain refresh rate at which subsequent images are presented; the rate can be as low as 24 Hz in cinematography. The basic phenomenon that allows us to create a natural perceptual flow from flickering images is referred to as apparent motion, a type of illusory motion.

Because of the fascination with illusions and its influence on culture, illusions have been guiding research on visual perception for a long time—and continue to do so. But this is not the only reason for the utilization of illusions in science. Illusions are a powerful tool for understanding mechanisms of sensory processing in the brain that are unexpected or counterintuitive. Many motion illusions where motion can be seen in static displays (often seen in the entertainment sections of magazines) depend on a specific configuration of color values in directly abutting picture elements. These configurations of picture elements are repeated and cover the entire display, in sum creating a striking motion impression. Psychophysical experiments showed that the key to the illusion is the configuration of neighboring elements, whose effects cannot be predicted by current models of visual processing. Additional neurophysiological measurements in the same study demonstrated that different picture elements were processed with different latencies in certain areas of the visual cortex, mimicking a motion signal (Conway et al. 2005). This suggested a neural explanation for the occurrence of the illusion and led to a revision of existing models of motion selectivity.

Another driving force for the use of illusions in research was a resurgence of interest in understanding conscious perception. At the beginning of the 1990s, Francis Crick and Christof Koch started to publish a sequence of conceptual papers advocating the investigation of consciousness with empirical, and especially neuroscientific methods (Crick & Koch 1990, 1995, 1998). Since then the number of papers on consciousness has grown steadily in the domain of cognitive neuroscience. Certain visual illusions lend themselves specifically to investigating the nature of conscious processing. Some of the most prominent paradigms display the characteristic of bistability or multistability: When presented to observers, conscious perception alternates between two (bistability) or multiple (multistability) interpretations although the

physical characteristics of the display do not change. Rubin’s face-vase illusion and the Necker Cube are just the most prominent among a multitude of examples for multistability (Kim & Blake 2005). The promise of using multistability is that it allows for disentangling the neural representation of the physical stimulus characteristics from the processes giving rise to conscious perception. The logic of the approach is that changes in neural activity accompanying switches in subjective experience during constant physical stimulation provide a guide to understanding the neural underpinnings of consciousness.

2 Hecht’s criticism of the illusion concept

In his target article “Beyond illusions: On the limitations of perceiving relational properties,” Heiko Hecht (this collection) begins with a discussion of the traditional concept of illusion and how it has been employed in the context of research on vision. In its most basic sense, an illusion refers to a difference between our representation of a given scene and its actual physical properties. In an interesting take on the utility of illusions in research, Hecht suggests that the mere discrepancy between our perception and the real world—what he calls illusion\textsubscript{d} (“d” for “discrepancy”)—is less useful than one might think. In simple terms, our perception is off to some degree in many cases. But still, on the other hand it is amazing how on-target it is most of the time: it is sufficiently accurate for an effective interaction with the world. For Hecht, the term “illusion” should be reserved for situations when discrepancies (illusion\textsubscript{d}) are manifest, i.e., when the error is part of the experience and we become aware of it. This is termed illusion\textsubscript{m} (“m” for “manifest”) and is supposed to be the more interesting case. The moment of insight for the train-ride illusion described above might be a good example. Interpreting relative motion between trains as self-motion is often an adequate interpretation, but the error is manifested in a striking fashion experimentally when we spot a part of the platform that indicates unmistakably that we are still in the same place.

In addition to the distinction between illusion\textsubscript{d} and illusion\textsubscript{m}, Hecht is concerned with cognitive illusions in comparison to the well-known perceptual illusions. His interesting observation is that when we move away from perception, the discrepancies between the real world and our judgments become even larger, sometimes to an absurd level. Humans are notoriously bad at everyday physics. Hecht mentions that we see nothing wrong with fabricated scenes that glaringly contradict Newtonian physics, and even our spontaneous actions reveal the same degree of error. Nevertheless, they are hardly ever noticed, i.e., illusion\textsubscript{d} rarely becomes illusion\textsubscript{m} in the cognitive domain. That this is especially the case for relational properties Hecht demonstrates with a series of his own experiments on physics judgments by university students. Even participants that should at least have some theoretical knowledge about the laws governing the real world (physics students) are surprisingly bad at finding the right answers to quizzes on balancing beams made of different materials with different weight distributions (Experiment 1) and on the slipperiness of surfaces (Experiment 2). In these examples, the students’ judgments are in stark contrast to the actual, real-world outcomes, which were also empirically tested in addition to deriving predictions from the laws of physics. So even though the paradigms were chosen to be experientially accessible and ecologically relevant, it seems that our cognitive system does not care about correctness or even rough approximations that would point it in the right direction. Even the mere ordering of solutions without providing quantitative details is seldom correct.

To summarize, Hecht suggests that the small deviations of our perceptual representations are no match for the sometimes extreme discrepancies found in the cognitive domain. Illusion\textsubscript{d} is the norm rather than the interesting exception in sensory processing because—at least in vision—the full three-dimensional representation of the world has to be derived from a limited array of two-dimensional information on the retinae. Hecht (this collection) refers to this as the “underspecification problem.” For an efficient solution to the underspecification prob-

lem, the system employs a range of assumptions and constraints on the makeup of the world to guide the reconstruction process. For Hecht, perception is therefore always fraught with cognitive elements. This is even more so when discrepancy is detected; illusion becomes illusion. Then, cognitive judgments are involved, and an explicit comparison process is initiated that allows us to capture the discrepancy and which makes it experientially available.

3 The role of illusions in vision research

Hecht provides compelling evidence for the error-prone nature of everyday judgments, especially when it comes to relational properties. His observation of an antagonism between the size of discrepancies and their detectability is interesting. Moving from the perceptual to the cognitive domain, the size of discrepancies increases, but at the same time we are less likely to notice those errors. But there are a few points of dissent I would like to discuss in what follows. (1) The discussion of the cognitive nature of perception is long-standing and won’t be solved in the near future, especially because the term “cognition” is notoriously imprecise. Nevertheless, I am not convinced that the cognitive aspect that is supposed to be part of perceptual as well as cognitive illusions in Hecht’s view is a necessary ingredient for a proper concept of illusion. (2) Hecht’s arguments are a welcome incentive to reflect upon the concept of illusion and its role for research. Although he does not negate the role of perceptual illusions for vision research, he is rather critical concerning the utility of traditional illusion research, especially with respect to the underspecification problem. Drawing on the vast body of research on apparent motion, I would like to provide an example of a positive research program that has accumulated valuable insights into the mechanisms underlying visual motion processing. This is not necessarily in contradiction to Hecht’s stance. The focus of research on illusions has focused more on the neural mechanisms of visual processing and specifically on the neural correlates of conscious perception. In this sense, the research lines can be seen as complementary.

Nevertheless, I would argue in conclusion that the term illusion is well anchored in the perceptual domain and plays an important guiding role for research on visual processing.

There is a long tradition in vision research of considering the influence of cognition on perceptual processes. The basis for the early investigations on vision and, more generally, on sensory processing in the 19th century and early 20th century was the distinction between sensation and perception. One of Helmholtz’s (1863) definitions captures the main line of thought:

Empfindungen nennen wir die Eindrücke auf unsere Sinne, insofern sie uns als Zustände unseres Körpers (speciell unserer Nervenapparate) zum Bewusstsein kommen; Wahrnehmungen insofern wir uns aus ihnen die Vorstellung äusserer Objecte bilden. ¹

The definition can be seen as a continuation of a philosophical tradition that has the intention of separating pure states of sensory reception from the more cognitive aspects concerned with the reconstruction of the outer world. Already at this time, different authors were aware of the fact that these definitions did not draw a clear dividing line between different types of sensory states. For example, Sigmund Exner (1875) refers to Helmholtz’s definition and points to several examples for which the distinction becomes muddled. His observant conclusion is that the philosophical concepts do not fare well in the field of brain physiology and that contradictions have to be resolved in future models of sensory processing (Exner 1875, p. 159). So despite its initial allure, the distinction between sensation and perception produced more problems than solutions.

An interesting recent model of the interaction between perception and cognition has been proposed by Vetter & Newen (2014). They review the current empirical literature on cognitive penetration of perceptual processing and

¹ English:
“We call the impressions on our senses sensations, insofar as we become aware of them as states of our body (especially of our nervous system); we call them perceptions insofar as we create representations of external objects.” [My translation]

find compelling evidence that cognitive penetration of perception is ubiquitous. They distinguish four stages of processing in the sensory (visual) hierarchy: (1) basic feature detection, (2) percept estimation, (3) learned visual patterns, and (4) semantic world knowledge. According to their account, almost all possible interactions between processing levels occur under normal conditions and top-down connections can be considered forms of cognitive penetration. They argue that it’s not a question of whether cognition influences perception, but rather of what type of interaction takes place in any given case. They advocate a move away from the general conceptual question of the cognition-perception relationship towards an empirically-based consideration of the interactions between different levels of the processing hierarchy.

Importantly, none of the stages characterized by Vetter & Newen (2014) capture the cognitive component Hecht has in mind. The realization that there is a discrepancy between percept and the real world is not something involved in the construction of the perceptual content itself. It seems that this is more along the lines of a metacognitive appraisal of the current situation. With reference to Metzinger’s (2003b) concept of phenomenal transparency (a naive-realistic stance towards the perceived world) referred to at the beginning of the commentary, it is now the complementary feature of phenomenal opacity—a situation in which the representational character of experience becomes available to the subject—that might play a role here. Metzinger (2003b) refers to cases of lucid dreaming and drug-induced hallucinations as prime examples of phenomenal opacity. Interestingly, it is not sufficient for him that we have accompanying reflexive thoughts on the nature of perceptual representations (the “philosopher’s stance”, as one could say), but we must also be attentively engaged with the perceptual content and recognize the illusory nature of the process. Therefore, it seems to be the case that neither the views of Vetter & Newen nor Metzinger’s concept of phenomenal opacity seem to capture the cognitive component Hecht has in mind. But in my view, such models of cognitive penetration are much more intimately linked with the illusion concept, because they provide an understanding of how the very nature of the experience is modulated by cognitive processes. Hecht’s model doesn’t seem to capture that aspect, since it functions more as a cognitive commentary on the impenetrable perceptual process. It is unclear why this metacognitive appraisal should be considered a hallmark of illusion experiences.

When Hecht argues for abandoning the term “illusion” in the perceptual domain, he also refers to Wertheimer’s classical work on apparent motion (1912) and contends that the Gestalt psychologists “avoided the term illusion” (Hecht this collection). It is true that, for example, Wertheimer (1912, pp. 167–168) himself mentions in a footnote that “illusion” should not be used to refer to a discrepancy relative to the physical world because his main concern is with mental states. (The German word in the original paper is “Täuschung,” which is indeed best translated as “illusion” in this context.) Nevertheless, the passage is not very clear on the reasons for rejecting the reference to discrepancy. Again, it seems that the distinction between sensation and perception (see above) is lingering in the background. Even assuming a correct sensory reception (sensation) of the apparent-motion inducers, something is added that goes beyond the raw sensory data. In a later section of the paper (Wertheimer 1912, p. 228), this becomes clearer when Wertheimer analyzes another possible meaning of “Täuschung,” i.e., failure of judgment (German: “Urteilstäuschung”). It is important for him that apparent motion is not a result of cognitive processes, of inferences of the type: “If an object was there just before and now is over here, it must have moved between the points.” He is convinced of the perceptual nature of the phenomenon and rejects the idea that cognition plays an important role. Again, there is some ambiguity with respect to the usage of the term “illusion” here. This being said, throughout the article Wertheimer uses the noun-form “Täuschung” thirty-five times and also refers to other motion illusions that were already as well known at the time as “Täuschung.” On my...
reading, his main intention was to prove that apparent motion is the result of a low-level perceptual process and that it is indeed illusory in nature.

Wertheimer’s 1912 paper, with its detailed psychophysical investigation of the apparent-motion phenomenon is commonly considered to be the founding event of the Gestalt movement (cf. Sekuler 1996; Steinman et al. 2000), although this might not be the complete picture (Wertheimer 2014). We have just passed the centenary of Wertheimer’s seminal article, but still there is much work to be done to provide a complete picture of the processes involved in apparent-motion perception at behavioral, computational, and neurophysiological levels of description. In my view, apparent motion is a paradigmatic case of an illusion that has fertilized the understanding of motion processing and continues to do so. Given the roughly one hundred years of research on apparent motion, it is worthwhile to take stock (briefly) and see where investigations associated with this paradigm have taken us.

Psychophysical investigations of apparent motion are too numerous to review extensively here. Early studies focused on describing the basic features of the phenomenon. Korte’s laws (1915) are still part of textbook knowledge in vision research; he described the influence of different stimulus characteristics (stimulus strength, spatial and temporal separation etc.) on the quality of apparent-motion perception. New varieties of apparent motion were described in the following, one of the most important ones being the motion quartet (Neuhaus 1930; von Schiller 1933; see video: http://www.open-mind.net/videomaterials/kohler-motion-quartet). This is a bistable version of apparent motion, where two frames with diagonally opposing dots at the corners of a virtual rectangle are flashed in alternation. The identical stimulus sequence can be interpreted as being in vertical or horizontal motion. During longer presentations of the unchanging stimulus, conscious perception will spontaneously switch between the possible alternatives. It is therefore an important example of a multistable display, which allows various interpretations with the same physical input. Early on, it was noticed that the integration of motion inducers in the motion quartet processed within brain hemispheres is facilitated relative to integration between hemispheres (Gengerelli 1948), a fact we will come back to later on. After a relative hiatus in the 50s and 60s, apparent motion again took center stage in the 70s. It was the basis for the work of Paul Kolers (1972) on configuration effects and for the first investigation of computational principles of motion perception by Shimon Ullman (1979). At the same time, distinctions between different types of apparent motion were introduced (Anstis 1980; Braddick 1974, 1980), later culminating in the three-layered hierarchical system of motion types proposed by Lu & Spering (1995, 2001).

Currently, in all domains (psychophysical, computational, neurophysiological) there are ongoing research endeavors cross-fertilizing each other in the search for mechanisms underlying illusory perception of motion. After the turn of the millennium, the broad availability of brain-imaging methods spurred the investigation of the neural mechanisms underlying apparent-motion perception. By and large, the same areas that process real motion are involved in the (Muckli et al. 2002; Sterzer et al. 2003; Sterzer et al. 2002; Sterzer & Kleinschmidt 2005), supporting the assumption that results from studies on apparent motion can be transferred to other types of motion processing. Another interesting result from studies using functional magnetic resonance imaging was that traces of the virtual apparent-motion path, the illusory motion between inducers, can already be seen in the primary visual cortex, the earliest stage of visual cortical processing (Larsen et al. 2006; Muckli et al. 2005). This effect is probably mediated through feedback connections from higher areas (Sterzer et al. 2006), explaining the fact that normal visual functioning is disturbed on the path of apparent motion (Yantis & Nakama 1998) and also supporting Wertheimer’s (1912) original claim that apparent motion is a perceptual phenomenon that does not depend on cognitive inferences Animal studies are starting to elucidate the more fine-grained neural...
mechanisms subserving apparent-motion processing. Neurophysiological investigations in the animal model demonstrated complex wave patterns of interactions between several cortical areas during the perception of apparent motion (Ahmed et al. 2008). This work also inspired a formal model of these interactions elucidating the computational principles underlying the representation of apparent motion in the brain (Deco & Roland 2010).

In my own recent research, I have specifically looked at interindividual differences in the perception of apparent motion and its anatomical basis. As mentioned above, for the bistable motion quartet there is a difference between perceiving apparent motion in the vertical and horizontal direction. Observers show a bias towards perceiving vertical motion when they fixate on the middle of the motion quartet (Chaudhuri & Glaser 1991). A possible explanation for this is that due to the way the visual field is represented in the visual cortex, vertical motion only requires integration within brain hemispheres, but horizontal motion depends on integration between hemispheres. In fact, we could demonstrate that the individual bias of observers of vertical motion could be partly predicted by the quality of the neural connections between brain halves, suggesting that interhemispheric integration is a relevant factor (Genç et al. 2011).

The very short summary of research on apparent motion demonstrates the various insights this simple paradigm has inspired over the course of the last century and beyond. It led to a detailed description of the involved brain areas, including interindividual differences, and to processing models being developed on the computational and neurophysiological level. As mentioned in the introductory section, one main concern in vision research associated with illusions is the interest in conscious perception and the property of multistability. Both aspects are also dominant in the apparent-motion field. The current state of research is just the starting point for investigations towards a deeper understanding of the exact mechanisms. Often, the results are still descriptive and qualitative in nature and don’t allow for very specific predic-
tions with respect to the involved neural machinery and dynamics. Yet the research line is promising and has the potential to lead to broadly applicable results. This might even be the case for the underspecification problem, the problem of reconstructing a full-fledged 3D world from a limited 2D input— one of Hecht’s main concerns. Multistability can be seen as one paradigm case in which the nervous system has to resolve ambiguity. For the Necker Cube, the motion quartet, and other multistable displays, the brain settles into a solution for a perceptual problem by resolving competition among alternatives. Therefore, research on multistability might help to elucidate the core mechanisms that give rise to the definitive subjective interpretations with which we represent the world.

4 Conclusion

In conclusion, Hecht’s distinction between illusion$_{a}$ and illusion$_{m}$ and his criticism of the naïve illusion concept in vision research is interesting. When we become aware of illusions, when we suddenly recognize the virtual character of our subjective world, certain metacognitive processes are initiated that are a worthwhile subject matter for further investigation. In some sense they become part of the experience, and an important question is whether and how the two aspects of the experience interact. Nevertheless, Hecht also agrees that perceptual representations are relatively immune to top-down control, i.e., even in the rare cases in which the illusory character becomes manifest, the perceptual processes are mostly modular and impenetrable in nature. Therefore, the question of illusory representation can be tackled independently of the question of metacognitive awareness, and continues to be an important guide for research on visual processing. Apart from looking at the more conceptual question of the level at which the term “illusion” should be applied, which is moot to some degree, I have tried to provide examples of relevant illusion$_{a}$ research that has made progress on the question of how the brain processes visual information. Even for the underspecification problem, there is opportunity for valuable insight, which hasn’t been exploited to full potential yet in current research.
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