Perceptual grouping in rapid visuomotor processing

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Publishing Note

The content of Chapters 2 and 3 has been published as research papers in *Vision Research* (reference: Schmidt, F., & Schmidt, T. (2013). Grouping principles in direct competition. *Vision Research, 88,* 9–21) and *Psychological Research* (reference: Schmidt, F., & Schmidt, T. (2014). Rapid processing of closure and viewpoint-invariant symmetry: Behavioral criteria for feedforward processing. *Psychological Research, 78,* 37-54), respectively. Both papers have been adapted to the requirements of my thesis; most changes have been made in the Introduction and Discussion. A manuscript for Chapter 4 is in preparation. In addition, several parts of Chapter 1 are based on Schmidt and Schmidt (2013, 2014) and Section 1.6 includes an excerpt from Schmidt, Haberkamp, and Schmidt (reference: Schmidt, F., Haberkamp, A., & Schmidt, T., (2011). Dos and don'ts in response priming. *Advances in Cognitive Psychology, 7(2)*). Reprint permission has been granted by the respective copyright owners.

Contents

Abstract

Perceptual grouping is an integral part of visual object recognition. It organizes elements within our visual field according to a set of heuristics (grouping principles), most of which are not well understood. To identify their temporal processing dynamics (i.e., to identify whether they rely on neuronal feedforward or recurrent activation), we introduce the primed flanker task that is based on a firm empirical and theoretical background. In three sets of experiments, participants responded to visual stimuli that were either grouped by (1) similarity of brightness, shape, or size, (2) symmetry and closure, or (3) Good Gestalt. We investigated whether these grouping cues were effective in rapid visuomotor processing (i.e., in terms of response times, error rates, and priming effects) and whether the results met theory-driven indicators of feedforward processing. (1) In the first set of experiments with similarity cues, we varied subjective grouping strength and found that stronger grouping in the targets enhanced overall response times while stronger grouping in the primes enhanced priming effects in motor responses. We also obtained differences between rapid visuomotor processing and the subjective impression with cues of brightness and shape but not with cues of brightness and size. These results show that the primed flanker task is an objective measure for comparing different feedforward-transmitted groupings. (2) In the second set of experiments, we used the task to study grouping by symmetry and grouping by closure that are more complex than similarity cues. We obtained results that were mostly in accordance with a feedforward model. Some other factors (line of view, orientation of the symmetry axis) were irrelevant for processing of symmetry cues. Thus, these experiments suggest that closure and (possibly) viewpoint-independent symmetry cues are extracted rapidly during the first feedforward wave of neuronal processing. (3) In the third set of experiments, we used the task to study grouping by Good Gestalt (i.e., visual completion in occluded shapes). By varying the amount of occlusion, we found that the processing was in accordance with a feedforward model only when occlusion was very limited. Thus, these experiments suggest that Good Gestalt is not extracted rapidly during the first feedforward wave of neuronal processing but relies on recurrent activation. I conclude (1) that the primed flanker task is an excellent tool to identify and compare the processing characteristics of different grouping cues by behavioral means, (2) that grouping strength and other factors are strongly modulating these processing characteristics, which (3) challenges a dichotomous classification of grouping cues based on feedforward vs. recurrent processing (*incremental grouping theory*, Roelfsema, 2006), and (4) that a focus on temporal processing dynamics is necessary to understand perceptual grouping.

Outline

When a visual scene is projected onto our retina the property of any object as a physical unit is lost. As a consequence, at the start of visual processing our environment is represented as a set of image fragments. This is in stark contrast to our experience of a unified visual percept that is organized into a number of coherent and unitary objects. One type of perceptual organization that generates this visual percept is perceptual grouping by which some elements within our visual field are perceived as belonging together. This occurs according to a set of heuristics (grouping principles). The present thesis aims to further understand the mechanisms that underly the different grouping principles.

In the first chapter, I introduce the phenomenon of perceptual grouping and recapitulate the progress in the field since its foundation by the Gestalt school. I conclude that although there were major achievements with respect to research methodology, the explanatory power of existing theoretical concepts is still limited and the empirical findings are heterogeneous. This is a result of several factors, for example, the diversity of grouping principles, interactions between different grouping principles, and the critical role of grouping strength and other modulating variables. In addition, for a long time grouping research focused on investigating the level of processing at which grouping occurs. This is an arguable approach because grouping operates at multiple levels in the visual processing hierarchy and findings cannot be translated into knowledge about physiological mechanisms. Generally, rather than investigating the *where* of visual processing, it is a promising approach to investigate the *when* of processing (e.g., the temporal processing dynamics). This change in focus is carried out by the *incremental grouping theory* (e.g., Houtkamp & Roelfsema, 2010; Roelfsema & Houtkamp, 2011). The theory introduces a classification of grouping principles into *base groupings* (i.e., neuronal feedforward activation, fast, in parallel) and *incremental groupings* (i.e., neuronal recurrent activation, slow, capacity-limited). In this thesis, we introduce the primed flanker task to investigate and compare different principles with an emphasis on their temporal processing dynamics. The task is designed against the background of the *rapid-chase theory* (e.g., Schmidt, Niehaus, & Nagel, 2006) that provides the methodological foundations to differentiate between feedforward and recurrent processes on the basis of behavioral priming data.

In the following chapters, we apply the task in three sets of experiments, testing the principles of grouping by (1) similarity of brightness, shape, and size, (2) symmetry and closure, and (3) Good Gestalt. The superordinate aim was to classify these grouping principles based on the distinction between base and incremental grouping that was introduced by the incremental grouping theory. Our findings serve to establish the primed flanker task as a useful method to disclose the processing dynamics of the investigated grouping principles. The results contribute to the knowledge about each of the investigated principles; they are discussed in detail in the respective chapters. For example, grouping strength turns out to play a major role for the processing dynamics of all grouping principles.

In the final chapter, I argue for the primed flanker task as a new method that is useful to investigate and compare different grouping principles. Then I further discuss the factor grouping strength that might even determine whether a principle is implemented as base or incremental grouping. Based on that finding I argue that these two types of grouping are located on a continuum. Any grouping principle might be a base grouping given that the initial feedforward sweep of activation carries information that is rich enough to meet the perceptual demands of the task at hand. Only if this first representation of the visual scene is not detailed or specific enough to complete the task, the response has to rely on more elaborated, recurrent, top-down processes (cf. Ahissar & Hochstein, 2004; Hochstein & Ahissar, 2002). I review further evidence for this notion from the literature on the processing of natural images and define modulating factors besides grouping strength. Then, I discuss two classical theories of perceptual grouping in the light of a general focus on temporal processing dynamics and of our findings. Finally, I give an outlook to future research and close by a summary and conclusion, including an evaluation of the primed flanker task and the incremental grouping theory.

1. General Introduction

In my thesis, I aim to investigate the temporal processing dynamics of perceptual grouping in vision. To this end, I introduce a new task that measures the impact of different grouping principles on rapid visuomotor processing. Generally, the results serve to establish the task as a novel method to identify the processing characteristics of these principles and compare them to each other. Specifically, the results provide valuable insights into the mechanisms of a number of specific principles (i.e., grouping by similarity of brightness, shape, or size; grouping by symmetry; grouping by closure; grouping by Good Gestalt).

In the following sections, I will discuss, first, the different principles of perceptual grouping, second, the measurement of those principles, third, the levels of the visual hierarchy at which grouping operates, fourth, the relationship between different grouping principles, and fifth, the physiological mechanisms of grouping. Sixth and finally, I will outline the rationale of the present experiments and detail our experimental approach.

1.1 Perceptual Organization and Grouping Principles

Vision is very important for humans as reflected in the rich visual representation of our environment and the importance of vision for action and orientation within this environment. The processing and interpretation of visual signals, to which a large amount of cerebral cortex is devoted to, is extremely efficient. This can be demonstrated with two examples. In the sensory domain, rod photoreceptors can detect light signals in the range of single photons (Field, Sampath, & Rieke, 2005). In the processing domain, the visual system performs a great deal of complex operations that are in striking contrast to the experienced immediacy and effortlessness of our visual percept. For example, 3-D percepts are derived from 2-D retinal images and objects can be recognized regardless of their respective orientation or perspective from which they are seen. These operations are implemented by a large network of strongly interconnected cortical areas (Felleman & Van Essen, 1991; Hegdé & Felleman, 2007).

To study stimulus processing within this visual network, it is useful (although in some respects simplistic) to differentiate between *low-level*, *mid-level*, and *high-level vision* (Marr, 1982). In low-level vision, physical stimulus or surface properties (e.g., luminance, color, contrast, orientation, edges) are extracted by receptive fields via hardwired connections. In mid-level vision the visual system starts to make inferences about the visual world (e.g., depth, perceptual organization): for example, single physical properties from low-level vision are integrated into larger perceptual units (i.e., shapes). Finally, in high-level vision the stimulus representations from mid-level vision are “mapped to meaning” in an active process of interaction between perception and cognition (e.g., objects, scenes, intentions, actions, cf. Henderson & Hollingworth, 1999). These three levels refer to different parts of the cortical (and retinal) network and together, they produce the unified visual percept that we experience.

The functional tasks of the cortical areas and the processing dynamics are reasonably well understood with respect to low-level vision. However, those of mid-level and high-level vision are not (Cavanagh, 2011). To this day, the question of how exactly humans recognize objects remains to be answered. Because the input for high-level vision (and thus object recognition) is provided by mid-level vision, it is necessary to understand the latter before we can gain more detailed knowledge about the former.

Some of the fundamental building blocks of mid-level vision were described a long time ago and have a long research tradition. Specifically, this is true for two components of perceptual organization: *perceptual grouping* and *figure-ground segregation*. Perceptual grouping is the process that determines which elements of the visual field are perceived as belonging together (e.g., Wertheimer, 1923). Figure-ground segregation describes the process by which the visual system distinguishes a figure from its background (e.g., Rubin, 1915). Note that both processes are closely linked because grouping together elements leads to their segregation from other (groups of) elements (*parsing*). Thus, grouping transforms the low-level input into larger units such as shapes, and figure-ground segregation determines their relative positions in the 3-D world by identifying them as a figure or background (Palmer, 1999; Wagemans, Elder et al., 2012). As a consequence, both processes are crucial for visual object recognition and for the physical interactions with our environment.

My thesis is concerned with the grouping process. Particularly, it focuses on different kinds of grouping by presenting a new objective measure to identify and compare their processing dynamics. *Perceptual grouping* was first described by the founders of the Berlin Gestalt school (Max Wertheimer, Kurt Koffka, and Wolfgang Köhler) more than 100 years ago (for a historical account see Ash, 1995; for a general review see Wagemans, Elder et al., 2012). The early Gestalt psychologists recognized the inherent accomplishment of the visual system of organizing the visual input and transforming it into the perception of objects. When our visual environment is projected onto the retina as a 2-D image, the property of an object as a physical unit is lost. As a consequence, the organization of our phenomenal world needs to be explained: in some way the visual system has to retrieve organization by identifying units. The Gestalt psychologists discovered a number of *grouping principles*, a set of heuristics which is used by the visual system to derive larger units from the low-level input received by the retina and the receptive fields. Each principle describes a specific *grouping cue* that leads to grouping of different elements in the visual field (e.g., a shared characteristic). The grouping principles are still widely accepted today.

However, only in recent years has a renewed interest in Gestalt psychology arisen (Wagemans, Elder et al., 2012; Wagemans, Feldman et al., 2012). In the following paragraphs, I briefly outline the grouping principles/cues, most of which were put forward in a seminal paper by Wertheimer (1923).[1] They are depicted in Figure 1.

Elements in the visual field are grouped together if they are spatially close (*grouping by proximity*, Schumann, 1900), share the same or similar color, brightness, shape, size or orientation (*grouping by similarity*, Müller, 1903; Rubin, 1922), or move in the same direction (*grouping by common fate*, Wertheimer, 1923). Elements are also grouped if they are part of a symmetric shape (*grouping by symmetry*, Schumann, 1900), are parallel (*grouping by parallelism*, Wertheimer, 1923), are part of a closed shape (*grouping by closure*, Wertheimer, 1923), or are aligned with each other along a smooth path (*grouping by good continuation/continuity* or *grouping by collinearity*, Wertheimer, 1923).[2] According to the early Gestalt psychologists all of these principles should result in an arrangement of elements that is *"prägnant"* or forming a *"Good Gestalt"*, that is, an arrangement as simple, as regular, and as well-structured as possible (*law of Prägnanz*, Koffka, 1935). This idea was later transformed into the *minimum principle* (Attneave, 1954; Hochberg & McAlister, 1953) and the *structural information theory* (Leeuwenberg, 1969).

This list by Wertheimer (1923) was complemented by more recent papers that described a number of additional grouping principles. In short, elements are also grouped together if they change simultaneously (*grouping by synchrony*, Alais, Blake, & Lee, 1998), lie within the same bounded area or region (*grouping by common region*, Müller, 1903; Palmer, 1992), or share a common border (*grouping by element connectedness*, Palmer & Rock, 1994a). Note that some of the principles result in the perception of grouped elements that each retain their status as a single unit (*element aggregation*) while others bind together elements into a percept of one common shape or object (grouping by common region, element connectedness and some forms of grouping by common fate) (*unit formation*, Palmer, 1999).

Together with other processes (e.g., figure-ground organization), the grouping principles contribute to the perceived organization of the visual field (e.g., into a number of objects) that is not contained in the physical low-level description of the stimulus input.[3] In that way grouping cues are cues for "objectness" (Todorovic, 2011) that (1) delineate the features (e.g., its color) belonging to the same object, and (2)

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[1] Note that although Wertheimer was the first to provide a comprehensive list of the grouping principles and exemplifying figures, he was not the first to describe every one of these principles (Vezzani, Marino, & Giora, 2012).

[2] Wertheimer (1923) and others also noted that elements are grouped together if the observer is used to experiencing them as part of a group. However, the Gestalt psychologists commonly assumed that this *grouping principle of past experience* is not as important because it is superseded by the other more stimulus-based principles.

determine which particular elements of the visual field will be perceived together, forming a group or an object. This process has been described also by the term *binding* (Treisman, 1996).

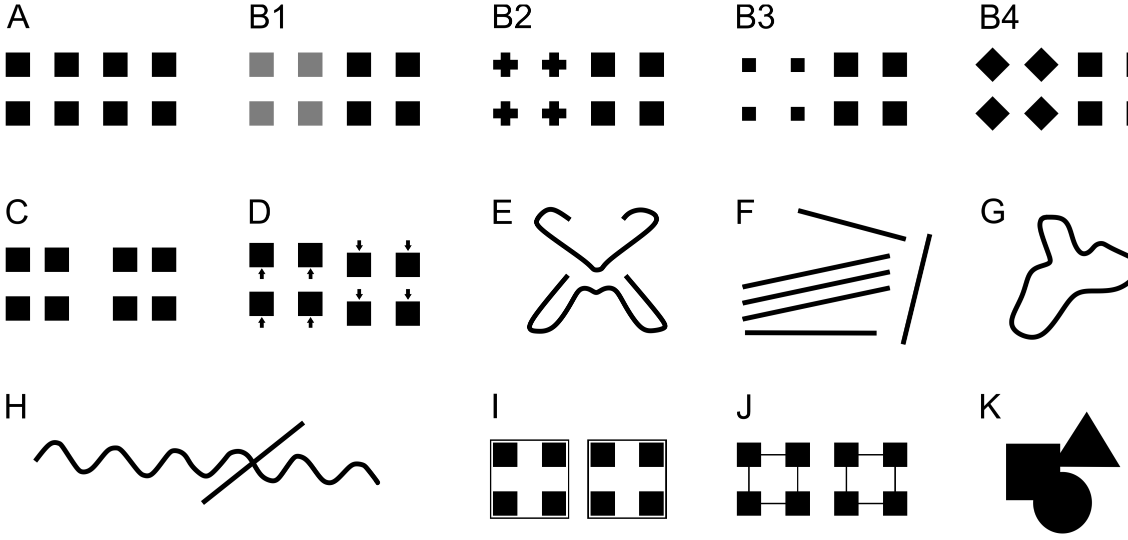

Figure 1. Schematic illustrations of the most prominent grouping principles. No grouping (**a**); grouping by similarity of color (**b1**), shape (**b2**), size (**b3**), and orientation (**b4**); grouping by proximity (**c**); grouping by common fate (**d**); grouping by symmetry (**e**); grouping by parallelism (**f**); grouping by closure (**g**); grouping by good continuation (**h**); grouping by common region (**i**); grouping by element connectedness (**j**); grouping by Good Gestalt (**k**). Note that in all cases, the grouping of elements leads to their segregation from other (groups of) elements.

The importance of grouping for perception is illustrated by several findings. First, grouping principles determine the organization of the stimulus input not only in vision but also in other modalities (e.g., in haptic perception, see Overvliet, Krampe, & Wagemans, 2012; for a review see Gallace & Spence, 2011). Second, grouping cues can precede or overrule processes of low-level vision, as is illustrated by experiments with vernier stimuli (Manassi, Sayim, & Herzog, 2012). Finally, the ecological importance of grouping is illustrated by animal camouflage in which animals share coloration and markings with their natural environment, grouping both together (by similarity) and making the animals more difficult to see for predators (Troscianko, Benton, Lovell, Tolhurst, & Pizlo, 2009).

In the following section, I discuss the different approaches and methods that can be used to measure perceptual grouping. I focus on the class of objective measures because I introduce the primed flanker paradigm as a new member of this class.

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[3] The opposite of grouping is *pop-out*, the effect that a single element stands out from its environment. Studying pop-out has a long and successful research tradition (Wolfe & Horowitz, 2004) but is only rarely linked to grouping.

1.2 Measurement of Perceptual Grouping

Although the early Gestalt psychologists made fundamental contributions to our modern understanding of visual object recognition, most notably by discovering and describing the processes of perceptual organization, their methods were not up to the standards of later psychophysical and behavioral research. The first descriptions of the grouping principles were mere demonstrations that used simple, often confounded stimuli, and all measures were subjective (i.e., phenomenally based) rather than objective (i.e., physically based). In subjective measures, observers classify internal perceptual states: responses cannot be compared with stimulus parameters and are thus observer-dependent. Later, different researchers tried to overcome this weakness by using experimental methods that either quantified the subjective reports of the participants, or yielded objective measures for the strength of the grouping effects. In objective measures, observers classify external stimuli: responses can be compared with stimulus parameters and are thus observer-independent (e.g., Palmer, 2003; Schmidt, 2013).

1.2.1 Subjective Measures

In the first alternative, participants are presented with displays in which elements are grouped by one or more grouping principles. Then, the proportion of trials in which different participants report perceiving each possible grouping outcome is identified (e.g., three-dimensionality ratings, see Hochberg & McAlister, 1953; orientation ratings, see Hochberg & Hardy, 1960; Hochberg & Silverstein, 1956). Often multistable *dot lattices* are used in which dots are arranged according to the proximity principle (and optionally according to one other grouping principle) into horizontal or vertical stripes. Then participants report the orientation in which they see the dots arranged. As a result, the strength of proximity grouping can be adjusted with respect to that of other dot-organizing principles (e.g., Claessens & Wagemans, 2008; Gepshtein & Kubovy, 2000; Kubovy, Holcombe, & Wagemans, 1998). Experimentally, the strength of two types of grouping can be quantified following two research strategies (Kubovy & van den Berg, 2008). The *proximity-first strategy* first measures the grouping strength of proximity on its own and only then studies its relation to other grouping cues (for a review and probabilistic model, see Kubovy & van den Berg, 2008). The *trade-off strategy* measures the strength of grouping cues in terms of each other. For example, participants are presented with stimuli whose vertical elements are grouped by proximity and horizontal elements by brightness. They then adjust the level of brightness until the grouping of vertical and horizontal orientation appears equally strong.

This approach yielded important findings, especially with respect to grouping by proximity (alone and in relation to other grouping principles). Most notably, it became possible to formulate a *Pure Distance Law* for grouping by proximity: the grouping strength follows a decaying exponential function of relative distances between dots, invariantly over lattices of all shapes (Kubovy et al., 1998). This finding was a milestone in the attempts to define and quantify one of the grouping principles described by the early Gestalt psychologists.

1.2.2 Objective Measures

However, the basis of these findings is still phenomenal, that is, they do not allow researchers to measure performance with respect to well-defined physical criteria. As a consequence, it is not possible to identify accuracy and response bias of participants (for a discussion see Palmer & Beck, 2007). In the alternative approach, performance of participants is specified in terms of objective variables such as response times and error rates. Participants again respond to stimuli that are arranged according to one or more grouping principles. It is possible to distinguish between a number of different experimental methods. Well-known examples are approaches using *configural superiority effects* (Pomerantz & Portillo, 2011; Pomerantz, Sager, & Stoever, 1977), *Garner interferences* (Garner, 1974), or the *repetition-discrimination task* (Palmer & Beck, 2007). In the following paragraphs, I briefly describe these different methods.

Configural superiority effects are defined as the performance difference between identification of an odd target element in (1) a display of four elements (*base display*), compared to (2) the same display of four elements with four identical context elements super-positioned (*composite display*). Typically, response times are slower and error rates are higher with the composite display compared to the base display. However, when in the composite display the target element groups together with a context element, response times are faster and error rates lower compared to the base display. This is due to the different amounts of cognitive resources that are needed to process ungrouped or grouped elements: If two elements do not group, they are processed independently (requiring more cognitive resources) while if they group they are processed together (requiring fewer resources). This effect is termed the configural superiority effect and is found for example in grouping by proximity and similarity of orientation (e.g., Pomerantz & Portillo, 2011).

Garner interference effects are defined as the performance difference between classification of a target element in (1) a display with two elements when only the target changes from trial to trial (*control condition*) compared to (2) a display with two elements when both elements change from trial to trial (*filter condition*). For example, participants are asked to classify the left one of two elements and are either presented with AA and BA (in the control condition) or with AA, AB, BA, and BB (in the filter condition). Typically, response times are slower and error rates are higher with the filter condition compared to the control condition (Garner interference) as a result of interference from irrelevant variation. However, also within the filter condition there are differences depending on the grouping of the two elements. If they group together, for example with curved lines of the sort ((, (),)(, and)), then response times are slower and error rates higher compared to when they do not group, for example with curved lines of the sort (⌒, (⌣,) ⌒, and) ⌣. Again, this is explained by the different amounts of cognitive resources that are needed to process ungrouped or grouped elements: If two elements do not group they are processed independently (requiring fewer cognitive resources because it is easier to attend selectively to the target element) while if they group they are processed together (requiring more resources because it is harder to attend selectively to the target element). This effect has been found, for example, for grouping by closure, parallelism, and bilateral symmetry (e.g., Pomerantz & Garner, 1973).

Finally, in the repetition-discrimination task, participants have to detect a pair of repeating elements in a row of alternating shapes as quickly as possible. The resulting response times depend strongly on whether or not the repeated element pair is grouped by some grouping cue. In addition, the response times correlated with subjective ratings of grouping strength. This effect has been found, for example, for grouping by common region, connectedness, proximity, and similarity of color (Beck & Palmer, 2002; Palmer & Beck, 2007).

All these findings illustrate that objective measures are suited to quantify different grouping principles. But what can these methods be used for apart from measuring the effect of different grouping cues (i.e., grouping strength) in terms of objective variables? One main aim of the researchers using them was to determine which physiological mechanisms perceptual grouping processes are based on. Traditionally, this culminated in the question at which level of the visual hierarchy grouping might operate (low-level, mid-level, or high-level vision).

1.3 Levels at which Perceptual Grouping Operates

For a long time, it was assumed that perceptual grouping is a part of low-level vision, operating on 2-D representations and physical properties of stimuli (e.g., Marr, 1982). More recently, researchers directly tested this by investigating grouping in relation to the perception of depth, transparencies, occluded elements, and other high-level processes (reviewed in Palmer, Brooks, & Nelson, 2003). In some cases, the traditional claim is supported by empirical findings (grouping by regularity, van den Berg, Kubovy, & Schirillo, 2011) but in other cases grouping occurs relatively late, for example, after the inclusion of information regarding binocular depth (grouping by proximity, Rock & Brosgole, 1964), transparency (grouping by similarity of brightness, Rock, Nijhawan, Palmer, & Tudor, 1992), or occlusion (grouping by similarity of shape, Palmer, Neff, & Beck, 1996).

Rock and Brosgole (1964) asked participants to indicate whether arrays of dots were grouped by proximity into rows or columns. They tilted the arrays in several steps into 3-D space to dissociate physical (i.e., retinal) and phenomenal distance. Thus, dots might be grouped into rows or columns depending on whether the grouping was based on retinal or phenomenal proximity (Fig. 2A). They found that the latter is at the core of grouping by proximity.

In a similar approach, Palmer et al. (1996) presented arrays with two (three) columns of full circles on one side of the display and two (three) columns of semicircles on the other and asked participants to indicate which columns are grouped together by similarity of shape. In the critical condition, they presented a central column of semicircles that was either sealed off by a bar or not. Thus, the central column might be grouped with the semicircles or the circles depending on whether the grouping was based on physical shape (semicircles) or phenomenal shape (full circles that are partly occluded by a bar) (Fig. 2B). The authors found that the latter is crucial for grouping by similarity of shape.

Equivalently, Rock et al. (1992) presented two (three) columns of bright elements on one side of the display and two (three) columns of dark elements on the other and asked participants to indicate which columns are grouped together by similarity of brightness. In the critical condition, they overlaid a central column of medium gray elements with shades and transparent filters to dissociate physical (i.e., absolute) luminance and phenomenal lightness (Fig. 2C) and found that phenomenal lightness is at the core of grouping by similarity.

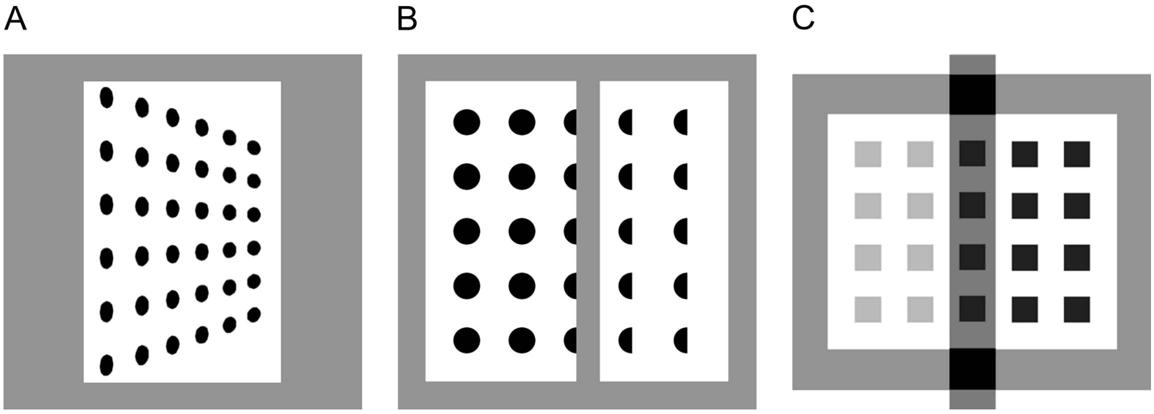

Figure 2. Schematic illustration of the stimulus material by Rock and Brosgole (1964) (**a**), Palmer et al. (1996) (**b**), and Rock et al. (1992) (**c**).

The computations that are needed for the phenomenal perception of stimuli in binocular depth, of partly occluded stimuli, or of stimuli in shades or behind transparent filters, are considered complex and late accomplishments as part of mid-level or even high-level vision. Thus, all these results demonstrate that some grouping occurs relatively late in the course of visual processing (and thus late in the visual hierarchy, Palmer, 2002).

Interestingly, Schulz and Sanocki (2003) showed that grouping can be early or late depending on the experimental setting. They presented participants with stimuli as those of Rock et al. (1992) with chromatic colors (red and blue) but varied the stimulus presentation times between 200 ms and 2,000 ms. They found that most participants grouped the central column according to physical color at brief presentation times but to phenomenal color at long presentation times.

To conclude, current findings suggest that "grouping operates at multiple stages in visual processing [...] and that this multi-stage view should be considered as the basis of future theories of perceptual grouping" (Palmer et al., 2003, p. 314). In other words, even though it is generally reasonable to consider grouping a part of mid-level vision, linking low-level and high-level vision, it might also be part of these earlier or later levels. However, the exact details of this (multi-)level view are unclear. First, we know that a number of factors are likely involved in determining the processing level at which perceptual grouping occurs – which poses a challenge mainly with respect to the experimental approaches used. Second, it is not possible to simply translate the findings on the basis of the (multi-)level view into physiological mechanisms – which generally calls this way to address grouping into question. If the finding that grouping is located on a particular level of vision cannot be related to specific mechanisms, it may be more sensible to use methods that allow for meaningful inferences. In the next two sections I detail those two problems of the (multi-)level approach and then discuss an alternative approach to investigate perceptual grouping, namely not to focus on *where* but on *when* grouping is implemented.

1.4 Complicating Factors: Relationship between Different Grouping Principles

There are at least two major factors that should be considered when thinking about the level at which the processing of grouping occurs. First, the way that the measurement of a grouping principle is operationalized in a given experiment is crucial. For example, grouping by similarity of brightness might be implemented by different mechanisms depending on the respective stimuli and their grouping strength. In general, grouping based on a grouping cue with higher grouping strength might occur at a different level of the visual hierarchy than might grouping based on a cue with lower grouping strength. Methods to measure grouping strength and thereby to control for it were discussed in Section 1.2.

Second, it is crucial to take into account that perceptual grouping is not a unitary process but a collection of different grouping principles. The early Gestalt psychologists were already aware of the fact that different grouping principles are neither equally effective nor of equal importance for our phenomenological impression. They explicitly formulated all principles as *ceteris paribus* rules, meaning that one can only accurately predict the organization of an array of elements by a grouping principle when everything else is equal (i.e., no other principle influences the organization, Palmer, 1999). For example, good continuation might only determine the outcome of grouping if the elements are not part of a closed shape. This leads to interesting research questions: Which grouping principles are more effective than other principles, that is, are more relevant in determining the phenomenological impression? Do different grouping principles rely on the same physiological mechanisms? Do different grouping principles need the same amount of cognitive resources (i.e., in terms of visual attention or processing time)?

Research indicates that the processing of different grouping cues varies fundamentally in its attentional demands and time course. For example, in a study by Kimchi and Razpurker-Apfeld (2004), two central target stimuli were presented in rapid sequence and had to be judged by participants as the same or different. At the same time, the task-irrelevant background elements were grouped according to different principles and could also change or remain the same. Response times in the same-different task depended on both a change of the unattended background and the particular cues that grouped the background elements. In line with other research, these findings suggest that different grouping cues have varying attentional demands (Behrmann & Kimchi, 2003; Han & Humphreys, 1999; Han, Humphreys, & Chen, 1999a).

In addition, the processing of different grouping cues varies profoundly in its time course. For example, it has been typically found that grouping by proximity occurs earlier and is more salient than grouping by shape (e.g., Ben-Av & Sagi, 1995; Han et al., 1999a, b; Quinlan & Wilton, 1998). This is supported by event-related potential data which show that grouping by proximity elicits earlier neuronal activity than that by shape (Han, Ding, & Song, 2002).

Generally, it seems that some forms of grouping and segmentation take place early, rapidly, and effortlessly, whereas others occur later, consume time, and require controlled attentional processing (e.g., Ben-Av & Sagi, 1995; Han, Jiang, Mao, Humphreys, & Gu, 2005; Kimchi & Razpurker-Apfeld, 2004; Palmer et al., 2003). In line with this, a review of neuroimaging studies by Sasaki (2007) suggests that different types of perceptual grouping also involve different areas of the visual processing stream.

1.5 Physiological Mechanisms of Grouping: Incremental vs. Base Grouping

The difficulty to pin down the level at which perceptual grouping operates is closely tied to the second major problem of a (multi-)level approach when searching for the physiological mechanisms perceptual grouping is based on. In contrast to early conceptualizations of the visual system, information processing is not only feedforward (i.e., does proceed from lower levels of the visual hierarchy to higher ones) but also recurrent (i.e., depends on neuronal feedback connections from higher to lower levels and on lateral/horizontal connections within one level, e.g., Felleman & von Essen, 1991; Bullier, 2004; Gilbert & Sigman, 2007). This stimulated a plethora of studies in visual perception that have been focused not only on spatial, hierarchical attributes of visual processing (*where*) but also on temporal aspects (*when*). Indeed, our visual percept changes rapidly in time and these changes provide valuable information about the cognitive and physiological mechanisms underlying the perceptual process of interest (Hegdé, 2008). An increasing number of theoretical accounts emphasize, for example, the difference between a temporally early phase of processing (mediated by neuronal feedforward activation) and a later phase of processing (mediated by neuronal feedback activation, e.g., Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000; Schmidt, Haberkamp, Veltkamp et al., 2011). Specifically, Lamme and Roelfsema (2000; see also Lamme, 2010) propose that a novel stimulus initially elicits a wave of neuronal feedforward activation (*feedforward sweep*) rushing through the visuomotor system: Each cell passes activation on to cells downstream before integrating any recurrent information from other cells about the signal (also see Bullier, 2001; VanRullen & Koch, 2003). Consequently, the wavefront of visually elicited activation is essentially devoid of information from recurrent processing, which develops only in the wake of the wave (Fig. 3).

Based on the distinction between these two processing phases, Roelfsema (2006; Roelfsema & Houtkamp, 2011) proposes a framework describing the basic mechanisms of perceptual grouping in terms of its temporal processing characteristics and its neurophysiology.[4] Historically, at least three major theoretical approaches can be distinguished that attempt to explain the neurophysiology of grouping (cf. Houtkamp & Roelfsema, 2010): (1) *Feedforward feature extraction*: Perceptual grouping is implemented by feature detectors that are tuned to specific lower-level features or feature conjunctions (*cardinal cells*, Barlow, 1972). (2) *Binding-by-synchrony*: Synchronous discharges of neurons label all image elements of the same perceptual group (Engel, König, Kreiter, Schillen, & Singer, 1992; Singer & Gray, 1995; but see Shadlen & Movshon, 1999; Roelfsema, Lamme, & Spekreijse, 2004). (3) *Spread of activation*: enhanced firing rates of neurons label the elements of a perceptual group in a gradual and time-consuming process (Houtkamp, Spekreijse, & Roelfsema, 2003).

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[4] Note that already the Gestalt school described perceptual grouping by the dynamic complexity of the brain (Köhler, 1920) which today would be termed as an interaction of neuronal feedforward and feedback activation.

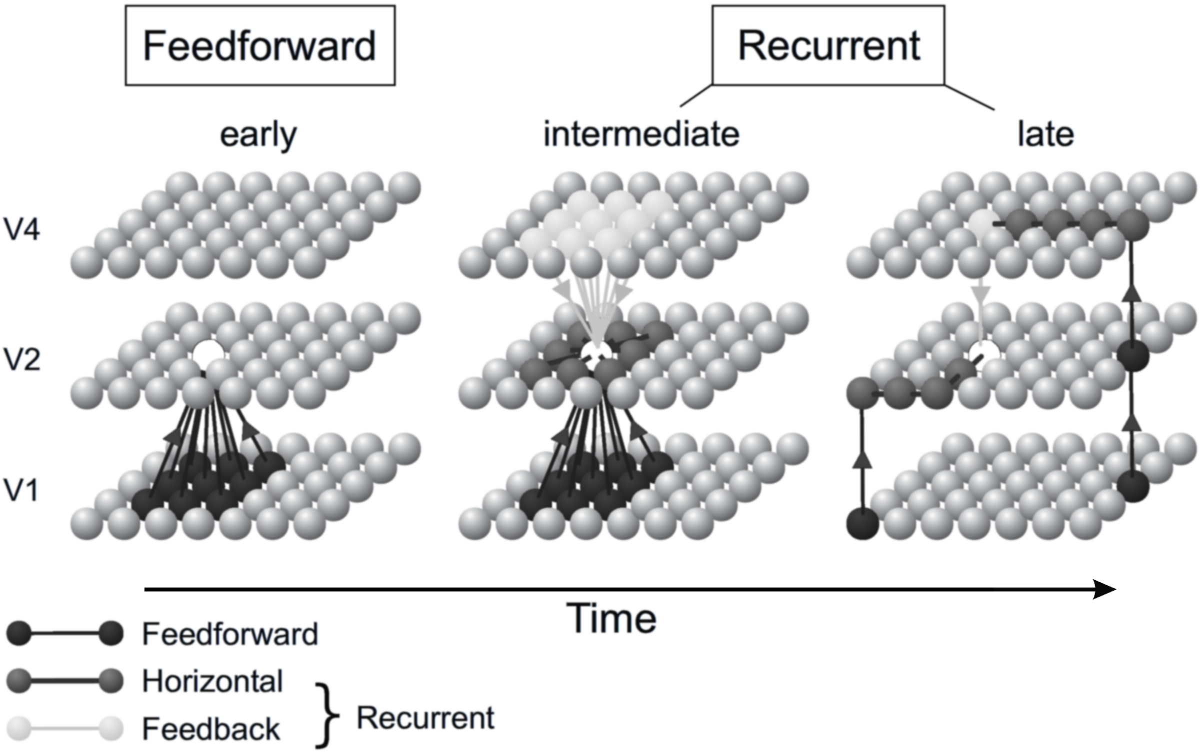

Figure 3. Schematic illustration of the connections between neurons for ascending areas within the visual processing hierarchy (V1, V2, and V4). When a novel visual stimulus is presented, neuronal responses are initially dominated by feedforward connections (dark gray). After a delay, horizontal (medium gray) and feedback connections (light gray) take effect. As time progresses, longer recurrent routes start to influence the neuronal responses. Adapted from Roelfsema (2006).

Roelfsema (2006; Roelfsema & Houtkamp, 2011) integrates these models into a framework comprising two mechanisms of grouping: *base grouping* and *incremental grouping*. Base grouping refers to feature extraction by multi-feature detectors during an initial feedforward sweep of visual processing (Lamme & Roelfsema, 2000). This form of perceptual grouping applies to relatively simple features or feature combinations, is rapid, and does not depend on recurrent processing loops. In psychological terms it is preattentive, that is, it does not rely on the allocation of visual attention. Base grouping is fundamental for visual processing because it occurs with all features and conjunctions of features for which tuned neurons (i.e., cardinal cells) are found (cf. Ullman, 1984). These neurons at higher levels of the visual hierarchy are invariant for size and location but are selective for specific feature or feature conjunctions that can be as complex as human faces or animals in natural scenes (cf. Logothetis & Sheinberg, 1996; Tanaka, 1996; Thorpe, Fize, & Marlot, 1996; Tsao & Livingstone, 2008). However, there are limits to the base grouping process. First, not all conceivable feature combinations can be coded by single neurons, and second, the receptive fields of the cardinal cells are so large that they may contain more than one object, resulting in competing object representations and intermingling of their features. Thus, when the visual system is confronted with unfamiliar objects or objects that are close together, incremental grouping becomes necessary. Incremental grouping refers to the notion of a gradual spread of enhanced firing rate. It relies on feedback processing from higher to lower visual areas, as well as on lateral/horizontal connections between neurons in the same area, and is therefore slower than base grouping (*incremental grouping theory*, Houtkamp & Roelfsema, 2010; Roelfsema & Houtkamp, 2011). In psychological terms this form of grouping is attentive and refers to a spread of visual attention.

The most influential precursor of the incremental grouping theory is the *feature-integration theory* (Treisman, 2006; Treisman & Gelade, 1980). In this framework, the detection and identification of the low-level features in a visual scene is assumed to occur in parallel and without the need for attentional resources. Different features are represented in separate topographical feature maps. Only by directing the spotlight of attention to a specific location, the features in this location are bound together in perception. Thus, for every feature conjunction not coded by tuned neurons, grouping is a serially working, attention-requiring, binding process – exactly as in the incremental grouping theory. However, there are also critical differences between both theories (for a discussion see Section 5.5 and Roelfsema & Houtkamp, 2011). Most importantly, the incremental grouping theory links the spread of attention at the psychological level to the spread of enhanced activity at the neurophysiological level and explains the mechanisms by which attention selects elements organized by the same grouping cues (Roelfsema & Houtkamp, 2011).

In sum, the incremental grouping theory provides a convincing and contemporary answer to the before-mentioned questions regarding differences between grouping principles as well as their physiological implementation. There are also promising attempts to implement the main features of the theory in a neurodynamical computational model that seems to fit well the empirical data (Korjoukov & Roelfsema, 2012). In the next paragraphs, I shortly review the existing experimental evidence that mostly stem from three lines of research.

The first cluster of findings that support the incremental grouping theory stems from *pathfinder* or *curve tracing tasks*. Participants are presented with stimuli consisting of two curved lines and are asked to judge whether two targets (e.g., two red dots) are placed on the same line or not (Jolicœur, Ullman, & MacKay, 1986). Although all the elements of each line are grouped together by good continuation, the response times typically increase linearly with the length of the lines. This finding indicates that perceptual grouping in these tasks is not instantaneous and based on a process with limited capacity. Empirically, the results can be explained by the hypothesized gradual spread of attention along the elements of each line (Houtkamp et al., 2003; Roelfsema, Houtkamp, & Korjoukov, 2010; for evidence from electrophysiology see Lefebvre, Dell'acqua, Roelfsema, & Jolicœur, 2011). This process of incremental grouping is transitive, meaning that if an element A is connected to an element B, and B is connected to C, than A is also connected to C. In neurophysiological terms, the transitivity is mirrored by a spread of enhanced firing rates along the neurons representing those elements: Single cell recordings of the primary visual cortex (V1) in monkeys performing pathfinder tasks showed cell clusters whose initial responses that were caused by feedforward connections were selective for the orientation of the element, while their later responses caused by recurrent connections propagated an enhanced response along the representation of the target line elements (Roelfsema et al., 1998, 2004). Specifically, neurons with a receptive field at the beginning of the target line enhanced their response at an earlier point in time than did the neurons with a receptive field further along the line (Roelfsema et al., 1998). The spread of firing rate proceeds along lateral/horizontal connections in the visual cortex that interconnect neurons coding contour elements that are well aligned (grouping by good continuation), that share similar features (grouping by similarity), or that are represented in neighboring receptive fields (grouping by proximity). The same results as those obtained in curve tracing tasks with monkeys were reported for humans when using real objects in natural scenes (Korjoukov et al., 2012).

In more recent studies, the two phases in the neuronal response to pathfinder displays are even more tightly linked to feedforward and feedback activation, respectively, by taking advantage of the specific cell structure in V1 and the neurotransmitter receptors that are thought to mediate feedforward vs. feedback signals. Specifically, it is known that feedforward and feedback connections in V1 are anatomically separate (e.g., Felleman & Van Essen, 1991; Rockland & Pandya, 1979). While sensory input (i.e., the feedforward connections) terminates in the middle cortical layer, input from other parts of the cortex (i.e., the feedback connections) projects mostly to the outer layers. In addition, the spread of the neuronal signal along projections within the visual system depends on specific neurotransmitters, particularly glutamate as an excitatory neurotransmitter. While the transmission of feedforward signals depends on α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptors with a fast time constant, that of recurrent signals is based on *N*-Methyl-D-aspartic acid (NMDA) receptors and neuromodulators (Acetylcholine, ACh) with a slow time constant. The two phases of incremental grouping in pathfinder tasks have been recently demonstrated by injecting glutamate antagonists in the respective layers of monkey V1: while NMDA antagonists selectively blocked the recurrent phase, AMPA blocked both feedforward and recurrent phases to an equal amount (van Kerkoerle, Self, & Roelfsema, 2009).

The second cluster of findings stems from *figure-ground tasks* in which a figure has to be segregated from its background, typically defined by different orientations of line textures. As in the pathfinder tasks, figure-ground segregation is implemented by two processes: a feedforward figure boundary detection that is followed by a recurrent process that fills in the figure (*filling-in* or *region growing*, Grossberg & Mingolla, 1985; Roelfsema, Tolboom, & Khayat, 2007). I will not go into more detail about this line of research because it is not concerned with perceptual grouping in a narrower sense. However, equivalent to the results from pathfinder tasks it has been shown that NMDA antagonists selectively block the recurrent phase of filling-in, while AMPA blocks both boundary detection and filling-in (Self, Kooijmans, Supèr, Lamme, & Roelfsema, 2012).[5]

The third cluster of findings stems from single-cell studies. Wannig, Stanisor, and Roelfsema (2012) demonstrated in monkey V1 that neuronal activation spreads to other neurons with neighboring or overlapping receptive fields according to the features that are shared by the presented stimuli. For example, an oriented bar activates neurons tuned to its orientation but the responses of neurons with neighboring receptive fields are enhanced only if their input contains signals from bars of the same and not other orientations (i.e., grouping by collinearity or similarity of orientation). Thus, the classical Gestalt cues are implemented by a local enhancement of neurons belonging to the same Gestalt.

Note that following Roelfsema's conceptualization the two phases of base and incremental grouping are sequential: prior base grouping is necessary for incremental grouping. This assumption is consistent with micro-stimulation of higher visual areas (FEF) in monkeys that only had an effect on lower visual areas (V1) when a stimulus was present in the receptive fields of the FEF neurons (e.g., Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008). Thus, incremental grouping requires previous base grouping (i.e., feedforward information processing). For a review and further discussion of the incremental grouping theory and its relationship to other theories of perceptual grouping see Roelfsema and Houtkamp (2011).[6]

1.6 Rationale and Experimental Approach

In the previous sections, I have described the perceptual organization that is at the core of object recognition in human vision. In the organizational process the visual system uses a set of heuristics (grouping principles) that were described in phenomenological terms by the Gestalt school. Since then, experimental tools were

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[5] These results are supported by multi-cell recordings that associate different phases of figure-ground segregation with activity in different cortical layers of V1 (Self, van Kerkoerle, Supèr, & Roelfsema, 2013).

[6] Note that base grouping may be experience-driven such that experience may define new base groupings. This would give this factor a much more central role in grouping than the early Gestalt psychologists thought. As a result, the dichotomy of base and incremental grouping would not be a complete one. I further discuss this point in Section 5.3.3.

developed to measure these principles and examine their impact on visual processing. It has been found that different principles have different characteristics and are based on just as different physiological mechanisms. I described the incremental grouping theory that was put forward to explain the discrepant sorts of grouping by supposing two classes of grouping processes: fast base grouping that is mediated by neuronal feedforward processes, and slow incremental grouping that is mediated by recurrent processes. In this section, I present a new objective measure that focuses on fast and temporally early phases of processing: the *primed flanker task.* The task is a variant of the *response priming paradigm* (Klotz & Neumann, 1999; Klotz & Wolff, 1995; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). Thus I first detail this paradigm's general characteristics and the theoretical background that render it particularly useful for the study of grouping processes (for overviews see Kohl, Schmidt, & Schmidt, 2010; Schmidt, Haberkamp, & Schmidt, 2011). After that, I describe the primed flanker task in more detail.

In response priming, participants are reacting to a target stimulus as quickly and accurately as possible. The target is preceded by a prime stimulus which is either mapped to the same response as the target (*consistent prime*) or to the alternative response (*inconsistent prime*). Typically, consistent primes will speed and inconsistent primes will slow responses to the target, leading to priming effects defined as the response time difference between consistent and inconsistent trials. If prime and target presentations follow each other at a *stimulus-onset asynchrony* (SOA) shorter than about 100 ms, the resulting priming function (the priming effect as a function of SOA) follows a prototypical pattern where priming effects increase approximately linearly with SOA (Vorberg et al., 2003).[7]

Generally, response priming effects occur because the prime activates the response assigned to it. This has been shown early on in the time course of lateralized readiness potentials (Eimer & Schlaghecken, 1998, 2003; Klotz, Heumann, Ansorge, & Neumann, 2007; Leuthold & Kopp, 1998; Mattler, 2003; Vath & Schmidt, 2007). These represent relative increases in EEG negativity over the motor cortices prior to response execution. They are stronger over the motor cortex contralateral to the responding hand, and hence the difference potential between the left and right hemispheres can be used as a measure of the selective preparation of a right-hand or left-hand response. Typically, the potentials start out time-locked to the prime, first develop in the direction specified by the prime, and only later proceed in the direction specified by the actual target. Such data suggest that the prime activates a response assigned to it, and has more time to drive the response on its own the more

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[7] For longer SOAs, the priming effect might increase further or, depending on stimuli and paradigm, reverse (i.e., inconsistent primes lead to faster responses and lower error rates, Eimer & Schlaghecken, 1998). The origin of this *negative compatibility effect* is debated (Jaskowski, 2008; Lingnau & Vorberg, 2005; Sumner, 2007).

time elapses between prime and target. Therefore, priming effects increase with prime-target SOA (for a mathematical model, see Mattler & Palmer, 2012; Vorberg et al., 2003). Similarly, priming effects in pointing responses make it possible to trace the prime's motor impact in the temporal as well as the spatial domain. Experiments that measured pointing movements show that inconsistent primes are not only able to delay the responses, but also to mislead them in the wrong direction. This diverting influence can lead to an initial finger movement towards the prime that only later reverses in direction of the correct target position (Schmidt, 2002; Schmidt et al., 2006; Schmidt & Schmidt, 2009). This is also evident in response force measures (Mattler, 2005).

In many cases, response activation by an inconsistent prime can result in a full-fledged movement towards the prime position (i.e., a response error). This results in a characteristic pattern of error probabilities with consistent primes rarely leading to errors and inconsistent primes leading to errors increasing with SOA. Therefore, error rates are of interest for at least two reasons. Firstly, they indicate response activation by the prime, just like the response time effects. Secondly, it is reasonable to assume that errors in inconsistent conditions are predominantly driven by prime information (e.g., Schmidt et al., 2006; Schmidt & Schmidt, 2010). As a result, priming effects in error rates are of similar importance as the response time effects and should be analyzed just as carefully. In sum, it is the close connection between priming effects and online motor control that distinguishes response priming from other types of priming effects. By this, response priming is also tightly linked to everyday reflex actions.

What makes the response priming paradigm (and the primed flanker task) especially useful for studying the processing of grouping cues? According to the incremental grouping theory by Roelfsema (2006; Roelfsema & Houtkamp, 2011) it is essential to distinguish between an initial phase of feedforward processing and a later phase of recurrent processing when investigating grouping. Crucially, there is a wealth of evidence that tightly links response priming effects to the phase of visual feedforward processing: The previously mentioned studies of primed pointing movements and lateralized readiness potentials show that the earliest processes of response activation are determined exclusively by prime information but are independent of all target information, and that only later processes of response activation are influenced by the actual target (Klotz et al., 2007; Schmidt et al., 2006; Schmidt & Schmidt, 2009; Vath & Schmidt, 2007). This evidence is explained by the *rapid-chase theory* of response priming (Schmidt et al., 2006; Schmidt, Haberkamp, Veltkamp et al., 2011) which proposes that prime and target signals elicit feedforward sweeps of neuronal activation that traverse the visuomotor system in strict sequence, without any temporal overlap. The motor response is initiated and driven by the prime signal until the subsequent target signal takes over response control. Priming effects increase with prime-target SOA because an inconsistent prime has progressively more time to activate the wrong response. In terms of online motor measures (e.g., pointing responses, but also force measures or lateralized readiness potentials), the properties of such a system can be described in terms of three rapid-chase criteria (Schmidt et al., 2006): (1) prime rather than target signals must determine the onset and initial direction of the response (*initiation criterion*); (2) target signals must influence the response before it is completed (*takeover criterion*); (3) movement kinematics must initially depend only on prime characteristics and be independent of all target characteristics (*independence criterion*).

Importantly, the rapid-chase theory also makes strong predictions for response time studies. Specifically, priming effects should increase with SOA (Vorberg et al., 2003) and the priming effects in fast responses should be at least as large as those in slower responses (Seydell-Greenwald & Schmidt, 2012). In contrast, priming effects that do not increase with SOA or priming effects that do increase in slower responses would contradict a rapid-chase account. First, when priming effects are not increasing with SOA, the initial processing of the prime signal is assumed to be corrupted by the processing of the target signal (i.e., both are not strictly sequential). Note that this interpretation is based on the precondition that increasing priming effects with SOA are not just the result of increasingly complete prime representations. Second, when priming effects are increasing in slower responses, the prime processing is also assumed to contradict a feedforward account. Because the visuomotor system is processing and responding to visual stimuli online, a feedforward prime signal should be more dominant in faster responses. In neurophysiological terms, the fastest responses are those most likely based on the first spikes of the feedforward sweep without any recurrent feedback. Consequently, a priming effect in the fastest responses that is as strong (or stronger) as in the slower responses suggests that it is driven by the first-arriving information alone. Note that such a finding precludes the possibility that increasing priming effects with SOA are due to increasingly complete prime representations because then priming effects should increase in slower responses.[8]

In sum, the response priming paradigm measures rapid visuomotor processes and can test for feedforward processing of prime stimuli by checking specific behavioral criteria. In response times, two predictions have to be tested (i.e., modulation of priming effects by SOA and by response speed) to assess whether visual processing can be said to be indistinguishable from pure feedforward processing. In the context of grouping processes, the paradigm offers the opportunity

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[8] Of course, the absolute speed of responses varies depending on participant, stimulus set, and task. However, participants are instructed to respond as fast as possible so that their respectively fastest responses are most probably reflecting the upper boundary of visuomotor performance.

to measure the feedforward phase of grouping (i.e., base grouping, Roelfsema, 2006; Roelfsema & Houtkamp, 2011).

Note that the fulfillment of the rapid-chase criteria does not imply that the visual system is strictly feedback-free (Lamme & Roelfsema, 2000) but establish it to be indistinguishable from a pure feedforward system. This is important because the notion of a pure feedforward processing stage in human vision is controversial. Recurrent mechanisms within and between visual areas can be rapid (Bullier, 2001, 2004; Roland, 2010; Sillito et al., 2006), and information might be processed at different rates in parallel streams (Chen et al., 2007; Merigan & Maunsell, 1993). This gives visual signals plenty of opportunity to cross or overtake each other. In the context of grouping processes, it is possible that two grouping cues such as symmetry and closure lead to different response speeds while both meeting the rapid-chase criteria, suggesting that both are based on feedforward processes but differ in speed or efficiency (Chapter 3; cf. Schmidt, Haberkamp, Veltkamp et al., 2011; Schmidt & Schmidt, 2009; Seydell-Greenwald & Schmidt, 2012). This conclusion would not be possible to draw based on raw response speeds (see for example, VanRullen & Koch, 2003).

Here, I propose the primed flanker task as a variant of the response priming paradigm that is particularly suited to study the processing of grouping cues – alone or in comparison – with respect to their time course, automaticity, and the influence of other variables. In this task, participants are reacting to one of two simultaneously presented targets as quickly and accurately as possible. The two targets are presented in the left and right periphery and the participant presses a left or right button depending on the position of the target with a predefined characteristic (e.g., one target is symmetric and the other asymmetric and participants are instructed to indicate the position of the symmetric one).

Targets are preceded by two primes to the left and right of the central fixation that are either consistent or inconsistent with respect to the task-relevant characteristic (e.g., the symmetric prime is on the same side as the symmetric target or on the opposite side).[9] This arrangement has several advantages. First, the response to the relevant stimulus dimension (e.g., symmetry) is based on the comparison of two stimuli (*two-alternative forced-choice task*, 2AFC task). This makes the task easier and allows for faster responses. Second, targets do not cover

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[9] Note that this spatial arrangement is similar to that of the classical flanker paradigm by Eriksen and Eriksen (1974). Indeed, the flanker paradigm might be a special case of the response priming paradigm: Both yield comparable results when the same time range is studied (cf. Mattler, 2003; Schwarz & Mecklinger, 1995). Even in their seminal 1974 paper, Eriksen and Eriksen showed that response times were the same for flankers identical to the targets and for nonidentical flankers assigned to the same response as the target, thus demonstrating flanker effects on a motor rather than on a perceptual level.

the same positions as the primes. This precludes masking and temporal integration effects that would complicate the interpretation of the results. Third, the task virtually rules out effects of spatial attention (Schmidt, Haberkamp & Schmidt, 2011). Because the relevant target appears equiprobably on the left and right side of fixation, participants are discouraged from using fixation strategies; also participants were instructed to maintain steady fixation, a simple experimental manipulation that has proven successful in comparable paradigms (e.g., Yantis & Jonides, 1990).

Importantly, because response priming works irrespective of whether primes are presented at identical or separate positions from the targets (Vorberg et al., 2003), the primed flanker task can be used to study response-time effects in a principled fashion provided by the framework of rapid-chase theory.

2. Grouping by Brightness, Shape, and Size

2.1 Introduction

2.1.1 General

In this chapter, we use the primed flanker task to directly compare the efficiency of different grouping cues in rapid visuomotor processing. Because the task measures the earliest output of visuomotor processing, it qualifies for comparing different base groupings. We test three types of grouping by similarity (brightness, shape, and size) because we assume that these are all extracted during an initial feedforward sweep of visual processing.

We complement this objective, visuomotor measure for comparing grouping strengths with a subjective measure: a scaling task in which the strength of two grouping cues is quantified in terms of each other. Even though a few earlier studies that compared different grouping principles varied grouping strength (e.g., Han & Humphreys, 1999; Kimchi, 2000), they did not measure the strength of grouping cues in terms of each other.

This design has three major advantages. Firstly, it allows to study the impact of competing grouping principles on objective measures of response activation (response times, error rates, and priming effects). Secondly, the task permits a detailed analysis of the role of grouping strength and its interaction with the grouping cues. Thirdly, the use of a speeded response task allows to compare grouping cues that can be assumed to involve fast grouping processes (base grouping rather than incremental grouping, Roelfsema, 2006).

2.2 Experiment 1: Brightness vs. Shape

2.2.1 General

We employed the primed flanker task in which a pair of primes at the center of the screen was succeeded by a pair of targets flanking the primes (Fig. 4). Primes and targets were grouped by either brightness or shape into rows (horizontal orientation) or columns (vertical orientation). Prime as well as target pairs always opposed each other in their orientation. Participants indicated as quickly and accurately as possible the side of the vertical target by pressing a left or right key. Primes were *consistent* with the required response (such that the vertical prime appeared on the side of the vertical target), or *inconsistent* (switched). This spatial arrangement should produce response priming effects, that is, faster responses in consistent trials and slower responses in inconsistent trials.

Primes and targets were either grouped by the same cue (all by brightness, all by shape) or by different cues. Grouping strength of both cues was chosen on the basis of a preceding *scaling task* where participants were asked to adjust the luminance contrast in the brightness stimuli until their perceived grouping strength was equivalent to that of the shape stimuli, or to half or twice of it (*ratio production*, Stevens, 1957).

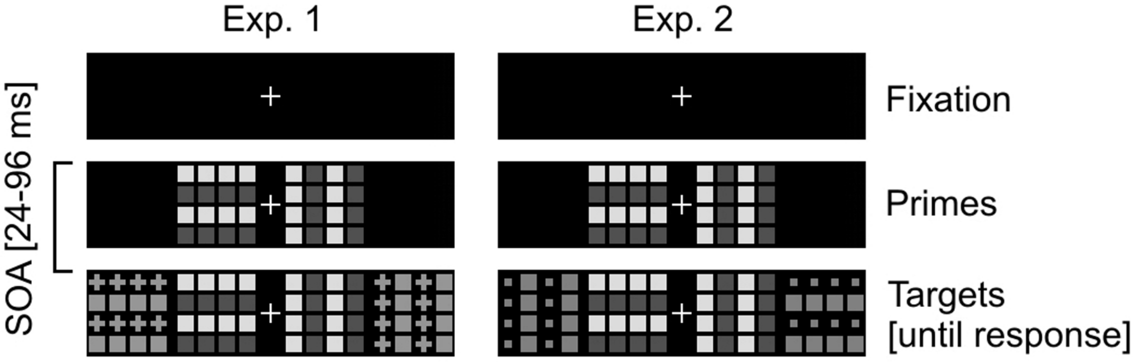

Figure 4. Stimuli and procedure in Experiments 1 and 2. Two primes and two flanking targets were presented in the sequence displayed. Participants responded to the orientation of the targets. Left panels: In Experiment 1, primes and targets were either grouped by brightness or shape. The two primes (or targets) always were grouped by the same grouping cue but were opposed to each other in their orientation (vertical or horizontal stripes). Here, a consistent trial is shown, where primes are grouped by brightness and targets by shape. Right panels: In Experiment 2, stimuli were either grouped by brightness or size. Here, an inconsistent trial is shown, where primes are grouped by brightness and targets by size.

2.2.2 Methods

Participants. Eight right-handed students from the University of Kaiserslautern, Germany (4 female, 4 male, ages 21-24), with normal or corrected vision participated in the experiment for payment of € 8 per hour. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association. Participants were debriefed after the final session.

Apparatus and Stimuli. The participants were seated in a dimly lit room in front of a CRT color monitor (1280 x 1024 pixels) with a monitor retrace rate of 85 Hz at a viewing distance of approximately 70 cm. They responded with their left and right index fingers via a standard keyboard. Stimulus presentation and timing was controlled by using Presentation® software (www.neurobs.com).

Stimuli grouped by brightness were 4 x 4 arrays of small squares (array diameter: 1.82° of visual angle; single square diameter: 0.34°; 1 cm ≈ 0.82° of visual angle). Because the squares in every second row or column shared the same luminance, stimuli appeared to be oriented horizontally or vertically. Stimuli grouped by shape were 4 x 4 arrays of small squares and crosses of the same size, again appearing as oriented horizontally or vertically (Fig. 4, lowermost left panel). Primes and targets were presented on the left and right of the fixation cross (diameter of 0.41°; 85.50 cd/m^2) against a dark background (0.28 cd/m^2). The distance between primes and fixation cross matched the distance between primes and flanking targets (0.45°).

Procedure: Scaling task. In each trial, participants were presented simultaneously with a central prime and a flanking target pair. Primes were grouped either by brightness or shape and targets were grouped by the respective other cue. Within each pair, the two primes and targets had different orientations (Fig. 4, lowermost left panel).

The task of the participants was to adjust the luminance contrast of the brightness stimuli until their grouping strength appeared as equally strong (*contrast = shape*), half as strong (*lower contrast*) or twice as strong (*higher contrast*) as the grouping strength of the shape stimuli. In the beginning of each trial all elements of the brightness stimuli had the same shade of gray, resulting in no grouping (RGB values 128/128/128 = 22.80 cd/m^2; RGB range of [0..255]). Participants increased the contrast between element rows (or columns) by pressing number 3 on the NUM keyboard, adding one RGB unit to each second row (or column) and subtracting one unit from the other rows (or columns). By pressing number 1 they decreased the contrast again. They confirmed their final decision by pressing the space bar. There was no time limit.

Each participant completed six scaling trials in each of the three grouping strength conditions in randomized order. Brightness stimuli were equally often presented at prime and target positions, and primes and targets were equally often consistent or inconsistent. Participants were instructed to focus on the fixation cross at all times.

Procedure: Primed flanker task. The primed flanker task succeeded the scaling task. In each trial, participants were first presented with the central fixation cross followed after a variable delay by a central prime pair. The flanking target pair succeeded primes at SOAs of either 24, 48, 72, or 96 ms. Primes and targets were either grouped by the same cue (*all bright* – both pairs grouped by brightness, *all shape* – both pairs grouped by shape) or by different cues (*bright primes* – prime pair grouped by brightness and target pair by shape, *shape primes* – prime pair grouped by shape and target pair by brightness). Within each pair, the two primes and targets had different orientations (Fig. 4, left panels).

The task of the participants was to indicate as quickly and accurately as possible the side of the vertical target by pressing a left or right key (2AFC task). Primes and targets were consistent or inconsistent with respect to the required response. Participants were instructed to ignore the primes. All stimuli remained on screen until participants had finished their response.[10]

The time interval from fixation to target onset was constant at 1000 ms to allow for optimal preparation to the target; summary feedback on response times and error rates was provided after each block. All stimulus combinations of consistency, prime-target SOA, prime grouping cue, and target grouping cue occurred equiprobably and pseudo-randomly in a completely crossed repeated-measures design. Grouping strengths were varied block-wise based on each participant's average values from the scaling task. The blocks were ordered such that each possible sequence of two blocks appeared equally often. Overall, every participant performed six 1-hour sessions of the primed flanker task, each consisting of one practice block followed by 54 blocks of 32 trials, accumulating to a total of 10,368 trials per participant.

Data treatment and statistical methods. In the primed flanker task, practice blocks and trials with response times shorter than 100 ms or longer than 1000 ms or with timing uncertainties larger than 1 ms were not analyzed. Those criteria eliminated 0.22% of trials. Repeated-measures analyses of variance (ANOVAs) were performed for mean response times and error rates. All were fully-factorial with factors of prime-target SOA (*S*), consistency (*C*), combination of grouping cues (*GC*), and grouping strength (*GS*). The priming effect is defined as the difference between mean response times or error rates in consistent compared to inconsistent trials and is characterized by the factor consistency. To analyze the data in more detail, planned repeated-measures contrasts were calculated. F values are reported with subscripts indicating the respective effect (e.g., F_{CxS} for the interaction of consistency and prime-target SOA), and statistical contrasts are denoted by naming the two contrasted conditions (e.g., all bright vs. all shape). All error rates were arcsine-transformed to comply with ANOVA requirements. Reported p values are Huynh-Feldt-corrected.

2.2.3 Results and Discussion

2.2.3.1 Scaling Task

The results for each participant and scaling instruction are displayed in Figure 5. In general, different participants were somewhat disparate in their perception of relative grouping strengths, especially in the *contrast = shape* and *higher contrast* conditions. At the same time they were consistent in their judgments (cf. the small standard errors across the six trials for each participant). In all participants, the adjusted contrast values increased monotonically with instructed grouping strength.

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[10] This ensured that primes were presented for longer than 100ms, the time that the visual system needs to arrive at a stable evaluation of the brightness of a stimulus (*Bloch's law,* e.g., Raab, 1962).

Both results indicate that the scaling task is an adequate way to obtain reliable subjective estimates of the relative grouping strengths of the two grouping cues.

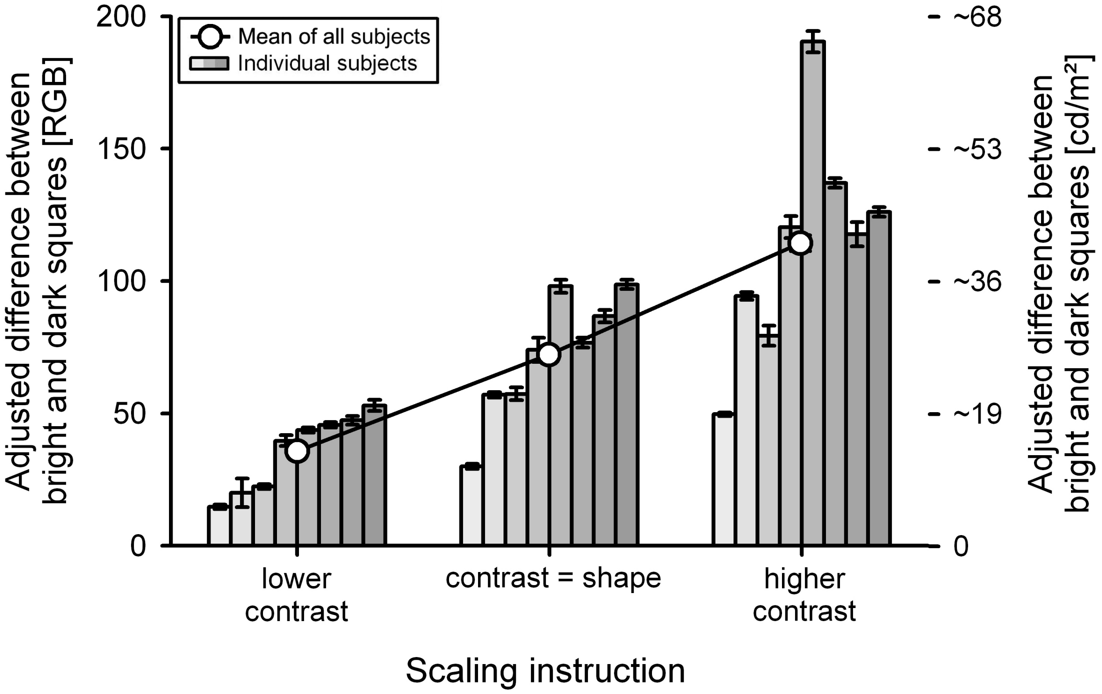

Figure 5. Results of the scaling task in Experiment 1. The bars denote for every participant the difference between bright and dark squares (in terms of their RGB values or their approximate luminances) that resulted from the respective scaling instructions. For example, a difference value of 50 is obtained with RGB values of 153/153/153 for the bright squares and 103/103/103 for the dark squares. The graph denotes participants' mean values, error bars denote the standard error of the mean.

2.2.3.2 Primed Flanker Task: Response Times and Error Rates

All conditions generated stable response priming effects in response times. An ANOVA with factors of prime-target SOA, consistency, combination of grouping cues, and grouping strength, confirmed that in consistent trials participants responded considerably faster compared to inconsistent trials [$F_{C}(1,7) = 46.80$, $p < .001$]. This effect increased with increasing SOA [$F_{CxS}(3,21) = 23.73$, $p < .001$]. As shown in Figure 6, inconsistent trials also produced more errors than consistent ones [$F_{C}(1,7) = 76.65$, $p < .001$] and this effect increased with increasing SOA as well [$F_{CxS}(3,21) = 26.46$, $p = .001$]. This was also true for individual participants (response times: $p_{C} < .001$ in eight out of eight participants; error rates: $p_{C} < .001$ in eight out of eight participants). The overall error rate in Experiment 1 was about 11.43% of all trials.

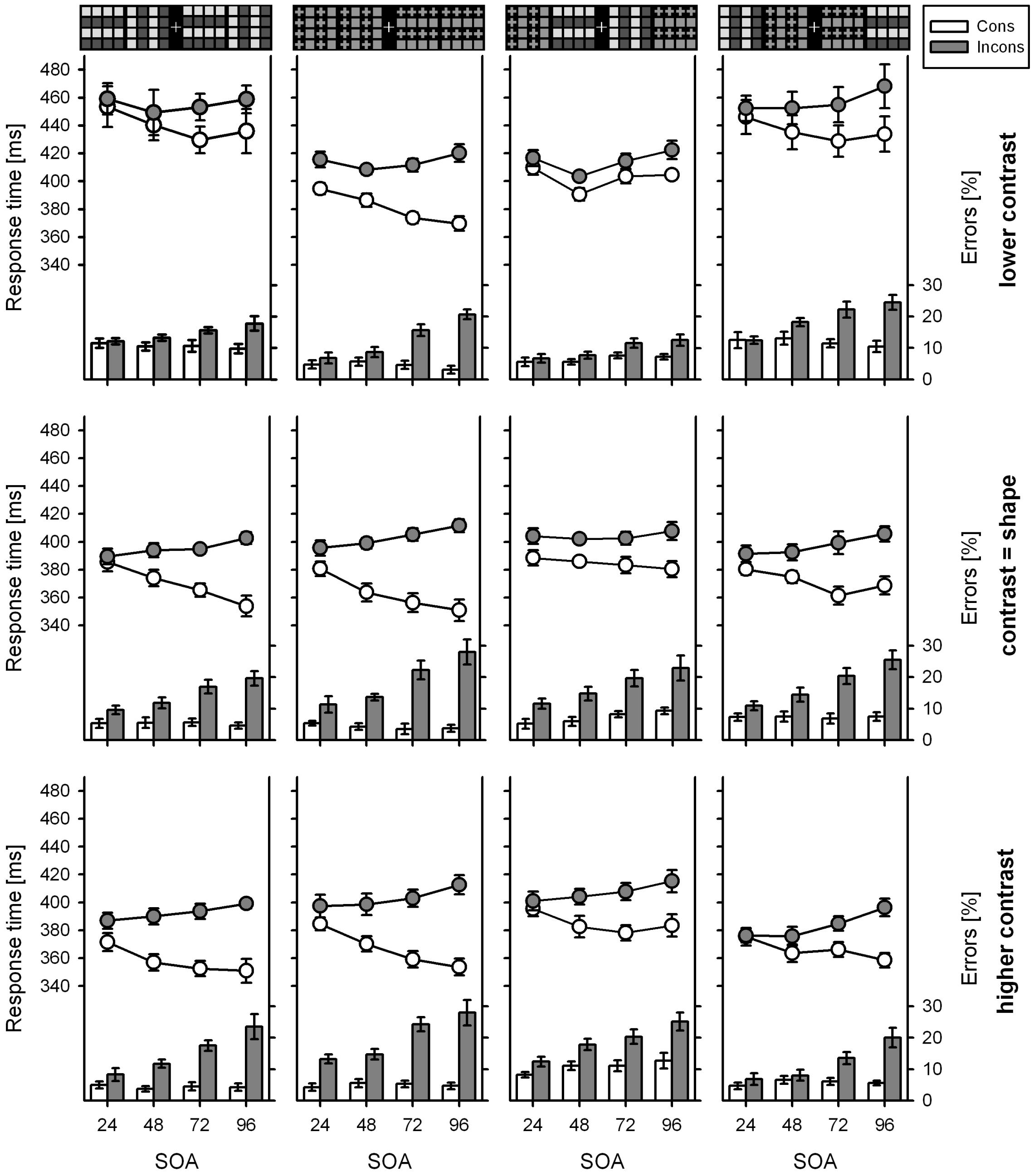

Figure 6. Results of the primed flanker task in Experiment 1. Panels show all possible combinations of grouping cues (columns) and the three different contrast conditions (rows). Each panel displays mean response times (line plots) and error rates (bar plots) in consistent (white) and inconsistent (gray) trials as a function of prime-target SOA. Error bars denote the standard error of the mean corrected for between-subjects variance (Cousineau, 2005; Loftus & Masson, 1994).

In general, priming effects in both measures were strongly modulated by the combination of grouping cues as well as their relative grouping strengths [response times: $F_{\text{CxGC}}(3,21) = 6.90$, $p = .002$; $F_{\text{CxGS}}(2,14) = 10.54$, $p = .002$; error rates:

$F_{\mathrm{CxGC}}(3,21) = 8.51$, $p < .001$; $F_{\mathrm{CxGS}}(2,14) = 9.38$, $p = .003$]. For direct comparison, net priming effects are displayed in Figure 7.

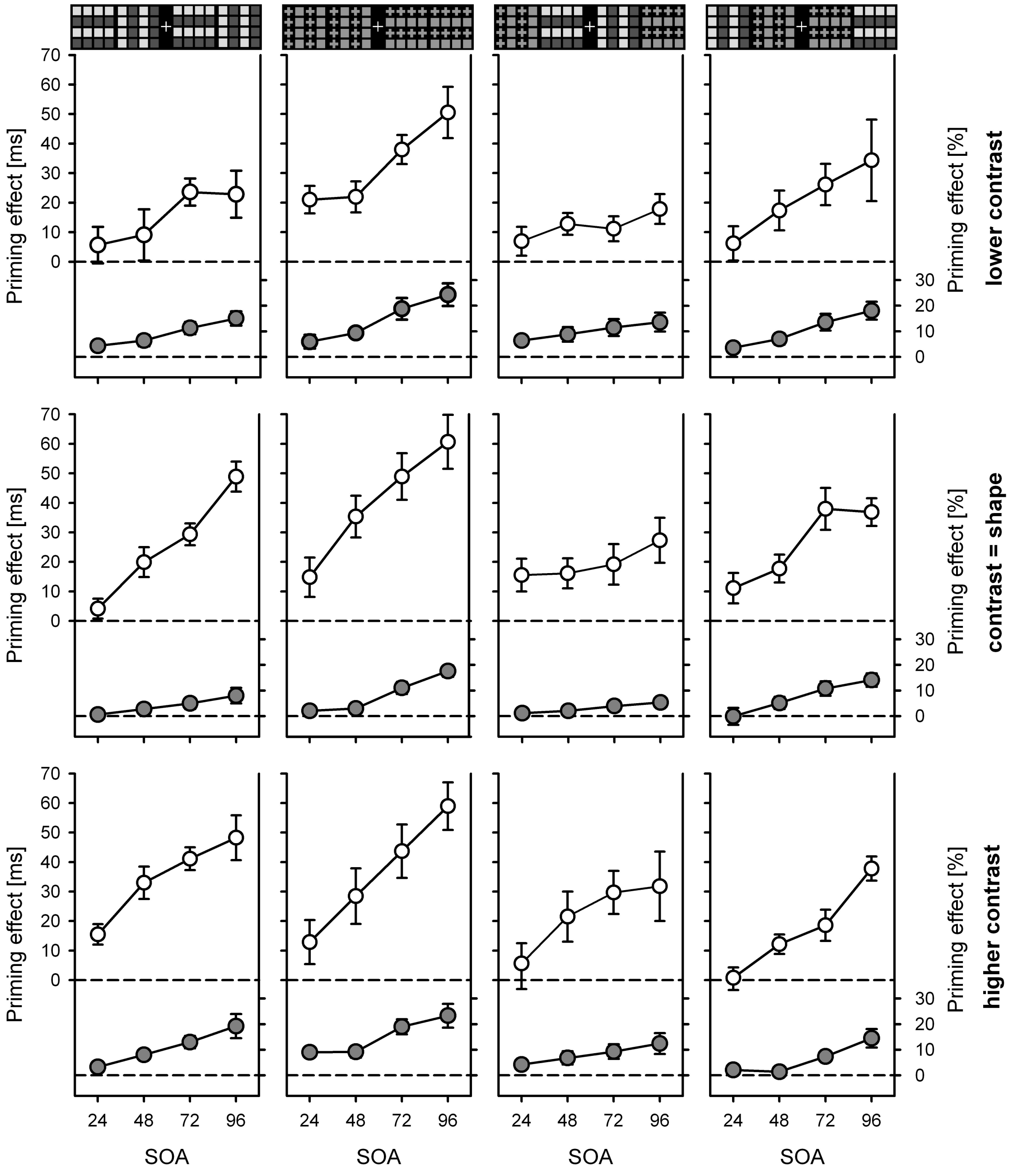

Figure 7. Priming effects for the primed flanker task in Experiment 1. Priming effects are defined as the differences between mean response times or error rates in consistent compared to inconsistent trials. Panels show all possible combinations of grouping cues (columns) and the three different contrast conditions (rows). Each panel displays priming effects in mean response times (white) and error rates (gray) as a function of prime-target SOA. Error bars denote the standard error of the mean.

2.2.3.3 Primed Flanker Task: Grouping Principles in Direct Competition

We compared the two grouping cues by examining the priming effects in response times for different combinations within each grouping strength condition. To rule out influences of the grouping cue of the target, we contrasted those combinations with the same targets but different primes.

In the lower contrast condition (Figs. 6 and 7, upper panels), shape primes yielded stronger effects compared to brightness primes when combined with shape targets [all shape vs. bright primes: $F_{\mathrm{CxGC}}(1,7) = 28.13$, $p = .001$]; this effect further increased with SOA [$F_{\mathrm{CxSxGC}}(1,7) = 5.70$, $p = .014$]. In contrast, shape and brightness primes yielded effects of the same magnitude when combined with brightness targets [all bright vs. shape primes: $F_{\mathrm{CxGC}}(1,7) = 1.13$, $p = .322$].

When the grouping strength of both cues was perceived as equal (Figs. 6 and 7, mid panels), this pattern was repeated: Again, shape primes yielded stronger effects compared to brightness primes when combined with shape targets [all shape vs. bright primes: $F_{\mathrm{CxGC}}(1,7) = 11.42$, $p = .012$]; this effect further increased with SOA [$F_{\mathrm{CxSxGC}}(1,7) = 7.05$, $p = .033$]. On the other hand, shape and brightness primes yielded effects of the same magnitude when combined with brightness targets [all bright vs. shape primes: $F_{\mathrm{CxGC}}(1,7) = .00$, $p = .971$].

These results were complemented by the fact that when all stimuli were grouped by shape compared to all stimuli grouped by brightness, priming effects were stronger in response times [all bright vs. all shape: $F_{\mathrm{CxGC}}(1,7) = 12.40$, $p = .010$] and by trend in error rates [all bright vs. all shape: $F_{\mathrm{CxGC}}(1,7) = 5.39$, $p = .053$]. Priming effects in response times also were by trend larger with shape primes and brightness targets compared to brightness primes and shape targets [bright primes vs. shape primes: $F_{\mathrm{CxSxGC}}(1,7) = 5.49$, $p = .052$]. Thus, although participants equalized the cues' subjective grouping strengths, stimuli grouped by shape produced stronger priming effects than stimuli grouped by brightness. Note that this difference is not a result of speed-accuracy trade-off because it was observed in response times as well as error rates, and both grouping cues produced similar levels of overall response times and error rates.

Finally, in the higher contrast condition (Figs. 6 and 7, lower panels), shape primes yielded stronger effects compared to brightness primes when combined with shape targets [all shape vs. bright primes: $F_{\mathrm{CxSxGC}}(1,7) = 26.13$, $p = .001$]. However, shape primes yielded also weaker effects compared to brightness primes when combined with brightness targets [all bright vs. shape primes: $F_{\mathrm{CxGC}}(1,7) = 17.86$, $p = .004$]. In other words, the increased grouping strength of the brightness primes compensated for their processing disadvantage, resulting in similar effects for both grouping cues. Put differently, the subjective grouping of the brightness stimuli has to be much stronger than that of the shape stimuli to drive priming effects with similar efficiency.

2.2.3.4 Primed Flanker Task: The Role of Grouping Strength

We examined the influence of subjective grouping strength (i.e., contrast modulation in brightness stimuli) on response times and priming effects for each of the different prime-target combinations (Figs. 8 and 9). Data were collapsed across SOA but larger priming effects went along with longer SOAs throughout all conditions [response times: all $F_{\mathrm{CxS}}(3,21) \geq 7.44$, all $p \leq .001$; error rates: all $F_{\mathrm{CxS}}(3,21) \geq 3.60$, all $p \leq .031$]. This was also true for individual participants (response times: $p_{\mathrm{CxS}} < .001$ in six out of eight participants; error rates: $p_{\mathrm{CxS}} < .001$ in seven out of eight participants).

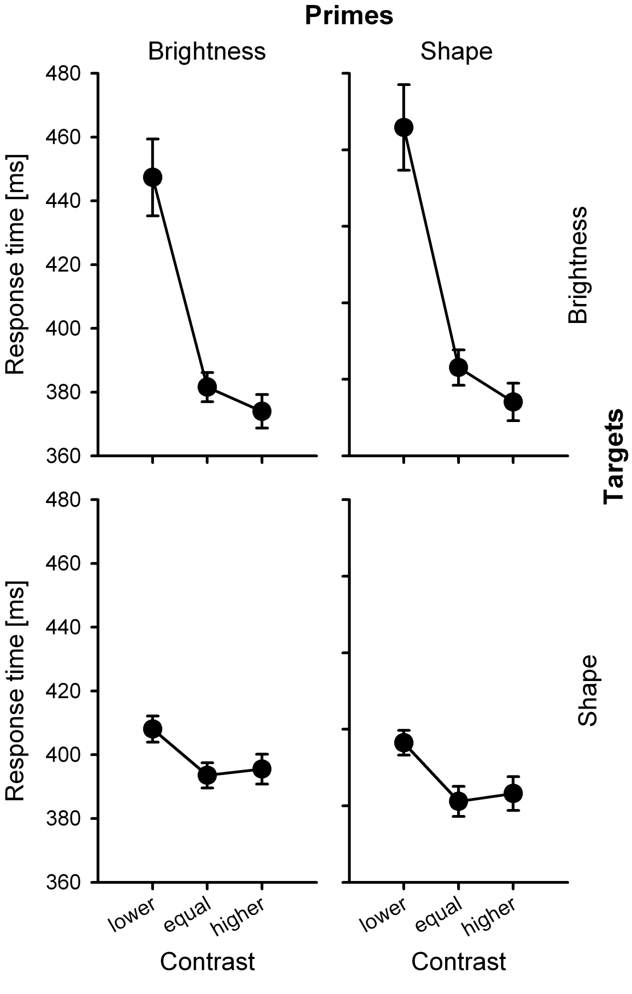

Figure 8. Response times for the primed flanker task in Experiment 1. The four graphs display the mean response times as a function of grouping strength for the four different grouping cue combinations of primes and targets. Error bars denote the standard error of the mean corrected for between-subjects variance (Cousineau, 2005; Loftus & Masson, 1994).

For overall response times (Fig. 8), we found a main effect of grouping strength [$F_{\mathrm{GS}}(2,14) = 21.54$, $p = .002$] as well as an interaction of grouping strength and prime-target combination [$F_{\mathrm{GCxGS}}(6,42) = 19.76$, $p = .002$]. Tests of simple effects (conducted for each prime-target combination separately) showed that when targets were grouped by brightness, responses accelerated with increasing grouping strength in the targets [brightness primes: $F_{\mathrm{GS}}(2,14) = 20.38$, $p = .002$; shape primes: $F_{\mathrm{GS}}(2,14) = 23.59$, $p = .002$]. When targets were grouped by shape, responses were also modulated by grouping strength, but this effect was much smaller and limited to the lower contrast condition [brightness primes: $F_{\mathrm{GS}}(2,14) = 10.26$, $p = .007$; shape primes: $F_{\mathrm{GS}}(2,14) = 11.12$, $p = .005$]. Note that the latter effects are induced by the block-wise contrast variation. In blocks where contrast was lower, grouping was more demanding and as a result response times were slowed down for all stimuli in that block. This was true even when primes and targets were not varied in their grouping strength (i.e., when both were grouped by shape).

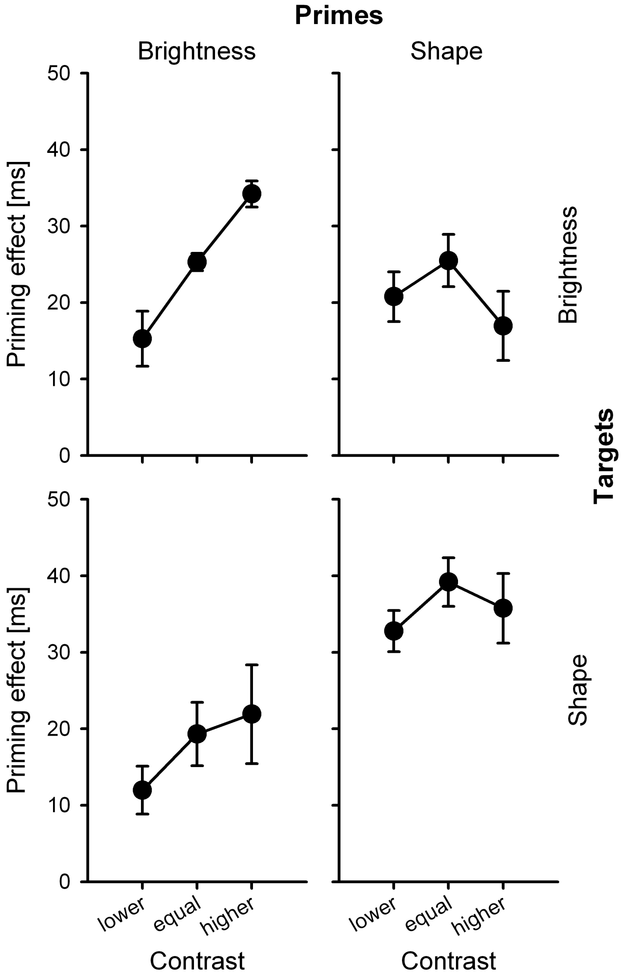

Figure 9. Response time priming effects for the primed flanker task in Experiment 1. The four graphs display the mean priming effects as a function of grouping strength for the four different grouping cue combinations of primes and targets. Error bars denote the standard error of the mean corrected for between-subjects variance (Cousineau, 2005; Loftus & Masson, 1994).

Priming effects in response times (Fig. 9) were modulated by both prime-target combination [$F_{\mathrm{CxGC}}(3,21) = 6.98$, $p = .002$] and grouping strength [$F_{\mathrm{CxGC}}(2,14) = 10.25$, $p = .002$]. The interaction of all three factors did not reach significance [$F_{\mathrm{CxGCxGS}}(6,42) = 2.21$, $p = .091$].

When primes and targets were both grouped by brightness, priming effects increased monotonically with their grouping strength [$F_{\mathrm{CxGS}}(2,14) = 17.22$, $p = .004$]. This pattern developed in the same direction with brightness primes combined with shape targets but was not significant [$F_{\mathrm{CxGS}}(2,14) = 1.06$, $p = .370$]. When primes were grouped by shape, priming effects were not systematically influenced by prime grouping strength [shape targets: $F_{\mathrm{CxGS}}(2,14) = 1.16$, $p = .342$; brightness targets: $F_{\mathrm{CxGS}}(2,14) = 1.86$, $p = .193$].

Together, these analyses suggest an appealing principle: Overall response times depend primarily on grouping strength of the targets but not of the primes, while priming effects depend primarily on grouping strength of the primes but less so on grouping strength of the targets.

2.3 Experiment 2: Brightness vs. Size

2.3.1 General

In Experiment 2, we further tested the paradigm with the grouping cue of size. Equivalently to Experiment 1, participants performed a scaling task and a subsequent primed flanker task comparing brightness with size stimuli.

2.3.2 Methods

Participants. One left-handed and seven right-handed students from the University of Kaiserslautern, Germany (3 female, 5 male, ages 21-25), with normal or corrected vision participated in the experiment for payment of € 8 per hour. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association. Participants were debriefed after the final session.

Apparatus and Stimuli. Apparatus, stimuli, and their arrangement were the same as in Experiment 1, except that shape stimuli were replaced by size stimuli. Those were defined by 4 x 4 arrays of squares, half of them the size of the brightness stimuli (diameter of 0.34°; 22.80 cd/m^2), half of them markedly smaller (diameter of 0.16°; 22.80 cd/m^2). Again, stimuli appeared to be oriented horizontally or vertically.

Procedures: Scaling task and primed flanker task. The scaling and the primed flanker tasks were identical to Experiment 1 except that size stimuli replaced the shape stimuli (Fig. 4, right panels).

Data treatment and statistical methods. Data treatment and statistical analyses were identical to those in Experiment 1. Outlier exclusion eliminated 0.10% of trials.

2.3.3 Results and Discussion

2.3.3.1 Scaling Task

The results are displayed in Figure 10. Again, the participants differed significantly in their perception of relative grouping strengths but were consistent in their respective judgments. The adjusted contrast values also increased monotonically with instructed grouping strength. As in Experiment 1, the results of each participant were used to define the stimuli grouped by brightness in the primed flanker task.

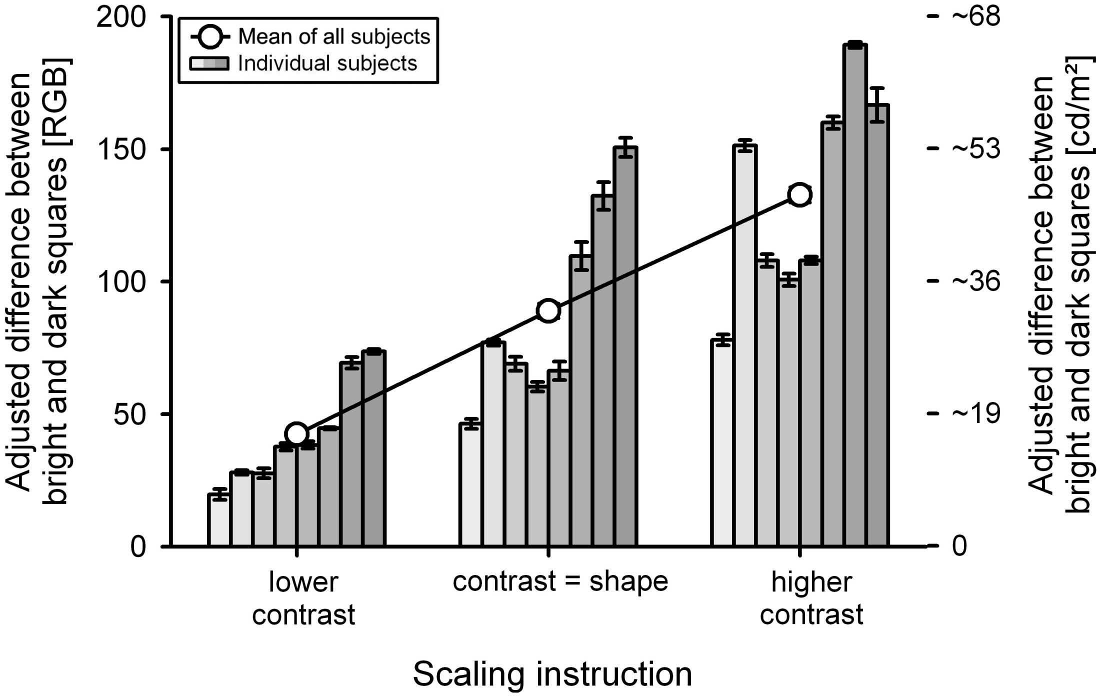

Figure 10. Results of the scaling task in Experiment 2. For specifications see Figure 5.

2.3.3.2 Primed Flanker Task: Response Times and Error Rates

As in Experiment 1, all conditions generated stable response priming effects in response times and error rates that increased with SOA [response times: $F_{\mathrm{C}}(1,7) = 42.48$, $p < .001$; $F_{\mathrm{CxS}}(3,21) = 37.52$, $p < .001$; error rates: $F_{\mathrm{C}}(1,7) = 28.98$, $p = .001$; $F_{\mathrm{CxS}}(3,21) = 27.69$, $p < .001$]. Again, these priming effects were strongly modulated by variations in grouping cues and their relative grouping strengths [response times: $F_{\mathrm{CxGC}}(3,21) = 4.51$, $p = .050$; $F_{\mathrm{CxGS}}(2,14) = 11.76$, $p = .001$; error rates: $F_{\mathrm{CxGC}}(3,21) = 19.30$, $p < .001$; $F_{\mathrm{CxGS}}(2,14) = 24.65$, $p < .001$] (Fig. 11). This was also true for individual participants (response times: $p_{\mathrm{C}} < .001$ in eight out of eight participants; error rates: $p_{\mathrm{C}} < .001$ in eight out of eight participants). The overall error rate in Experiment 2 was about 9.59% of all trials.

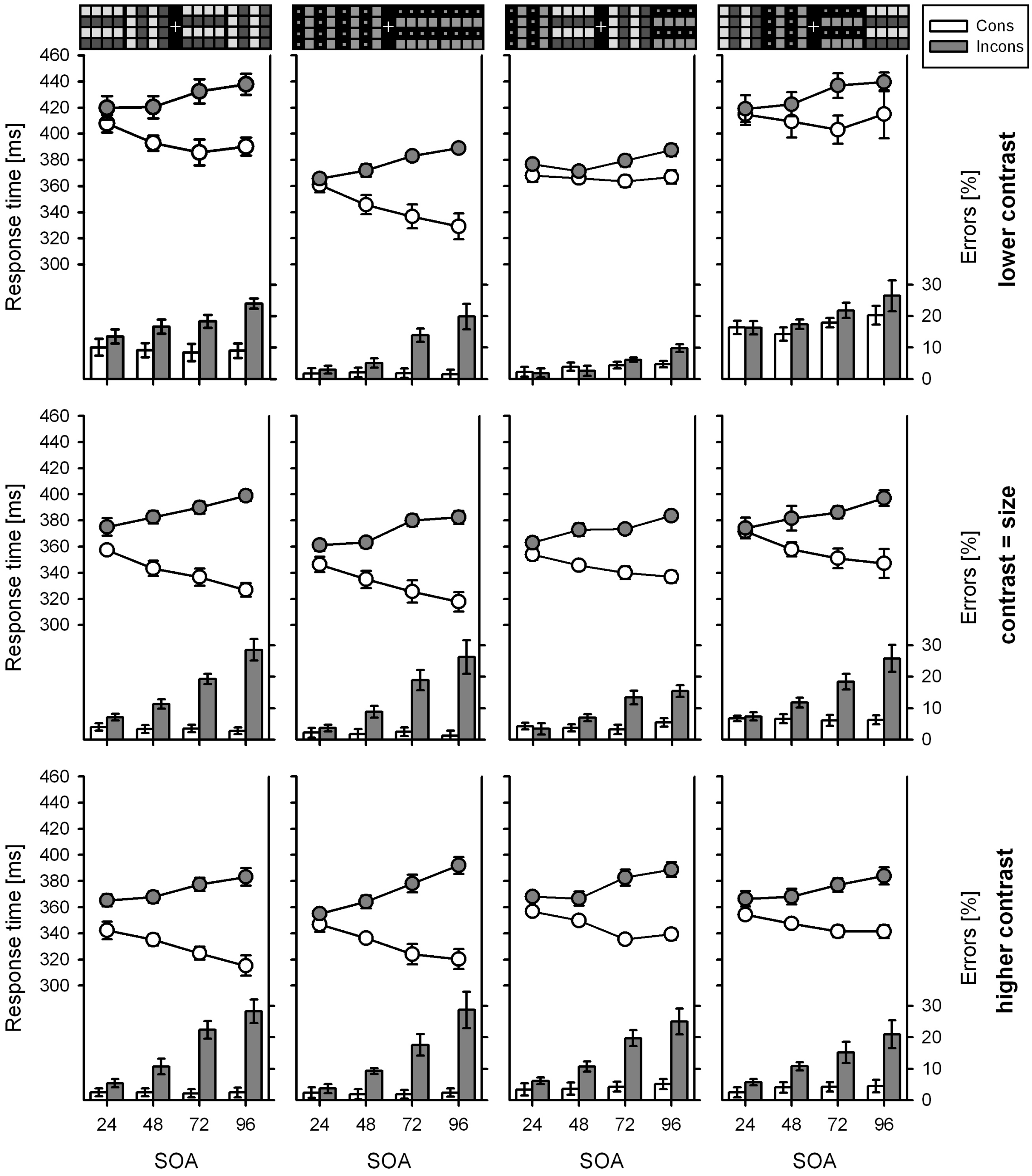

Figure 11. Results of the primed flanker task in Experiment 2. For specifications see Figure 6.

2.3.3.3 Primed Flanker Task: Grouping Principles in Direct Competition

Again, we compared both grouping cues by examining the priming effects in response times for different combinations within each grouping strength condition. For direct comparison, net priming effects are displayed in Figure 12.

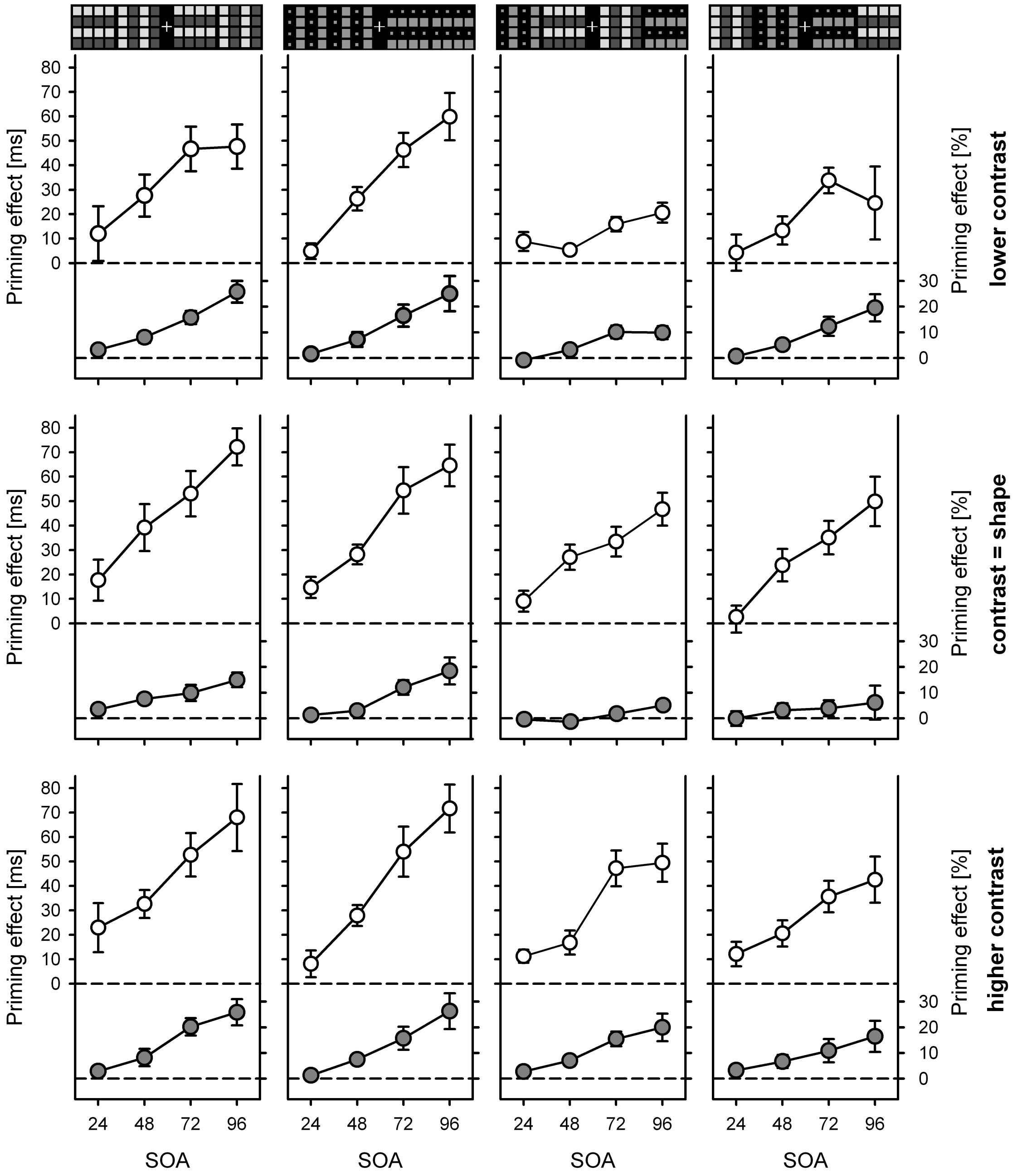

Figure 12. Priming effects for the primed flanker task in Experiment 2. For specifications see Figure 7.

In the lower contrast condition (Figs. 11 and 12, upper panels), size primes yielded stronger effects compared to brightness primes when combined with size targets [all size vs. bright primes: $F_{\mathrm{CxGC}}(1,7) = 18.32$, $p = .004$] and this effect increased further with SOA [$F_{\mathrm{CxSxGC}}(1,7) = 29.97$, $p = .001$]. In contrast, size and brightness primes yielded effects of the same magnitude when combined with brightness targets [all bright vs. size primes: $F_{\mathrm{CxGC}}(1,7) = 1.60$, $p = .247$]. This pattern resembles the results of Experiment 1.

When the grouping strength of both cues was perceived as equal (Figs. 11 and 12, mid panels), size primes yielded stronger effects compared to brightness primes when combined with size targets [all size vs. bright primes: $F_{\mathrm{CxGC}}(1,7) = 9.59$, $p = .017$] and this effect further increased with SOA [$F_{\mathrm{CxSxGC}}(1,7) = 4.14$, $p = .035$]. Size and brightness primes yielded effects of the same magnitude when combined with brightness targets [all bright vs. size primes: $F_{\mathrm{CxGC}}(1,7) = 4.22$, $p = .079$]. Again, this resembles the results of Experiment 1. However, this time we observed effects of the same magnitude for brightness primes and targets compared with size primes and targets [all bright vs. all size: $F_{\mathrm{CxGC}}(1,7) = 1.66$, $p = .238$]. Priming effects were also not different for brightness primes combined with size targets and size primes combined with brightness targets [brightness primes vs. size primes: $F_{\mathrm{CxGC}}(1,7) = .10$, $p = .757$]. Thus, when grouping strengths were perceived as equally strong neither of the two grouping cues was consistently producing stronger priming effects in visuomotor processing.

Finally, in the higher contrast condition (Figs. 11 and 12, lower panels), size primes again yielded stronger effects compared to brightness primes when combined with size targets [all size vs. bright primes: $F_{\mathrm{CxGC}}(1,7) = 6.07$, $p = .043$], that increased with SOA [$F_{\mathrm{CxSxGC}}(1,7) = 4.33$, $p = .016$]. In contrast, size and brightness primes yielded effects of the same magnitude when combined with brightness targets [all bright vs. size primes: $F_{\mathrm{CxGC}}(1,7) = 4.63$, $p = .068$]. Thus no systematic difference was found between priming effects induced by brightness and size groupings.

2.3.3.4 Primed Flanker Task: The Role of Grouping Strength

In Figures 13 and 14, response times and priming effects in response times for the different prime and target combinations are displayed as a function of grouping strength. Again, data were collapsed across SOA for these analyses; however, increasing SOAs always increased priming effects [response times: all $F_{\mathrm{CxS}}(3,21) \geq 5.48$, all $p \leq .034$; error rates: all $F_{\mathrm{CxS}}(3,21) \geq 17.35$, all $p \leq .001$ and $F_{\mathrm{CxSxGS}}(6,42) = 4.24$, $p = .008$]. This was also true for individual participants (response times: $p_{\mathrm{CxS}} < .001$ in eight out of eight participants; error rates: $p_{\mathrm{CxS}} < .001$ in eight out of eight participants).

For overall response times (Fig. 13), we found main effects of prime-target combination [$F\text{GC}(3,21) = 6.99$, $p = .021$] and grouping strength [$F\text{GS}(2,14) = 52.25$, $p < .001$], as well as an interaction of both factors [$F\text{GCxGS}(6,42) = 28.14$, $p < .001$]. Tests of simple effects (conducted for each prime-target combination separately) showed that when targets were grouped by brightness, response times accelerated with target grouping strength [brightness primes: $F\text{GS}(2,14) = 49.84$, $p < .001$; size primes: $F\text{GS}(2,14) = 45.73$, $p < .001$]. When targets were grouped by size, responses were modulated by grouping strength [brightness primes: $F\text{GS}(2,14) = 13.09$, $p = .002$; size primes: $F\text{GS}(2,14) = 12.23$, $p = .006$]. Again, this effect was considerably smaller and limited to the lower contrast condition, replicating the findings of Experiment 1 and reflecting the more demanding grouping in these blocks.

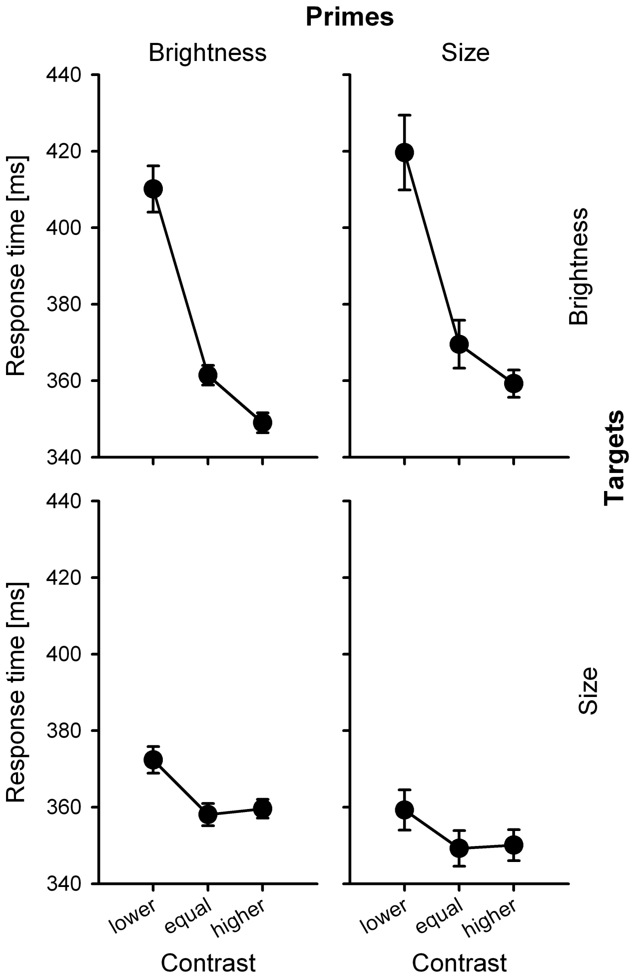

Figure 13. Response times for the primed flanker task in Experiment 2. For specifications see Figure 8.

Priming effects in response times (Fig. 14) were modulated by grouping strength [$F_{\text{CxGS}}(2,14) = 11.63$, $p = .001$] and by trend by prime-target combination [$F_{\text{CxGC}}(3,21) = 4.33$, $p = .056$]. The interaction of all three factors did not reach significance [$F_{\text{CxGCxGS}}(6,42) = 1.70$, $p = .145$].

With brightness primes, priming effects were smaller with lower grouping strength, independently of the targets [brightness targets: $F_{\text{CxGS}}(2,14) = 8.77$, $p = .004$; size targets: $F_{\text{CxGS}}(2,14) = 11.89$, $p = .001$]. With size primes, priming effects were not modulated by prime grouping strength when combined with size targets [size targets: $F_{\text{CxGS}}(2,14) = 2.20$, $p = .173$] but that effect was significant when size primes were combined with brightness targets [brightness targets: $F_{\text{CxGS}}(2,14) = 4.39$, $p = .033$]. Note, however, that this effect seems to rest on a single data point (lower-contrast condition, consistent trials, longest SOA) that has a somewhat elevated error variance, so we have reasonable doubt that the effect is replicable.

In sum, these analyses support the conclusion from Experiment 1 that overall response times depend on grouping strength of the targets but not of the primes, while priming effects depend primarily on grouping strength of the primes but less so on grouping strength of the targets.

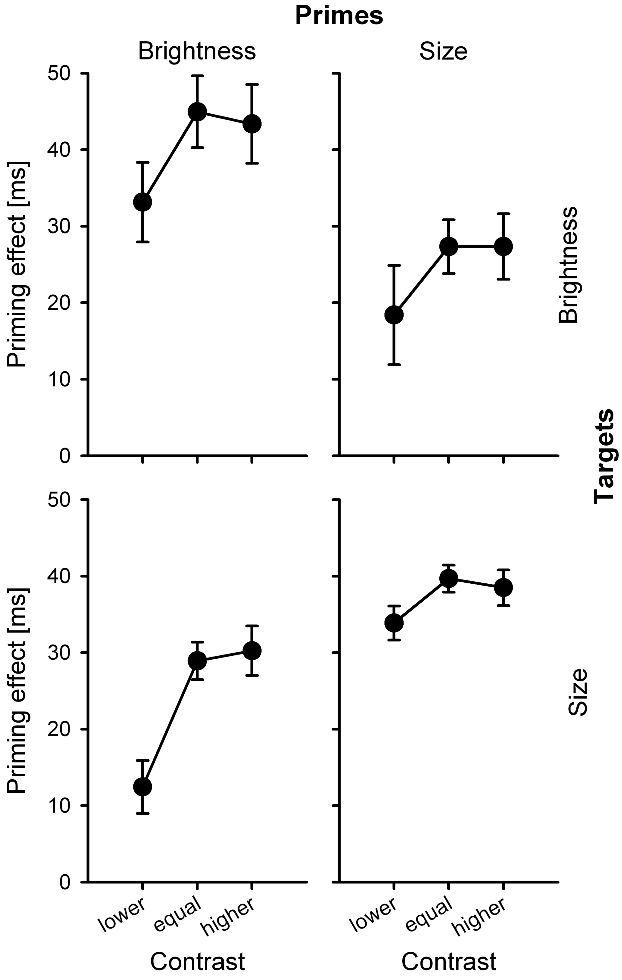

Figure 14. Response time priming effects for the primed flanker task in Experiment 2. For specifications see Figure 9.

2.3.4 Synopsis of the Results in Experiments 1 and 2

Overall, Experiments 1 and 2 showed strong modulations of response times, error rates, and priming effects by the combinations of grouping cues and their respective grouping strengths. In Experiment 1, shape primes produced larger priming effects even when the subjective grouping strength of both cues was equalized. Only when the grouping strength of the brightness primes was further increased did they lead to priming effects of similar magnitude as those induced by shape primes. In Experiment 2, priming effects with size primes did not differ from those with brightness primes. Together, the two experiments suggest a useful rule of thumb: Grouping strength of the primes mainly determines the magnitude of the priming effects, whereas grouping strength of the targets mainly determines the overall response times.

2.4 General Discussion

We used a primed flanker task with a concomitant scaling task to compare the visuomotor processing dynamics of different grouping cues under conditions of controlled subjective grouping strengths. Our results serve to establish the task as a new objective measure to compare different principles of fast, automatic grouping, linking the feedforward dynamics of the grouping processes to the feedforward activation of associated motor responses. In addition, our data clearly show that comparisons between different grouping principles are extremely difficult to interpret if nothing is known about the relative grouping strengths.

2.4.1 The Scaling Task

Firstly, the scaling task proved to be a useful tool for controlling subjective grouping strength before comparing different grouping cues. It is easy to implement, produces reliable individual estimates of relative grouping strength, and avoids mismatches between tasks (by using the same stimulus settings as in the primed flanker task).

2.4.2 The Primed Flanker Task

Secondly, the primed flanker task produced large and reliable priming effects in response times and error rates that increased with prime-target SOA, and more importantly, strongly depended not only on the relative grouping strengths of primes and targets but also on the cues that grouped them. Therefore, obtained priming effects are suited to trace out the visuomotor processing dynamics of different grouping cues over the course of the prime-target SOA.

The primed flanker task is an *objective* measure of grouping anchored in the domain of visuomotor processing and in that respect comparable to the *repetition discrimination task* by Palmer and Beck (2007). In that task, participants have to detect a pair of repeating elements in a row of alternating shapes as quickly as possible, and the resulting response times depend strongly on whether or not the repeated element pair is grouped by some grouping cue. This effect has been demonstrated, for example, for grouping by common region, connectedness, proximity, and similarity of color (Beck & Palmer, 2002; Palmer & Beck, 2007). However, the repetition discrimination task is not suited to directly investigate the role of grouping strength and compare different grouping principles in rapid visuomotor processing. In contrast, our results shed further light on both.

2.4.3 Comparing the Grouping Cues

Our experiments reveal a number of commonalities, but also some discrepancies, regarding the processing of the studied grouping cues. As a rule of thumb, for all grouping cues, increases in grouping strength in the targets lead to faster response times, and increases in grouping strength in the primes lead to larger priming effects (similar relationships between grouping strength and processing speed were reported by Han & Humphreys, 1999, and Kimchi, 2000). Such behavior is in accord with a simple feedforward model of response priming, which explains priming effects by sequential response activation that occurs in turn by primes and targets. For instance, in the accumulator model proposed by Vorberg et al. (2003), a prime consistent with the subsequent target activates the correct response ahead of the target, whereas an inconsistent prime would lead to activation of the incorrect response that would need to be counteracted by the target. This model directly predicts that stronger prime signals should augment priming effects by deepening the response conflict, while stronger target signals should speed the overall response times.

All of the grouping cues yield fast response times similar to choice responses to simple color or shape stimuli, and they are all able to induce rapid visuomotor activation (i.e., response priming effects). This suggests that those groupings are extracted in a highly automatic fashion and are implemented by base grouping mechanisms, that is, feedforward feature extraction, rather than incremental grouping, that is, a time-consuming spread of enhanced firing rates (Roelfsema, 2006). This is supported by the fact that our task asked for the processing of local groupings and not for their transitive combination (i.e., a chain of local groupings that would result in incremental grouping, cf. Roelfsema & Houtkamp, 2011). In addition, Wannig et al. (2011) tested the visual processing of stimuli similar to ours in monkey visual cortex and observed a rapid spread of neuronal activity according to grouping by color similarity, consistent with a base grouping account.

Although all grouping principles studied here seem to involve base grouping, the primed flanker task is able to assess their processing efficiency in comparison. Indeed, Experiment 1 reveals that grouping by shape produces stronger priming effects than grouping by brightness. Only when the perceived grouping strength of the brightness stimuli is much stronger than that of the shape stimuli, the magnitude of priming effects reaches similar levels. This is not the case for grouping by size in Experiment 2: With subjective grouping strengths equalized, the obtained priming effects are of similar magnitude for brightness and size stimuli.

This pattern of findings allows for two alternative interpretations. First, it might demonstrate a precedence in visuomotor processing of shape groupings over brightness and size groupings under conditions of equalized grouping strength. Second, it might demonstrate a dissociation between the subjective impression of grouping strength and the objective modulation of priming effects in speeded responses.

The first interpretation would provide further evidence for the notion that grouping is not a unitary process but that the processing of different grouping cues varies in critical aspects such as attentional demands or time course (e.g., Kimchi & Razpurker-Apfeld, 2004; Palmer et al., 2003; Sasaki, 2007). More specifically, we might assume that the grouping cues of size and brightness are processed less efficiently than grouping by shape. To our knowledge, our primed flanker task is the first to demonstrate such differences in the processing of different forms of grouping by similarity.[11] On a neurophysiological level, it is well known that the neuronal translation of visual shape or contour information differs considerably from that of surface brightness (e.g., DeYoe & Van Essen, 1988). In agreement with our findings, the processing of (even complex) contours or shapes can be implemented within a feedforward architecture (e.g., Riesenhuber & Poggio, 1999; Roelfsema & Houtkamp, 2011). Evidence from masking and neurophysiological studies also supports the notion of a fast processing of contour information and a slower one of surface/lightness information (Arrington, 1994; Breitmeyer et al., 2006; Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999). Thus, the visual system first makes use of contour or shape information, which consequently exerts a stronger influence on temporally early processes, that is, yields larger priming effects. Later on, by filling-in processes, brightness information becomes accessible and may be incorporated into perceptual grouping processes.

The alternative interpretation would imply that it is not possible to directly compare subjective and objective measures, even if both refer to the same stimuli. In keeping with the experimental literature on masked priming, we propose that the physical parameters that determine grouping strength affect both the temporally early visuomotor response to the stimulus and the later subjective impression formed about the stimulus. However, even though we find that both these output systems are sensitive to this aspect of the stimulus, there is no guarantee that grouping strength is represented in both systems in the same way. This leads to an important caveat to our approach: Equating different stimulus features for their subjective impression of grouping strength does not necessarily imply that the features are also equated in the visuomotor system. Conversely, it is an open question whether physical parameters leading to identical effects in an objective priming measure would lead to the same subjective impression of grouping strength. Note that this applies to all objective measures of grouping strength and does by no means diminish their explanatory power in the study of grouping processes.

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[11] At first glance, this seems to be in contrast to an earlier study by Ben-Av and Sagi (1995) in which participants indicated the orientation of masked grouping arrays, yielding similar results for grouping by brightness and shape. However, while our findings relate to the processing speed of different grouping cues, those of Ben-Av and Sagi (1995) relate to the efficiency of their identification.

2.4.4 Summary

In conclusion, the primed flanker task was introduced as a new objective measure to compare grouping cues in their impact on fast visuomotor processing. The current results once again demonstrate the fundamental role of grouping strength for the processing of grouping cues and disclose specific processing characteristics of different similarity cues. First, grouping strength strongly modulates the extent to which a grouping cue influences speeded visuomotor processing. Second, we found that even with the subjective grouping strength equalized, grouping by shape still has a stronger impact on rapid visuomotor processes than grouping by brightness.

3. Grouping by Symmetry and Closure

3.1 Introduction

3.1.1 General

In this chapter, we use the primed flanker task to investigate the efficiency of grouping cues in rapid visuomotor processing that are more complex than grouping by similarity: symmetry (e.g., Schumann, 1900) and closure (e.g., Wertheimer, 1923). Perceived figures or shapes may be either symmetric or asymmetric (i.e., are reflected along their central axis or not),[12] and may possess contours that are either enclosed or open.

Although there are successful computational models of symmetry and closure processing (van der Helm & Leeuwenberg, 1996, 1999; Wagemans, van Gool, Swinnen, & van Horebeek, 1993), the physiological mechanisms are still unclear. Symmetry processing may be accounted for by a number of different mechanisms at multiple stages of the visual hierarchy (Julesz, 2006; Wagemans, 1995), while closure processing may proceed by integrating contour elements in a piecemeal fashion based on recurrent neuronal processing (e.g., via horizontal connections in V1, see Bauer & Heinze, 2002; or feedback connections from areas higher in the visual hierarchy, see Roelfsema, 2006; Zipser, Lamme, & Schiller, 1996).

Both cues are important for the low-level processing of visual scenes because of similar reasons. Symmetry is a common attribute of both natural and man-made environments and makes it easier to identify objects irrespective of their particular position and orientation in the visual field (e.g., Enquist & Arak, 1994). Just as well, closure is an inherent attribute of most objects in our visual environment and can thus serve as a valid cue for identifying objects and segregating them from other objects and from the background (e.g., Koffka, 1935).

The importance of these two grouping cues in visual processing is made clear firstly in their role in figure-ground segregation[13] and secondly in the speed and effortlessness of their processing. The latter point is of importance for the current chapter: Research suggests that symmetry as well as closure are primitives in early

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[12] Here, we focus on bilateral (mirror, reflection) symmetry only, because this form of symmetry is the most salient, most investigated and most relevant to humans (Treder, 2010). We will use the term "symmetry" to refer to "bilateral symmetry".

[13] Figure-ground segregation is the process by which the visual system distinguishes a figure from its background. It is crucial for object recognition and for physical interactions with our environment. The identification of an image area as a figure or background strongly depends on the visual attributes of that area. Importantly, an area that is symmetric or enclosed is more likely to be seen as a figure than an (adjacent) area that is asymmetric (e.g., Bahnsen, 1928; Machilsen, Pauwels, & Wagemans, 2009) or open (e.g., Koffka, 1935; Kovács & Julesz, 1993).

vision that are extracted quickly and effortlessly (for reviews on symmetry processing see Treder, 2010; Wagemans, 1995, 1997; a classic study on the processing of closure is Treisman & Paterson, 1984). At first glance, this finding is surprising since both figural cues are relatively complex compared to other grouping cues: The symmetry or closure of a stimulus is only provided by the spatial relationships between its multiple components (e.g., in the case of symmetry, mirrored angles within a figure) and is not a property of a single stimulus component. Nevertheless, both cues are readily available and do not seem to require a time-costly computation or recombination of stimulus components.

In this study, we test the notion that symmetry as well as closure processing can be based on an temporally early read-out during the first feedforward wave of neuronal processing (Lamme & Roelfsema, 2000). We do this by using the primed flanker task, which allows us to draw conclusions about the time course of processing of consecutive stimuli from the time course of motor priming effects and from the distributions of response times (cf. Schmidt, Haberkamp, Veltkamp et al., 2011; Schmidt et al., 2006). We show that symmetry and closure can be processed not only relatively quickly, but consistent with specific predictions from a simple feedforward processing model. We next examine whether closure and symmetry are processed automatically, in the sense of intruding into visuomotor processing even when being task-irrelevant. Then, testing the limits of feedforward processing, we apply the primed flanker method to investigate the role of view-point invariance in symmetry processing and of the orientation of the symmetry axis. In the following sections, we first review findings that describe common characteristics of symmetry and closure processing and then detail our experimental approach.

3.1.2 The Speed and Automaticity of Symmetry Processing

In symmetry processing, it has been shown that the detection of symmetry in polygonal shapes or random dot patterns is noise-resistant (Barlow & Reeves, 1979; Dakin & Herbert, 1998; Jenkins, 1983; Wagemans, van Gool, d'Ydewalle, 1991) and possible at brief stimulus presentation times (Carmody, Nodine, & Locher, 1977; Julesz, 2006; Niimi, Watanabe, & Yokosawa, 2005; for an early overview see Wagemans, 1995). For example, participants can detect symmetry in dot patterns with presentation times of 13 ms (Niimi et al., 2005) and in masked polygonal shapes with presentation times of 25 ms (Carmody et al., 1977).

Additionally, a number of studies suggest that the processing of symmetry may even be automatic (Baylis & Driver, 1994; for a summary see Treder, 2010).[14] For example, Koning and Wagemans (2009) presented participants with two three-

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[14] Note that here we are focusing on one specific aspect of automatic processing, that is, the extent to which symmetry affects performance even though it is not relevant for the task (cf. Treder, 2010).

dimensional objects and instructed them to judge whether or not their facing contours are symmetric. Interestingly, even task-irrelevant contours speeded responses when they were symmetric. Equivalently, Lachmann and van Leeuwen (2005, 2008) asked participants to classify simultaneously presented pairs of five-dot patterns as either same (identical) or different (non-identical or identical rotated/reflected). As a result, response times also differed between non-identical and rotated/reflected stimuli although both belonged to the same response category. Because participants were not able to voluntarily preclude the influence of symmetry, both studies suggest that processing of symmetry is to some extent independent of cognitive control. This notion is also supported by a study of Driver, Baylis, and Rafal (1992). A patient with hemispatial neglect, an attentional deficit for one side of the visual field as a result of a brain lesion, classified symmetric areas as figures (and not as background) although he was not able to consciously perceive the symmetry. This finding corresponds to that of healthy participants, suggesting that symmetry processing is possible without visual awareness, and further supports the notion of its automaticity.

All of the studies discussed up to this point suggest that symmetry can be extracted from images by the visual system early on as a simple or primitive property. Does this also apply to closure?

3.1.3 The Speed of Closure Processing

In closure processing, it has been shown that the detection of closed contours compared to open contours is easier and more accurate (Mathes & Fahle, 2007), even with relatively brief stimulus presentation times of 150-160 ms (Kovács & Julesz, 1993; Saarinen & Levi, 1999). In addition, visual search for closed contours is faster and more efficient than that for open contours (Elder & Zucker, 1993, 1998; Kanbe, 2008; Mori, 1997; Treisman & Paterson, 1984; Treisman & Souther, 1985). For example, the time to search for a concave target between convex distractors increased more strongly with the number of distractors when all stimuli were open compared to when they were closed (Elder & Zucker, 1993) and decreased when the level of closure increased (Elder & Zucker, 1998). Kanbe (2008) used a large set of carefully designed line figures that controlled for a number of variables that may have contributed to earlier findings. In a same-different task, participants were faster when both figures were closed compared to when both were open.[15]

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[15] The notion of closure as a basic feature that is detected and processed by the visual system in a parallel fashion is not without controversy (e.g., Enns, 1986). In addition, there is no unequivocal evidence that the processing of closure is automatic.

3.1.4 Symmetry and Closure as Non-Accidental Properties

The processing advantages of symmetry and closure are presumably due to their significance in object recognition (e.g., Marino & Scholl, 2005; Treder, 2010). Effective object recognition must be viewpoint-invariant, that is, an object must be recognized from different angles and perspectives (at least when "degenerate" perspectives are excluded, e.g., looking straight at the tip of a knitting needle). Therefore, image properties that remain invariant as the viewing perspective changes are of special importance for the processing system. In addition, image properties that are non-accidental are diagnostic: When these properties are present in the retinal image, it is unlikely that they are not present in the original object.

Closure is an invariant image property, at least under certain restrictions. Any three-dimensional projection of a closed contour defined on a flat surface remains a closed contour (as long as the surface is not viewed directly from the side); therefore, closure is viewpoint-invariant. A restriction applies when the contour is defined on a curved surface: Here, closure is viewpoint-invariant only as long as the contour is not self-occluding (Palmer & Ghose, 2008). Closure is a non-accidental image property as well, because closure in the retinal image will indicate closure in the original object contour – unless a contour that is actually open is accidentally viewed from a degenerate perspective from which it appears closed.

Symmetry is not invariant. When a contour on a flat surface is viewed from a point of view perpendicular to the surface, mirror symmetry is given if for any point s on the symmetry axis and any point c on the contour, the reflection of the vector c-s about the symmetry axis is again a point on the contour. In a rectangular reference frame defined by the symmetry axis, those two vectors form equal angles with the symmetry axis. However, when for example the surface is tilted in 3-D space, it is easy to see that these angles do not remain equal (e.g., the projection of a square tilted backwards in 3-D space is a trapezoid, not a square). Therefore, symmetry is not viewpoint-invariant. It is, however, non-accidental: When the retinal image is symmetric, it is unlikely that it results from a particular view of an asymmetric object.

Are observers able to detect skewed symmetry, that is, do they notice that some asymmetrical image contour could be turned into a symmetric image by an appropriate change in perspective? Although it was shown that skewed symmetry is an important perceptual cue, for example, to determine object orientation in depth (Niimi & Yokosawa, 2008), its processing differs from that of non-skewed symmetry. In a series of experiments, Wagemans et al. demonstrated that symmetry detection in skewed stimuli – measured by sensitivity and speed – decreases with an increase in skewing angle (Wagemans, 1993; Wagemans et al., 1991, 1992; Wagemans et al., 1993). Importantly, Wagemans (1993) showed that these decreases level off when the skewed stimuli are polygonal shapes instead of dot patterns. Responses were speeded also once more when those skewed polygonal shapes were presented within frames that could be interpreted as the contour of the plane in which they were placed, thus giving additional cues about the appropriate three-dimensional transformations needed to restore symmetry.

3.1.5 Symmetry Processing and the Orientation of the Symmetry Axis

A final factor that has repeatedly been reported to play an important role for the processing of bilateral symmetry is the orientation of the symmetry axis (e.g., Palmer & Hemenway, 1978; Rock & Leaman, 1963; Wenderoth, 1997). Specifically, symmetric stimuli with one symmetry axis (as in our study) are more easily detected and yield faster responses if their axis is oriented vertically, compared to other orientations, including a horizontal one (e.g., Wenderoth, 1994; Wenderoth & Welsh, 1998). Importantly, the response time advantage of vertical over horizontal symmetry axes is also present when stimuli with different axis orientations are presented in separate experimental blocks, thus allowing participants to anticipate the axis orientations of upcoming stimuli (Wenderoth, 2000).

In summary, both symmetry and closure are important features that affect the speed and efficiency of contour processing. What is still missing is a principled method for assessing whether the processing dynamics for either cue are consistent with feedforward processing, that is, are extracted during the first processing wave that sweeps the visual system (Lamme & Roelfsema, 2000). In the following section, we detail our experimental approach and explain how motor measures of processing can be employed to address the issue of feedforward vs. recurrent processing of symmetry and closure.

3.1.6 Visuomotor Processing Dynamics as a Test of Feedforward Processing

We adopted the primed flanker task (Chapter 2) to study the processing of the two grouping cues with respect to their time course, automaticity, and the influence of other variables. Participants had to respond to the symmetrical (or closed) one of two target shapes presented simultaneously to the left and right of the fixation point. This pair of target shapes was preceded by a pair of prime shapes at positions adjacent but non-overlapping with those of the targets (Fig. 15A).

As described before, this task can be used to study response-time effects in a principled fashion provided by the framework of rapid-chase theory: priming effects should increase with prime-target SOA (Vorberg et al., 2003) and they should be at least as large in fast responses as in slower responses (Seydell-Greenwald & Schmidt, 2012). In contrast, priming effects that fail to increase with SOA or that increase in slower responses would contradict a rapid-chase account. Again, note that in the rapid-chase framework, issues of feedforward vs. recurrent processing are addressed not merely by looking at the raw response speed (VanRullen & Koch, 2003), but by examining the functional rapid-chase criteria. For example, it is possible that two grouping cues such as symmetry and closure lead to different response speeds while both meeting the rapid-chase criteria, suggesting that both are based on feedforward processes but differ in speed or efficiency (Schmidt, Haberkamp, Veltkamp et al., 2011; Schmidt & Schmidt, 2009; Seydell-Greenwald & Schmidt, 2012).

In three experiments, participants responded to the symmetry or closure of target contours that were preceded by response-consistent or inconsistent prime contours. The first two experiments explored the capability of each of the perceptual cues to produce response priming effects with sets of irregular (jagged) contours (Experiment 1) and regular (smooth) contours (Experiment 2). In Experiment 3, we tested the viewpoint-invariance of symmetry processing by skewing the stimuli in three-dimensional space. Moreover, in Experiments 2 and 3 the stimuli's symmetry axes were varied. Based on a wealth of empirical findings regarding the speed and efficiency of symmetry processing (summarized in Treder, 2010) and closure processing (e.g., Elder & Zucker, 1993, 1998), we expected that both cues can produce priming effects in fast visuomotor responses. However, while there is good evidence that symmetry processing show signs of automaticity (Treder, 2010) there is no such evidence for closure. Furthermore, in symmetry processing, we expected the priming effects to be modulated by the orientation of the symmetry axis and the skewing of the stimuli. Most importantly, however, we expected conclusive evidence as to whether the temporal dynamics of priming would be consistent with rapid-chase theory, that is, whether or not the processing dynamics of symmetry and closure are consistent with feedforward processing.

3.2 Experiment 1

3.2.1 General

Participants were asked to respond as quickly and accurately as possible to one of two target contours that were presented simultaneously in the left and right periphery. Either one of the targets was symmetric and the other asymmetric (symmetry task) or one of the targets was closed and the other was open (closure task). Targets were preceded at varying SOAs by two prime contours near the center of the screen (Fig. 15A). The primes were either consistent or inconsistent with respect to the relevant grouping cue (e.g., the symmetric prime was on the same side as the symmetric target or on the opposite side).

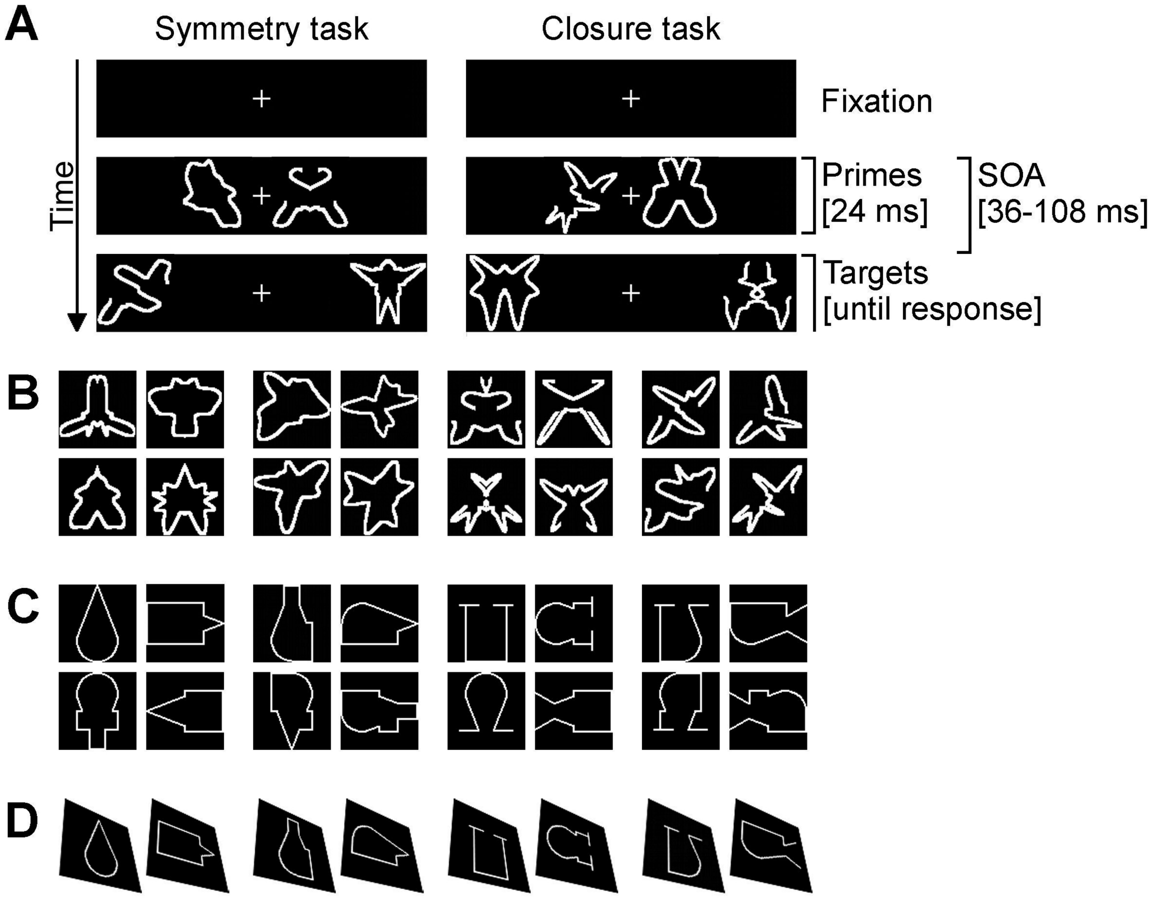

Figure 15. Procedure and stimuli in Experiments 1, 2, and 3. Two primes and two targets were presented in the sequence displayed (**a**). In the symmetry task, participants responded to either the symmetric or asymmetric target and in the closure task to either the closed or open target. The two primes (and targets) always opposed each other in the response-relevant dimension. Primes and targets on the same side of the fixation cross could be either mapped to the same response (consistent) or opposite responses (inconsistent). Examples of the stimuli in Experiments 1 (**b**), 2 (**c**), and 3 (**d**). Note that primes in the first session of Experiment 3 are presented on dark backgrounds that are skewed with the same angles as the primes (30° slant, 30° tilt, projected onto the frontal plane).

A lot of studies on symmetry processing used dot patterns in which a number of dots are mirrored along a central symmetry axis. However, for our purposes, simple contour stimuli are more suited because compared to dot patterns (1) they can be symmetric/asymmetric (e.g., Palmer & Hemenway, 1978) as well as closed/open (e.g., Elder & Zucker, 1993), (2) they have been shown to be more robust against three-dimensional skewing (Sawada & Pizlo, 2008; Wagemans, 1992, 1993), and (3) they more closely resemble the appearance of real-world objects. Importantly, the same contour stimuli were used in both tasks such that the only difference between tasks were the participants' instructions.

We investigated the capacity of symmetry and closure stimuli for priming speeded motor responses and provoking response errors as predicted by rapid-chase theory. We were especially interested in the earliest parts of the response time distributions which are indicative of temporally early visuomotor processes (e.g., feedforward processes). However, we did not attempt a quantitative comparison between the grouping principles because the stimuli were not matched for grouping strength.[16]

3.2.2 Methods

Participants. Eight right-handed students from the University of Kaiserslautern, Germany (3 female, 5 male, ages 21-28), with normal or corrected vision participated in the experiment for payment of € 6 per hour. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association. Participants were debriefed after the final session.

Apparatus and Stimuli. The participants were seated in a dimly lit room in front of a color monitor (1280 x 1024 pixels) with a monitor retrace rate of 85 Hz at a viewing distance of approximately 70 cm. They responded with their left and right index fingers via a standard keyboard. Stimulus presentation and timing was controlled by using Presentation® software (www.neurobs.com).

We generated a pool of 80 irregular contour stimuli using a routine developed by Garrigan, Fortunato, and LaSala (2010). Each stimulus was either symmetric or asymmetric and closed or open. This resulted in four classes, each containing 20 stimuli: (1) closed and symmetric, (2) closed and asymmetric, (3) open and symmetric, and (4) open and asymmetric (Fig. 15B). All had an aspect ratio of about 1:1 (1.82° x 1.82° of visual angle; 1 cm ≈ 0.82° of visual angle) and were presented in white (60.00 cd/m^2) against a dark background (0.13 cd/m^2). All symmetric stimuli had a vertical symmetry axis. Primes and targets were arranged to the left and right of the center of the screen. The edge-to-edge distance between fixation cross (diameter of 0.41°; 60.00 cd/m^2) and primes was about 0.41°, the distance between fixation cross and targets was about 2.46°.

Procedure. The experimental procedure is depicted in Figure 15A. Each trial started with the appearance of the central fixation point. After a varying delay, two primes were displayed for 24 ms to the left and the right of the center. Subsequently, the targets were presented to the left and the right of the prime positions at prime-target SOAs of 36, 60, 84, or 108 ms and remained on screen until the participant's response. In each trial, the prime was either consistent or inconsistent with the target

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[16] While grouping strength can be easily matched for some grouping dimensions (e.g., similarity in brightness or size, Chapter 2), matching is difficult to achieve with more complex grouping principles. Imagine, for example, participants adjusting the amount of symmetry in a given figure such that it is equal to the perceived amount of closure in another figure.

with respect to the required motor response. All stimulus combinations of consistency, prime-target SOA and position of the relevant target occurred equiprobably and pseudo-randomly in a completely crossed repeated-measures design.

We employed two tasks in separate sessions with the order of the tasks counterbalanced across participants. In the symmetry task, participants had to decide as accurately as possible whether the symmetric (or asymmetric) target was presented on the left or right of the center by pressing a left or right button. In the closure task, they did the same for the closed (or open) target. The relevant target type was counterbalanced across participants. In each trial of the symmetry task, one prime was picked randomly from one of the two classes of symmetric stimuli (closed or open) and the other was picked from one of the two classes of asymmetric stimuli (closed or open). The targets were selected in the same way. In half of the trials, the symmetric prime and target were on the same side of the center (consistent trials), in half of the trials they were on opposite sides of the center (inconsistent trials). Correspondingly, in each trial of the closure task, one prime and one target were picked from one of the two classes of closed stimuli and the other prime and target were picked from one of the two classes of open stimuli. In a particular trial, primes and targets were never the same. The time interval from trial start to target onset was constant at 1,000 ms to allow for an optimal preparation for each response to the target. Targets remained on screen until participants gave their response. Participants were instructed to ignore the primes. After each block, summary feedback on response times and error rates was provided. Participants performed two 1-h sessions, each consisting of one practice block followed by 54 blocks of 32 trials, accumulating to a total of 3,456 trials per participant.

Data treatment and statistical methods. Practice blocks were not analyzed and trials were eliminated if response times were shorter than 100 ms or longer than 1,000 ms. This criterion eliminated 0.25 and 1.00% of trials in the symmetry and closure tasks, respectively. Note that response time distributions are analyzed based on raw response times. Errors were not included in the response time analyses. Repeated-measures ANOVAs were performed with Huynh-Feldt-corrected p values. ANOVAs were fully factorial with factors of consistency (C) and prime-target SOA (S). F values are reported with subscripts indicating the respective effect (e.g., F_{CxS} for the interaction of consistency and prime-target SOA). All error rates were arcsine-transformed to comply with ANOVA requirements.

3.2.3 Results and Discussion

3.2.3.1 Priming Effects

Both tasks in Experiment 1 produced response priming effects in response times and error rates (Fig. 16A).

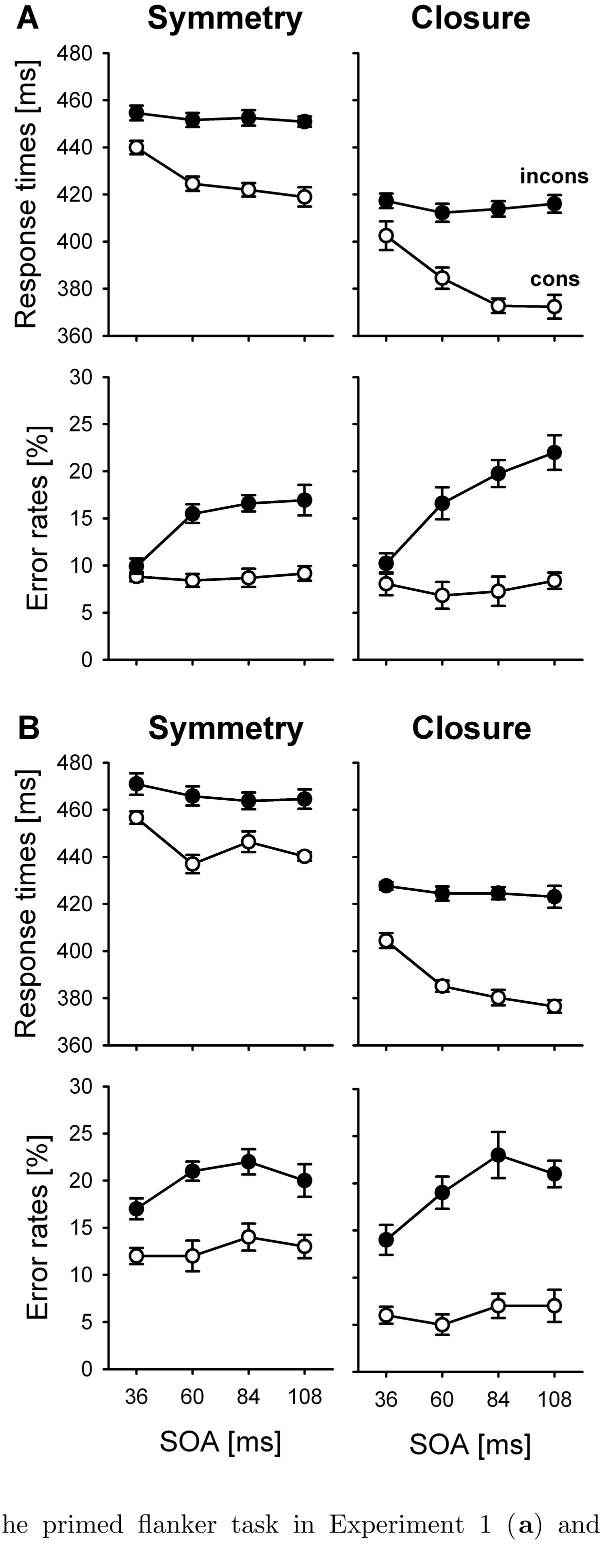


Figure 16. Results of the primed flanker task in Experiment 1 (**a**) and Experiment 2 (**b**). The results of the symmetry task are displayed in the left panels, of the closure task in the right panels. Mean response times and error rates in consistent (white) and inconsistent (black) trials are displayed as a function of prime-target SOA. Error bars denote the standard error of the mean corrected for between-subjects variance (Cousineau, 2005; Loftus & Masson, 1994).

Separate ANOVAs affirmed faster responses and lower error rates in consistent compared to inconsistent trials in the symmetry task [$F_{\mathrm{C}}(1,7) = 37.70$, $p < .001$, and $F_{\mathrm{C}}(1,7) = 32.89$, $p = .001$, for response times and error rates, respectively] and in the closure task [$F_{\mathrm{C}}(1,7) = 38.32$, $p < .001$, and $F_{\mathrm{C}}(1,7) = 18.54$, $p = .004$]. In other words, participants responded faster and made fewer errors when primes and targets on the same side of the fixation cross were corresponding in the task-relevant dimension, compared to when they were opposed. The response priming effect was further modulated by the prime-target SOA: The more time elapsed between prime and target presentation, the stronger were the priming effects in response times and error rates in the symmetry task [$F_{\mathrm{CxS}}(3,21) = 7.70$, $p = .001$, and $F_{\mathrm{CxS}}(3,21) = 7.19$, $p = .003$] and in the closure task [$F_{\mathrm{CxS}}(3,21) = 9.80$, $p = .001$, and $F_{\mathrm{CxS}}(3,21) = 11.02$, $p < .001$]. This corresponds to earlier findings in response priming experiments (cf. Schmidt, Haberkamp, Veltkamp et al., 2011; Vorberg et al., 2003).

Finally, with increasing SOA, overall response times became faster and error rates increased in the symmetry task [$F_{\mathrm{S}}(3,21) = 6.34$, $p = .006$; $F_{\mathrm{S}}(3,21) = 5.99$, $p = .004$] as well as the closure task [$F_{\mathrm{S}}(3,21) = 5.55$, $p = .028$; $F_{\mathrm{S}}(3,21) = 17.86$, $p < .001$].

At the same time, priming effects did not depend on task instruction (e.g., it was irrelevant whether participants responded to symmetry or asymmetry). Separate ANOVAs yielded no significant interactions of the factor task instruction (*TI*) and consistency for the symmetry or closure task [$F_{\mathrm{CxTI}}(1,7) = .01$, $p = .922$, and $F_{\mathrm{CxTI}}(1,7) = .83$, $p = .392$].

Response times were about 40 ms slower when participants had to respond to the symmetry of the stimuli compared to their closure. Because the cues were not matched for grouping strength (Chapter 2), these differences were not analyzed further.

3.2.3.2 Response Time Distributions

Our results imply that both grouping cues are processed quickly enough to affect speeded motor responses. To study this processing in more detail, we analyzed the response time functions in both tasks. We *vincentized* response times by sorting them into multiple ordinal bins of data (Ratcliff, 1979), separately for each participant and condition (defined by the levels of consistency and SOA in the symmetry and closure task), starting from the fastest response times all the way through the slowest ones. We use deciles, so that each bin summarizes 10% of the cumulative distribution (Fig. 17A, B) (note that the first and last bins are excluded because they are likely to be distorted by outliers). As a result, the priming effect can be looked at as a function of response speed and SOA. Most importantly, rapid-chase theory predicts a priming effect in the fastest responses that does not increase in slower responses, consistent with feedforward processing of symmetry and closure.

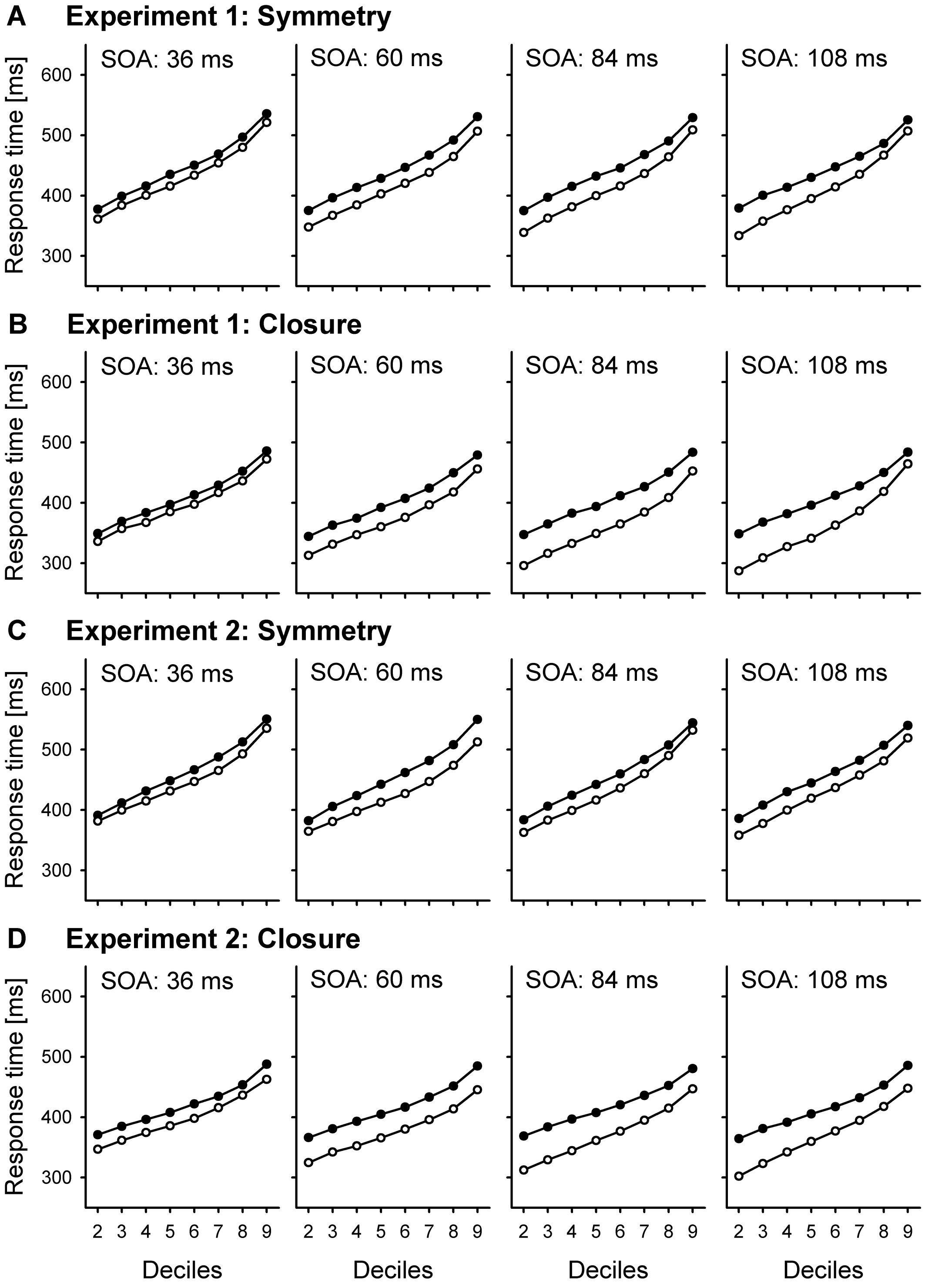


Figure 17. Response time functions for Experiment 1 (**a**, **b**) and Experiment 2 (**c**, **d**). Response times in consistent (white) and inconsistent trials (black) are displayed as a function of response speed (bins 2-9), separately for each task and SOA. It is a strong prediction of rapid-chase theory that priming effects should be present in the fastest responses and should not increase any further in slower responses.

For statistical analysis, the response time bins 2-9 in each task were subjected to a repeated-measures ANOVA with factors of consistency (*C*), prime-target SOA (*S*), and decile (*D*). We will only report the interactions of consistency and decile. The analysis in the symmetry task (Fig. 17A) revealed an interaction of factors of consistency and decile [$F_{\mathrm{CxD}}(7,49) = 4.49$, $p = .037$] and one of consistency, SOA and decile [$F_{\mathrm{CxSxD}}(21,147) = 2.38$, $p = .030$], showing a decrease of the priming effect in slower responses, particularly in SOAs of 84 and 108 ms. This result pattern was repeated in the closure task (Fig. 17B) with interactions of consistency and decile [$F_{\mathrm{CxD}}(7,49) = 4.57$, $p = .042$] as well as of consistency, SOA and decile [$F_{\mathrm{CxSxD}}(21,147) = 3.78$, $p = .007$].

Thus, in all SOA conditions of both tasks, the fastest responses show the strongest priming effect. This pattern is predicted by rapid-chase theory and is consistent with a feedforward system where prime and target signals traverse the visuomotor system in strict sequence, without mixing or overlapping (Schmidt et al., 2006; Vath & Schmidt, 2007).

3.2.3.3 Effects of Task-Irrelevant Cues

Finally, we tested for the automaticity of symmetry and closure processing by investigating the influence of the respective task-irrelevant cue in both tasks. For example, in the symmetry task we analyzed whether response times were the same for trials in which primes and targets were consistent with respect to closure, compared to trials in which primes and targets were inconsistent with respect to closure. ANOVAs did not show any significant main or interaction effect of the task-irrelevant cue's consistency on response times, either in the symmetry task [$F_{\mathrm{C}}(1,7) = .81$, $p = .398$; $F_{\mathrm{CxS}}(3,21) = .64$, $p = .600$] or in the closure task [$F_{\mathrm{C}}(1,7) = 1.45$, $p = .268$; $F_{\mathrm{CxS}}(3,21) = .25$, $p = .854$]. Thus, in both tasks the respective irrelevant cue was efficiently ignored by the visual system (Seydell-Greenwald & Schmidt, 2012; Tapia, Breitmeyer, & Shooner, 2010).

3.3 Experiment 2

3.3.1 General

Experiment 1 showed that symmetry as well as closure can drive response priming effects consistent with a simple feedforward system, with their temporal dynamics predicted by rapid-chase theory. In Experiment 2, we generalized and extended those findings by investigating the potential role of the symmetry axis. To this end, we presented participants with newly constructed regular stimuli that had either a horizontal or vertical symmetry axis. Stimuli with the same symmetry axis were blocked to minimize the potential influence of attentional scanning strategies (cf. Wenderoth, 1994). Again, participants were asked to respond to the symmetry or closure of target stimuli that were preceded by consistent or inconsistent primes.

3.3.2 Methods

Participants. Eight right-handed students from the University of Kaiserslautern, Germany (2 female, 6 male, ages 21-25), with normal or corrected vision participated in the experiment for payment of € 6 per hour. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association. Participants were debriefed after the final session.

Apparatus and Stimuli. Apparatus, experimental environment and stimulus arrangement were the same as in Experiment 1. For Experiment 2, we generated a pool of 128 contour stimuli. Again, each stimulus was either symmetric or asymmetric and closed or open resulting in four classes, each containing 32 stimuli: (1) closed and symmetric, (2) closed and asymmetric, (3) open and symmetric, and (4) open and asymmetric (Fig. 15C). All had an aspect ratio of about 2:1 (1.82° x 0.91° of visual angle) and were presented in white (60.00 cd/m^2) on a dark background (0.13 cd/m^2). The symmetry axis of the symmetric primes and targets varied block-wise (either both horizontal or both vertical).

Procedure. The procedure was the same as that in Experiment 1 (cf. Fig. 15A). Again, participants performed the two tasks in two 1-h sessions, each consisting of one practice block followed by 54 blocks of 32 trials, accumulating to a total of 3,456 trials per participant.

Data treatment and statistical methods. Practice blocks were not analyzed. In the symmetry and in the closure task, 0.20 and 0.06% of trials were eliminated due to response times shorter than 100 ms or longer than 1,000 ms. Statistical methods correspond to those adopted in Experiment 1 with the further factor of symmetry axis (*SA*).

3.3.3 Results and Discussion

3.3.3.1 Priming Effects

As in Experiment 1, we observed response priming effects in response times and error rates in the symmetry task [$F_{\mathrm{C}}(1,7) = 18.85$, $p = .003$, and $F_{\mathrm{C}}(1,7) = 25.37$, $p = .002$, for response times and errors, respectively] and the closure task [$F_{\mathrm{C}}(1,7) = 107.84$, $p < .001$, and $F_{\mathrm{C}}(1,7) = 49.73$, $p < .001$] (Fig. 16B). In the closure task, this effect increased with SOA in response times as well as error rates [$F_{\mathrm{CxS}}(3,21) = 7.27$, $p = .002$, and $F_{\mathrm{CxS}}(3,21) = 3.08$, $p = .050$]. However, in the symmetry task, the priming effects in response times or error rates did not depend on SOA [$F_{\mathrm{CxS}}(3,21) = 1.78$, $p = .181$, and $F_{\mathrm{CxS}}(3,21) = .74$, $p = .497$].

Finally, as in Experiment 1, with increasing SOA, overall response times became faster and error rates increased in the symmetry task [$F_{\mathrm{S}}(3,21) = 5.45$, $p = .006$, and $F_{\mathrm{S}}(3,21) = 3.59$, $p = .031$] as well as in the closure task [$F_{\mathrm{S}}(3,21) = 11.51$, $p < .001$, and $F_{\mathrm{S}}(3,21) = 5.37$, $p = .007$]. In addition, priming effects did not depend on task instruction (TI), either in the symmetry or in the closure task [$F_{\mathrm{CxTI}}(1,7) = .13$, $p = .730$, and $F_{\mathrm{CxTI}}(1,7) = .27$, $p = .619$]. Again, response times were about 50 ms slower in the symmetry than in the closure task.

3.3.3.2 Response Time Distributions

These results again imply that symmetry and closure are analyzed quickly enough to affect speeded motor responses. This conclusion is also supported by the response time functions in both tasks (Fig. 17C, D). We performed repeated-measures ANOVA with factors of consistency (*C*), prime-target SOA (*S*), and decile (*D*) for response time bins 2-9, reporting only the interactions of consistency and decile. The analysis in the symmetry task (Fig. 17C) revealed neither an interaction of factors of consistency and decile nor one of consistency, SOA and decile [$F_{\mathrm{CxD}}(7,49) = 1.42$, $p = .276$; $F_{\mathrm{CxSxD}}(21,147) = 1.77$, $p = .093$]. Thus, the priming effect was the same in the fastest responses as in the slower ones. In contrast, in the closure task (Fig. 17D) we observed an interaction of consistency and decile [$F_{\mathrm{CxD}}(7,49) = 6.19$, $p = .029$], showing that the priming effect was strongest in the fastest responses. This effect was particularly observed in the two longer SOAs of 84 ms and 108 ms, as supported by a three-way interaction of consistency, SOA and decile [$F_{\mathrm{CxSxD}}(21,147) = 5.25$, $p < .001$]. Thus, in both tasks we observed a priming effect in the fastest responses that did not increase (or even decreased) in slower responses. Again, this is consistent with the idea that processing of closure and symmetry is based on sequential visuomotor feedforward activation by primes and targets (Schmidt et al., 2006).

3.3.3.3 Effects of Task-Irrelevant Cues

We also tested for the automaticity of processing in both tasks by investigating the role of the task-irrelevant cue. Again, ANOVAs revealed no significant effects on response times either in the symmetry task [$F_{\mathrm{C}}(1,7) = .59$, $p = .467$; $F_{\mathrm{CxS}}(3,21) = .76$, $p = .517$] or in the closure task [$F_{\mathrm{C}}(1,7) = 2.31$, $p = .173$; $F_{\mathrm{CxS}}(3,21) = .57$, $p = .572$], showing that the task-irrelevant cue was efficiently ignored by the visual system (Seydell-Greenwald & Schmidt, 2012; Tapia et al., 2010). Finally, we investigated the potential role of the symmetry axis for symmetry processing. We observed no significant interactions of symmetry axis and consistency in the symmetry task, that is, priming effects in response times and error rates were independent of axis orientation [$F_{\mathrm{CxSA}}(1,7) = 3.98$, $p = .086$; $F_{\mathrm{CxSA}}(1,7) = .37$, $p = .562$]. In addition, we observed no main effect of symmetry axis on response times [$F_{\mathrm{SA}}(1,7) = .49$, $p = .831$]. However, participants made fewer errors when primes and targets were reflected horizontally compared to vertically [$F_{SA}(1,7) = 8.19$, $p = .024$]. We discuss this finding later on with reference to the results of Experiment 3.

3.3.4 Conclusion

With respect to the processing of closure, we replicated the findings of Experiment 1. However, in the symmetry task priming effects failed to increase with prime-target SOA, violating a prediction of rapid-chase theory. This might be an effect of the new stimulus set, which slows responses by another 20 ms compared to Experiment 1. It is indeed possible that processing has become too slow in this task to be conclusively explained by a simple feedforward model, and that more extensive recurrent processing is involved here. Though we still found that priming effects were fully present in the fastest responses and did not increase any further in slower responses (consistent with a feedforward account), we did not replicate the finding from Experiment 1 that the fastest responses produced notably larger priming effects than the slower ones. This casts further doubt on whether symmetry was indeed processed in a strictly feedforward fashion. Finally, contrary to the studies reporting a processing advantage of vertical symmetry axes (e.g., Wenderoth, 1994; Wenderoth & Welsh, 1998), we observed no response-time difference between vertical and horizontal symmetry axes.

3.4 Experiment 3

3.4.1 General

Beside the symmetry axis, another factor has been shown to strongly influence the processing of symmetric stimuli: the viewpoint of the observer (e.g., Koning & van Lier, 2006; Wagemans, 1995). When bilateral symmetric stimuli as in Figure 15C are seen from a non-orthogonal line of view, their actual projections on the retina are skewed, for example, as in Figure 15D. Skewing has been shown to interfere with the visual processing of symmetric stimuli but less so when stimuli are polygonal shapes or are presented within frames that could be interpreted as the contour of the plane in which they were placed (Wagemans, 1993; cf. the black frames in Fig. 15C and D).

In Experiment 3, we extended our findings on symmetry processing by investigating the role of viewing position in our task. We generated skewed versions of the stimuli in Experiment 2 and used them as primes. In the first session of Experiment 3, they were presented within frames whereas in the second session this cue was removed. Finally, we again varied the symmetry axis block-wise between horizontal and vertical orientation. In this way, we could track the roles of skewing, framing, and symmetry axis, as well as their interactions, on response times, error rates and priming effects.

3.4.2 Methods

Participants. Eight right-handed students from the University of Kaiserslautern, Germany (1 female, 7 male, ages 22-24), with normal or corrected vision participated in the experiment for payment of € 6 per hour. Six of them took part in Experiment 2, two were not on hand any more and were substituted by naïve participants. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association. Participants were debriefed after the final session.

Apparatus and Stimuli. Apparatus, experimental environment, and stimulus arrangement were the same as in Experiments 1 and 2. For Experiment 3, we generated a pool of 128 skewed prime stimuli. We rotated the symmetric and asymmetric stimuli of Experiment 2 by 30° about the vertical mid-line and the horizontal mid-line and calculated the resulting projections on the frontal plane (Fig. 15D). The resulting stimuli were not symmetric in terms of mirror symmetry but only in terms of skewed symmetry. They carried symmetry information that could be retrieved by an appropriate change in viewing perspective (e.g., Wagemans et al., 1992). Note that target stimuli were not skewed. Primes and targets had an aspect ratio of about 2:1 (1.82° x 0.91° of visual angle) and were presented in white (60.00 cd/m^2) on a dark background (0.13 cd/m^2).

In the first session of Experiment 3 this background constituted a frame (1.82°x 0.91° of visual angle) for primes and targets on an otherwise white monitor (60.00 cd/m^2). This frame was rectangular for targets but skewed for primes, providing the visual system with information about the angles of the three-dimensional transformation (cf. Wagemans, 1993). In contrast, in the second session of Experiment 3, primes and targets were presented on a dark background without frames revealing the skewing angles. In both sessions, the symmetry axis of the symmetric primes and targets varied block-wise (either both horizontal or both vertical).

Procedure. The procedure was the same as that in Experiments 1 and 2 (cf. Fig. 15A), using the newly constructed prime stimuli. Participants performed the task in two 1-h sessions (session 1 with framed, session 2 with non-framed stimuli) each consisting of one practice block followed by 54 blocks of 32 trials, accumulating to a total of 3,456 trials per participant.

Data treatment and statistical methods. Practice blocks were not analyzed. 0.05 and 0.01% of trials were eliminated due to response times shorter than 100 ms or longer than 1,000 ms in the first and second session, respectively. Statistical methods correspond to those adopted in Experiment 2 with the further factor of framing (F).

3.4.3 Results and Discussion

3.4.3.1 Priming Effects

In a first step, we performed separate analyses for the results within each session (Fig. 18).

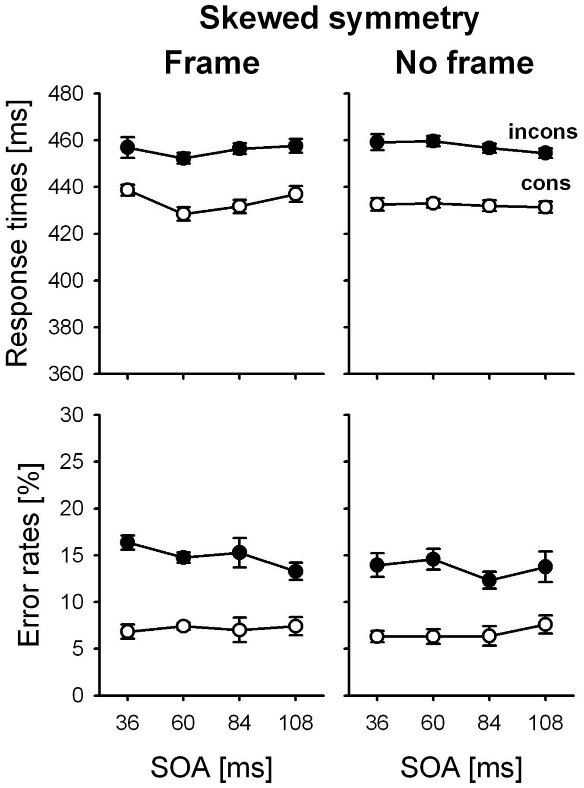


Figure 18. Results of the primed flanker task in Experiment 3. In session 1, primes were presented within frames that provided information about their skewing angles. In session 2, primes were presented without frames. For further specifications see Fig. 16.

With framed primes, we observed priming effects in response times and error rates [$F_{\mathrm{C}}(1,7) = 43.53$, $p < .001$, and $F_{\mathrm{C}}(1,7) = 54.33$, $p < .001$, respectively]. Priming effects did not depend on orientation of the symmetry axis [$F_{\mathrm{CxSA}}(1,7) = .04$, $p = .849$, and $F_{\mathrm{CxSA}}(1,7) = .75$, $p = .416$]; neither did response times [$F_{\mathrm{SA}}(1,7) = 1.84$, $p = .217$]. However, a vertical symmetry axis led to fewer errors compared to a horizontal one [$F_{\mathrm{SA}}(1,7) = 11.13$, $p = .012$]. No other effects reached significance; in particular, priming effects did not increase with SOA in any condition [response times: $F_{\mathrm{CxS}}(3,21) = .49$, $p = .692$; $F_{\mathrm{CxSxSA}}(3,21) = 1.24$, $p = .322$; error rates: $F_{\mathrm{CxS}}(3,21) = 1.26$, $p = .312$; $F_{\mathrm{CxSxSA}}(3,21) = 1.55$, $p = .232$]. In addition, priming effects did not depend on task instruction (*TI*) [$F_{\mathrm{CxTI}}(1,7) = 4.77$, $p = .065$].

With non-framed primes, we again observed priming effects in response times and error rates [$F_{\mathrm{C}}(1,7) = 151.39$, $p < .001$, and $F_{\mathrm{C}}(1,7) = 45.03$, $p < .001$, respectively]. Moreover, responses were faster and, again, produced fewer errors when the symmetry axis was vertical compared to horizontal [$F_{\mathrm{SA}}(1,7) = 17.13$, $p = .004$, and $F_{\mathrm{SA}}(1,7) = 36.04$, $p < .001$, respectively]. No other effects reached significance; in particular, priming effects did not increase with SOA in any condition [response times: $F_{\mathrm{CxS}}(3,21) = .43$, $p = .678$; $F_{\mathrm{CxSxSA}}(3,21) = 2.01$, $p = .165$; error rates: $F_{\mathrm{CxS}}(3,21) = .99$, $p = .411$; $F_{\mathrm{CxSxSA}}(3,21) = .53$, $p = .664$]. In addition, priming effects in response times did not depend on task instruction [$F_{\mathrm{CxTI}}(1,7) = .00$, $p = .998$].

3.4.3.2 The Role of Framing

In a second step, we compared session 1 and session 2 to test for the potential influence of framing on response times, error rates and priming effects. Although we observed significant priming effects in response times as well as error rates [$F_{\mathrm{C}}(1,7) = 102.42$, $p < .001$, and $F_{\mathrm{C}}(1,7) = 51.02$, $p < .001$, respectively] that effect was neither modulated by SOA nor framing [response times: $F_{\mathrm{CxS}}(3,21) = .31$, $p = .780$; $F_{\mathrm{CxF}}(1,7) = 1.60$, $p = .247$; $F_{\mathrm{CxSxF}}(3,21) = 2.04$, $p = .144$; error rates: $F_{\mathrm{CxS}}(3,21) = 1.20$, $p = .329$; $F_{\mathrm{CxF}}(1,7) = 1.30$, $p = .291$; $F_{\mathrm{CxSxF}}(3,21) = .62$, $p = .610$]. In contrast to Experiment 2, we observed no main effect of SOA [$F_{\mathrm{S}}(3,21) = 1.65$, $p = .209$; $F_{\mathrm{S}}(3,21) = .61$, $p = .615$]; however, there were main effects of symmetry axis on error rates [$F_{\mathrm{C}}(1,7) = 20.56$, $p = .003$] and response times [$F_{\mathrm{SA}}(1,7) = 10.60$, $p = .014$] as well as an interaction effect of symmetry axis and framing on response times [$F_{\mathrm{SAxF}}(1,7) = 8.47$, $p = .023$]. Specifically, participants were slightly faster and made fewer errors when responding to stimuli with a vertical symmetry axis compared to those with a horizontal one; and that difference in speed was more pronounced with non-framed stimuli compared to framed ones (11.13 ms vs. 3.42 ms). Error rates did not significantly differ between both sessions of Experiment 3 [$F_{\mathrm{F}}(1,7) = .29$, $p = .606$] (session 1: 11.04% and session 2: 10.15%), making a speed-accuracy trade-off unlikely.

3.4.3.3 The Role of Skewing

Finally, we compared the results in Experiment 2 and the two sessions of Experiment 3 for the six participants that took part in both experiments. Would their response times, error rates and priming effects differ for non-skewed (Experiment 2), framed skewed (Experiment 3, session 1), or non-framed skewed primes (Experiment 3, session 2)?

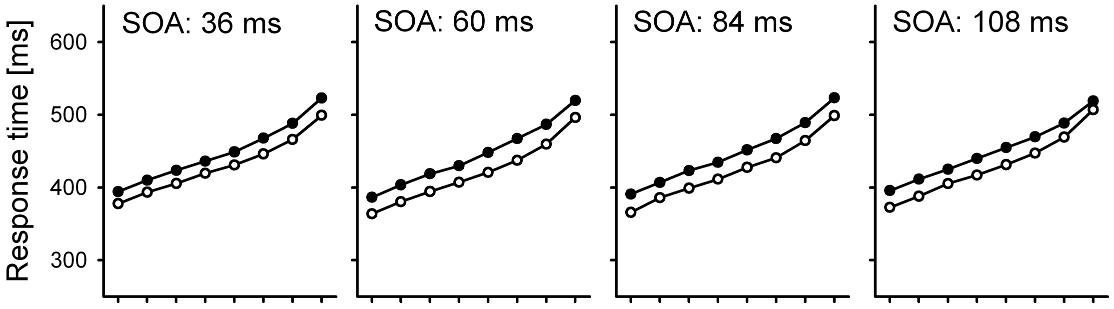
Interestingly, that was not the case: we observed no influence of the factor experiment (*EXP*) on these measures [response times: $F_{\mathrm{EXP}}(2,10) = .30$, $p = .658$; $F_{\mathrm{CxEXP}}(2,10) = .91$, $p = .435$; error rates: $F_{\mathrm{EXP}}(2,10) = 4.74$, $p = .076$; $F_{\mathrm{CxEXP}}(2,10)$

$= .03$, $p = .901$] although the power with six participants was sufficient to discover the priming effects in response times [$F_{\mathrm{C}}(1,5) = 29.45$, $p = .003$] and error rates [$F_{\mathrm{C}}(1,5) = 78.36$, $p < .001$]. The only difference between experiments was observed when taking the symmetry axis into account. Specifically, in Experiment 2, participants made more errors when the symmetry axis of primes and targets was vertical compared to horizontal; in contrast, in the two sessions of Experiment 3, they made fewer errors when responding to vertical targets preceded by vertical primes [$F_{\mathrm{SAxEXP}}(2,10) = 6.02$, $p = .048$]. Note, however, that this effect is small and only observed in plain error rates, not in priming effects or response speeds [response times: $F_{\mathrm{SAxEXP}}(2,10) = .84$, $p = .440$; $F_{\mathrm{CxSAxEXP}}(2,10) = 1.11$, $p = .368$; error rates: $F_{\mathrm{CxSAxEXP}}(2,10) = .61$, $p = .519$]. Therefore, we refrain from a further interpretation of this interaction effect.

3.4.3.4 Response Time Distributions

Analyses of the response time functions revealed no significant interactions of the factors consistency and decile either in session 1 or in session 2 (Fig. 19A, B) [$F_{\mathrm{CxD}}(7,49) = .62$, $p = .528$, and $F_{\mathrm{CxD}}(7,49) = .49$, $p = .670$, respectively].

A **Experiment 3: Skewed symmetry (Frame)**



B **Experiment 3: Skewed symmetry (No frame)**

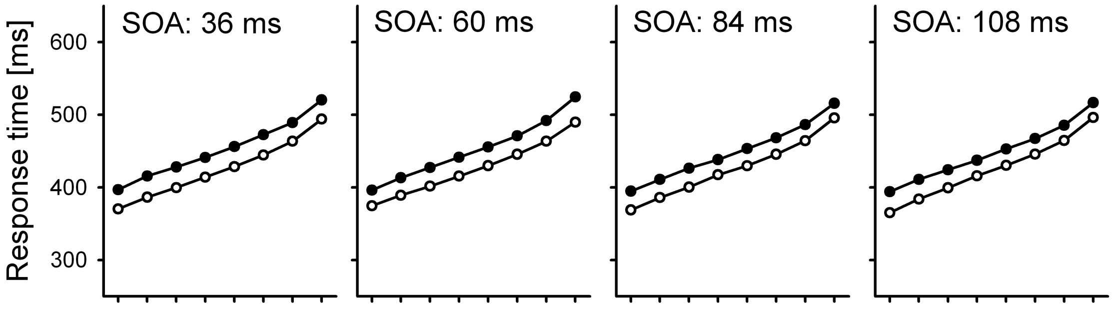


Figure 19. Response time functions for sessions 1 and 2 of Experiment 3. In session 1, primes were presented within frames that provided information about their skewing angles (**a**). In session 2, primes were presented without frames (**b**). For further specifications see Fig. 17.

So again, priming effects were present in the fastest responses and did not increase any further in slower responses. Furthermore, an overall repeated-measures ANOVA for the results of the six participants that participated in both experiments showed no influence of the factor experiment (*EXP*) on the interactions of consistency and decile [$F_{\mathrm{CxDxEXP}}(14,70) = 1.52$, $p = .232$], meaning that skewing had no relevance for the temporally early processing of the symmetry primes.

3.4.4 Conclusion

In summary, we observed no influence of the skewing of the primes on participants' performance. It also did not matter whether skewed primes were non-framed or framed (providing the visual system with information about the skewing angles in three-dimensional space). This finding is surprising because it suggests that symmetry information is viewpoint-independent, at least to some degree. In contrast to Experiment 2, we observed an influence of the symmetry axis on response speed when stimuli were skewed: Stimuli with a (skewed) vertical symmetry axis were processed faster and with fewer errors than those with a horizontal one. This effect of axis orientation was eliminated when the stimuli were framed. Finally, note that similar to the results of Experiment 2 the priming effects in Experiment 3 did not increase with SOA, violating an important prediction of rapid-chase theory. We discuss this issue in the next section.

3.5 General Discussion

We adopted a primed flanker task to explore the processing characteristics of symmetry and closure in visuomotor responses. This task has some features which makes it particularly suited to study grouping cues in temporally early visuomotor processing. It allows to investigate (1) the time course of cue processing – by varying the prime-target SOA but also by analyzing the response time functions (i.e., contrasting temporally early and later phases of processing); (2) the automaticity of cue processing – by testing for an influence of task-irrelevant grouping on participants' responses; (3) the role of particular variables for cue processing – by varying, for example, symmetry axes, skewing, and framing of prime/target stimuli.

Most importantly, we observed considerable priming effects in the symmetry and closure tasks that were present in the fastest responses and did not increase any further in slower responses. These effects were based purely on the stimuli's respective response categories; repetition priming was ruled out because in a particular trial primes and targets were never identical. Thus, the visual system processed the primes in a way that allowed for their classification into symmetric vs. asymmetric or closed vs. open contours. Together, these findings show that the symmetry or closure of primes is extracted rapidly enough to not only influence visuomotor processing of the targets, but also the fastest responses in particular.

In the following sections, we place our findings in the context of previous studies and of our expectations and discuss their implications for the processing characteristics of symmetry and closure.

3.5.1 Temporally Efficient Processing of Symmetry and Closure

One measure of efficiency of temporally early visual processing is the minimal amount of presentation time the system requires to generate a reliable response. In line with our expectations, the temporal efficiency of closure and symmetry corresponds to earlier findings with brief stimulus presentations. For example, participants have been shown to reliably discriminate between simple symmetric and asymmetric shapes with presentation times as brief as 25 ms (Carmody et al., 1977), and in random dot patterns for presentation times as brief as 13 ms (Niimi et al., 2005; other exemplary studies summarized in Wagemans, 1995). On the other hand, the closure of contours has been shown to be relevant when responding to stimuli that are presented for 150-160 ms (Kovács & Julesz, 1993; Saarinen & Levi, 1999). Our findings suggest that the distinction between closed vs. open contours is already possible at presentation times of 24 ms. Carefully note that this does not mean that the required processing time is just as short: In principle, any brief signal, once in the system, may be processed for an unlimited amount of time. Rather, presentation time limits the amount of temporal summation that can take place to form a reliable signal in the first place.

3.5.2 Closure and Symmetry: Rapid-Chase Processes?

Rapid-chase theory proposes that prime and target signals traverse the visuomotor system in strict sequence, like two cars in a close chase. Thus, the first processing wave reaching executive motor areas exclusively carries prime information, and therefore the motor activation triggered by the prime signal must precede even the earliest target-related motor activation. In contrast to other feedforward models (e.g., Thorpe et al., 1996; VanRullen & Koch, 2003) the theory does not preclude quick recurrent processing between and within visual areas – both are widely spread in the visual system (e.g., Bullier, 2001; Roland, 2010) – as long as primes and targets still lead to strictly sequential motor outputs. It also allows for different overall speeds of processing for different stimulus properties (e.g., slower processing of symmetry than of closure) as long as behavior meets the functional requirements for a rapid-chase process. Therefore, processing does not have to be extraordinarily fast (*ultra-rapid*, VanRullen & Thorpe, 2001) to be considered feedforward.

Our results indicate that response activation by closure meets the criteria of rapid-chase theory (Schmidt et al., 2006; Vath & Schmidt, 2007). In the closure task of Experiments 1 and 2, priming effects were present in the fastest responses and did not increase any further in later phases of processing, which is a strong prediction of rapid-chase theory. Moreover, priming effects increased markedly with prime-target SOA in response times as well as error rates, consistent with the notion that the prime signal has progressively more time to drive the response process into the correct or incorrect direction.

The case is less clear for symmetry processing. Results from Experiment 1 are clearly consistent with a rapid-chase process, showing priming effects to increase with SOA and to be largest in the fastest responses. However, neither Experiment 2 nor Experiment 3 clearly replicate the increase with SOA; and instead of observing priming effects to be largest in the fastest responses, we find them to be constant across all response time bins. Additionally, it is obvious that responses are relatively slow in general, at least if compared to the responses to the closure cue, and actually slowest in Experiments 2 and 3. All things considered, the evidence for feedforward processing of symmetry is somewhat mixed. However, Experiment 1 suggests that symmetry processing is able to meet the rapid-chase criteria if the task is simple enough to allow for fast responses.

3.5.3 Reentrant Processing of Symmetry

For symmetry processing, neuroimaging studies suggest that a widespread network of interacting extrastriate visual areas is involved (including V3A, V7, and the lateral occipital complex, Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005; Tyler et al., 2005). Thus, in terms of these studies a pure feedforward account may not be able to explain symmetry processing. Note, however, that neuroimaging has a relatively poor temporal resolution so that temporally early phases of processing cannot be differentiated from later ones. It may well be that there are early and late phases of symmetry processing; indeed, it was hypothesized earlier that the visual system may rely on several neural mechanisms at multiple stages of the visual hierarchy with potentially different time courses to detect and encode symmetry (Julesz, 2006; Wagemans, 1995). In line with that, even though later phases may involve a wide-spread network of visual areas, symmetry processing in fast responses may be explained in terms of low-level segmentation processes (i.e., by an interaction of oriented spatial filters or receptive fields, e.g., Barlow & Reeves, 1979; Dakin & Herbert, 1998; for a model see Rainville & Kingdom, 2000).

Our results complement findings from earlier studies on the temporal dynamics of symmetry processing in event-related potentials (ERPs), where participants' neuronal responses to symmetric and asymmetric stimulus displays are compared. From this contrast it is possible to determine the earliest point in time when symmetry-specific processing starts. While our data disagree with studies showing only late symmetry-specific activation between 500 and 1,000 ms after stimulus presentation (with abstract geometric stimuli, Höfel & Jacobsen, 2007; Jacobsen & Höfel, 2003), they are in accordance with other studies that observed symmetry-specific activation starting around 220 ms after stimulus presentation (with dot patterns, Norcia, Candy, Pettet, Vildavski, & Tyler, 2002; with checker stimuli, Oka, Victor, Conte, & Yanagida, 2007). Only neuronal activation as early as detected in the latter studies can possibly account for fast visuomotor responses like those observed in our experiments.

3.5.4 Reentrant Processing of Closure

For closure processing, recurrent neuronal activation seems to be important as well. Specifically, processes of contour integration (which provide the basis for the detection of closure) are mediated by horizontal connections between cells in V1 (Bauer & Heinze, 2002) as well as by feedback from extrastriate areas higher in the visual hierarchy (Zipser et al., 1996). Still, Houtkamp and Roelfsema (2010) and Roelfsema (2006) assume that closed contours are processed by feedforward mechanisms (base grouping) while open contours are not (incremental grouping). In our experiments, we presented closed and open contours simultaneously in all experiments. For this reason, we cannot differentiate between responses to those two stimulus classes. Nevertheless, our results suggest that discrimination between closed and open contours can be achieved within the feedforward process described by rapid-chase theory (Schmidt et al., 2006).

3.5.5 Automaticity of Symmetry and Closure Processing

Although our findings illustrate the speed of symmetry and closure processing, they do not argue for its automaticity.[17] This finding is in line with our expectations for closure processing but not for symmetry processing. In a strict sense, automatic processing would imply that a grouping cue inevitably influences participants' responses even though it is not relevant for the task. In contrast, we found that the respective response-irrelevant grouping cue was completely ineffective (i.e., when participants were instructed to focus on one of the cues, the other cue had no influence on their response times, error rates, or priming effects). Task-irrelevant symmetry cues did not influence responses in the closure task. This finding is in contrast to the general claim that "symmetry detection is a visual process that is constantly applied to any visual input and it affects the way we perceive our visual environment" (Treder, 2010, p. 1514). How can our results be reconciled with earlier studies reporting automaticity of symmetry processing (e.g., Koning & Wagemans, 2009)?

Fast motor responses generally have been shown to depend critically on action-trigger sets that are established under top-down control at the beginning of an

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[17] Note that priming effects per se are no evidence for automaticity because primes are spatially close to the targets, stem from the relevant stimulus set, and are highlighted by abrupt onset (cf. Pashler, 1999, p. 60).

experiment (Kiesel, Kunde, & Hoffmann, 2007). A general finding in response priming with multiple concurrent stimulus dimensions is that priming effects are controlled exclusively by the task-relevant feature but are unaffected by the task-irrelevant feature (Seydell-Greenwald & Schmidt, 2012; Tapia et al., 2010). For instance, Seydell-Greenwald and Schmidt (2012) studied response priming by illusory contours or by the line elements inducing those contours. When participants responded to the orientation of an illusory contour in the target, priming depended only on the orientation of the illusory contour in the prime, but not on the orientation of any inducing line elements. When participants instead responded to the inducers in the target, priming depended only on the inducers in the prime but not on any illusory contours (even though stimuli were identical in both tasks). Thus, if once set up for one cue (e.g., closure), the other cue (e.g., symmetry) loses access to the response process.

This conclusion seems to be in contradiction to some studies that also investigated fast visuomotor processing and obtained response times in a range similar to ours (Bertamini, 2010; Koning & Wagemans, 2009; van der Helm & Treder, 2009). In those experiments, participants are asked to judge as quickly as possible whether the facing or non-facing contours of two objects are symmetric. Typically, responses are speeded by the symmetry of the objects' task-irrelevant contours, seemingly contradicting our results. However, those participants were asked to actively search for symmetries, allowing the task-irrelevant features access to the motor process. In contrast, in our experiments participants were asked to search for an entirely different cue (i.e., closure). Thus, only with an appropriate presetting of the visuomotor system, symmetry is detected and processed also in task-irrelevant parts of the stimuli.

3.5.6 Symmetry Processing and the Orientation of the Symmetry Axis

In contrast to our expectations for symmetric stimuli, we found neither an influence of the symmetry axis nor of the three-dimensional transformation (framed or non-framed) on fast visuomotor processing. However, our data revealed an unexpected interaction of the factors symmetry axis, skewing, and framing on response times and error rates. When symmetric stimuli were skewed and non-framed, a vertical symmetry axis led to faster responses and fewer errors compared to a horizontal one. In the following section, we discuss these results and compare them to earlier studies.

The orientation of the symmetry axis was repeatedly shown to modulate detection performance and speed in symmetry processing; specifically, a vertical axis was superior to other orientations, including a horizontal one (e.g., Wenderoth, 1994; Wenderoth & Welsh, 1998). We presented stimuli with horizontal and vertical symmetry axes in blocks to preclude the use of attentional scanning strategies (cf.

Wenderoth, 1994), a technique that should still lead to faster responses to stimuli with vertical compared to horizontal orientations of the symmetry axis (Wagemans et al., 1992; Wenderoth, 2000). Why did that difference not show up in our Experiments 2 and 3?

The superiority of vertical symmetry axes is not without controversy. A number of studies with random dot patterns did not find a superiority effect (e.g., Fisher & Bornstein, 1982), or even reported that horizontally oriented stimuli were processed more easily (Jenkins, 1983; Pashler, 1990). Wagemans et al. (1992) have already stated that ‘‘the orientational effects on symmetry detection are not as simple and as universal as implicitly assumed’’ (p. 502). Many experimental factors may co-determine the effects of symmetry axes on output measures (e.g., random dot patterns vs. contour stimuli, large vs. small stimulus set, detection task vs. reaction time task, central vs. peripheral stimulus presentation, slow vs. fast responses, cf. Locher & Wagemans, 1993). For example, in contrast to contour stimuli as used in our experiments, random dot patterns are more difficult to process (Sawada & Pizlo, 2008) and also lead to slower response times (Wagemans, 1993). Nevertheless, some studies reported faster responses to contour stimuli with a vertical axis compared to those with a horizontal axis (e.g., Friedenberg & Bertamini, 2000) so that further research is needed to explain why we did not find any effect. In this context, it is interesting that we observed an effect of symmetry axis on response times and error rates in the expected manner (i.e., vertical axis better than horizontal axis) when stimuli were skewed (Experiment 3). We first describe the general role of the factors skewing and framing and after that we discuss their interaction with the symmetry axis.

3.5.7 Viewpoint-Invariance of Symmetry Processing

In contrast to evidence from earlier studies which showed a strong influence of skewing on performance and speed in symmetry detection (e.g., Wagemans, 1993; Wagemans et al., 1992), and also in contrast to our expectations, we found that skewing the primes did not change the magnitude of priming effects. Thus, it seems that the visuomotor system not only makes efficient use of the symmetry or asymmetry in briefly presented primes, but also possesses at least some degree of viewpoint-invariance. Although we only tested one specific level of three-dimensional transformation (30° slant and tilt) – more variance in skewing angles might well produce effects on response times in line with earlier results – it is remarkable that priming effects were in no way diminished by this transformation of the primes. Because primes were denoted as irrelevant by the task instruction, few resources should have been invested in their processing, which should have increased the vulnerability of the system to skewing. However, note that the priming effects in Experiment 3 were comparatively small and did not increase with SOA, violating a prediction of rapid-chase theory. Thus, we cannot rule out that the processing of skewed symmetry involves mechanisms beyond basic visuomotor feedforward activation.

In contrast to Wagemans (1993), we also did not find any effect of framing. This is not surprising given that our results show that the visuomotor system is able to extract prime symmetry irrespective of skewing. If the priming effects are of the same magnitude for skewed and non-skewed primes – without frames revealing the skewing angle – there might be no room for any further processing advantage when frames are provided.

Finally, we observed an interaction of symmetry axis, skewing and framing: No effect of symmetry axis was found in responses to non-skewed primes, whereas skewed primes with a vertical symmetry axis led to faster responses and fewer errors compared to those with a horizontal axis. This effect was stronger when primes have been shown without a frame. Although several studies reported interacting effects of symmetry axis and skewing on output measures, the exact type of this interaction is complex (Wagemans, 1993; Wagemans et al., 1991, 1992).

3.5.8 Summary

In conclusion, by using contour stimuli in a primed flanker task, we showed that the grouping cue of closure is processed rapidly and as predicted by rapid-chase theory, consistent with a simple feedforward processing model (Schmidt et al., 2006). In the case of symmetry, the evidence is equivocal, even though the data suggest that symmetry processing is able to meet the rapid-chase criteria if the task allows for fast responding.

Symmetry processing was not modulated by skewing or framing of the primes; also the symmetry axis was only of relevance when primes were skewed and presented without a frame, suggesting some degree of viewpoint-invariance in the temporally early processing of symmetry. Additionally, when participants responded to one of the two grouping cues, the respective other cue was irrelevant for the visuomotor response. Thus, we conclude that closure cues and (possibly) viewpoint-independent symmetry cues can be processed in a feedforward fashion if the task set allows for an unambiguous mapping of stimulus features to speeded motor responses.

4. Grouping by Good Gestalt

4.1 Introduction

4.1.1 General

In this chapter, we investigate the processing time course of the law of *Good Gestalt* (or *Prägnanz*) that subsumes a number of basic grouping principles. We do this by measuring rapid visuomotor responses to occluded shapes because the process by which these shapes are separated from their occluders relies on Good Gestalt cues. The difficulty of this process is controlled by varying the number of occluders and the amount of spatial overlap of shapes and occluders.

4.1.2 Good Gestalt and Visual Completion

The law of Good Gestalt has been put forward by the Gestalt school in order to encompass the numerous principles of grouping (Koffka, 1935; Wertheimer, 1923). The law states that within a visual scene, elements are bound together such that the perceived object is as simple, regular, and as well-structured as possible.[18] In this sense, it subsumes a number of basic grouping principles. *Grouping by element connectedness* (i.e., by elements that share a common border), *grouping by good continuation* or *collinearity* (i.e., by elements that are aligned with each other along a smooth path), and *grouping by proximity* (i.e., by elements that are spatially close) are well-studied examples.

The law of Good Gestalt has specific implications for our perception. A shape or figure satisfying the criteria of a Good Gestalt is preferred by the visual system. For example, it can be more easily distinguished from other objects in a visual scene and extracted as a whole even when it is not fully visible.

This, in turn, links the concept of Good Gestalt tightly to the research on *visual completion*. In this field, investigation focuses on the extent to which humans can perceive objects that are partly occluded. This ability is of immediate and crucial importance for everyday life in which an object is often occluded by either other objects or by (more proximate) parts of the object itself. Indeed, humans are very good at this task and can easily infer not-visible object parts based on earlier experiences and general perceptual principles (Good Gestalt being one of them, e.g., Dinnerstein & Wertheimer, 1957). The process of visual completion is especially easy

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[18] Note that this originally quite vague definition was revised later on and subject to strict formalizations (cf. the *minimum principle*, e.g., Attneave, 1954; Hochberg & McAlister, 1953; the *likelihood principle*, e.g., Pomerantz & Kubovy, 1986; or the *simplicity principle*, e.g., Leeuwenberg, 1969). However, the differences between these accounts and that of the Gestalt school are not important for our purposes.

for simple shapes (e.g., triangles, rectangles, and circles) because all of them are believed to be *Good Gestalten* as defined above.

4.1.3 Self-Splitting Objects

As noted before, our visual percept changes rapidly in time and these changes provide valuable information about the cognitive and physiological mechanisms underlying the perceptual process of interest (cf. Hegdé, 2008; Schmidt, Haberkamp, Veltkamp et al., 2011). Here, we investigate the time course of a special case of visual completion: that of *self-splitting objects* (Kellman & Shipley, 1991; Petter, 1956). When several 2-D objects are combined into a single object by superimposing objects with the same surface features, observers typically perceive a configuration of several distinct objects (e.g., when superimposing a white triangle and a white rectangle on a dark background, cf. Fig. 20C). This is true at least when the objects are not too complex and the observer has previous experience with them.

In every self-splitting object there are areas where the superimposed 2-D objects cross and in which, as a consequence, the objects' physically defined contours have gaps. In our perception, these gaps are spanned by interpolated contours. As a result of our adaptation to a visual environment where no overlapping objects are lying in the same depth plane, we perceive the different objects in a certain depth ordering, displaying the so-called Petter's effect: those contours crossing the smaller gap appear in front while those crossing the larger gap are seen behind (Petter, 1956). This results in the nearer contour having illusory contours (*modal completion*) and the farther contour having occluded contours (*amodal completion*).

The mechanisms underlying these two completion processes are still under debate. The main controversy arises around whether modal and amodal completion are separate processes (Anderson, 2007a, b, c), whether both are the result of a common mechanism of object interpolation across gaps (*identity hypothesis*, Kellman, Garrigan, & Shipley, 2005; Kellman, Garrigan, Shipley, & Keane, 2007), or whether both are the result of a common mechanism of surface creation (Kogo & Wagemans, 2013).

The origin of the perception of self-splitting objects is even more unclear because it involves both modal and amodal completion processes (*quasi-modal*, Kellman et al., 2005). Nevertheless, because we know that the law of Good Gestalt plays a major role in the processing of self-splitting objects, it is expedient to use these stimuli to measure the law's time course and processing characteristics.

4.1.4 The Time Course of Visual Completion

Although previous studies did not measure the time course of processing of self-splitting objects, they measured that of visual completion through psychophysical methods (e.g., Bruno, Bertamini, & Domini, 1997; Guttman, Sekuler, & Kellman, 2003; Murray, Sekuler, & Bennett, 2001; Ringach & Shapley, 1996; Sekuler & Palmer, 1992) as well as in electrophysiological and imaging studies (e.g., Lerner, Hendler, & Malach, 2002; Sugita, 1999). For example, Guttman et al. (2003) used a *primed-matching technique* in which participants have to indicate as fast as possible whether two simultaneously presented target shapes are the same. This response is known to be faster when a preceding prime shape is identical to the targets. The authors presented as targets complete shapes (circles or squares) or notched shapes (circles or squares). Primes were either the target shapes or a circle occluded by a square (or a square occluded by a circle) for which contours matched the notch in the notched targets. First, they observed the standard effect: responses were faster to complete targets preceded by complete primes and to notched targets preceded by notched primes. Second, and more importantly, they found that responses were faster to complete targets preceded by notched primes but only when prime presentation times were longer than about 200-250 ms.

Overall, it has been shown that visual completion develops roughly in the first 50-200 ms after stimulus presentation although the actual results strongly depend on task and stimulus characteristics as well as individual differences. Most prominently, the time to completion is shorter when the amount of occlusion is smaller (e.g., Shore & Enns, 1997). This led to the formulation of the *Temporal Variation Hypothesis*, stating that the visual system can interpolate a greater amount of occluded information with longer processing times (Guttman et al., 2003). In all probability, this also applies to self-splitting objects: The processing time for separating the shapes that are part of the objects is likely to increase with the number of objects and the amount of overlap between them. To control for this effect, we used objects that were composed of a varying number of shapes.

4.1.5 Measuring the Time Course of Good Gestalt

In order to determine the processing dynamics of the law of Good Gestalt, we employed the primed flanker task (Chapter 2). This task has two advantages over the primed-matching paradigm that was used in previous studies for measuring the time course of visual completion for occluded objects (e.g., by Guttman et al., 2003; for a discussion of the shortcomings of the primed-matching paradigm, see Murray et al., 2001). First, response priming effects are usually large, very robust, and not diminished by training. Second, the mechanisms underlying response priming are well understood and the existing theoretical accounts allow for a classification of the findings with respect to neuronal feedforward vs. feedback processing (cf. Schmidt, Haberkamp & Schmidt, 2011; Schmidt, Haberkamp, Veltkamp et al., 2011). For example, Seydell-Greenwald and Schmidt (2012) asked their participants to respond to the orientation of illusory and real-contour targets that were preceded by illusory and real-contour primes. They found that both target types were primed by illusory contours, and that this effect was fully present in the fastest responses. Thus, illusory contours activate rapid motor responses and meet the predictions of the rapid-chase theory. These behavioral results are in accordance with neuronal processing in a feedforward manner without time-consuming intracortical feedback. In the same manner, we can use response priming with keypress responses to investigate whether shape targets are primed by simple geometric shapes that are part of self-splitting objects.

To sum up, we wanted to know whether the visual system can extract simple geometric shapes from self-splitting objects in rapid visuomotor processing. Furthermore, we wanted to know whether this already occurs in the earliest (feedforward) phases of processing (Chapter 3; Seydell-Greenwald & Schmidt, 2012) and whether it is modulated by the amount of occlusion of the simple shapes.

4.2 Experiment

4.2.1 General

In the primed-flanker task (Chapter 2), participants were asked to respond as quickly as possible to the upward or downward pointing one of two target triangles that were presented simultaneously in the left and right periphery. Targets were preceded at varying time intervals (SOA) by two prime triangles in the center of the screen that could be either consistent or inconsistent regarding their orientation (e.g., the upward prime triangle could be on the same side as the upward target triangle or on the opposite one). The two primes (and targets) always opposed each other in their orientation (Fig. 20A). Importantly, prime triangles were occluded by one to three other shapes (i.e., square, rectangle, and/or circle) in the same plane and luminance, reducing the number of their visible edges and contours. Primes and targets were either defined by outline contours (Fig. 20B) or filled contours (Fig. 20C).

We investigated the capacity of self-splitting objects for priming speeded motor responses and response errors and analyzed these priming effects as a function of the response time distributions. Generally, primes should trigger priming effects only if the visual system is able to extract the triangle shapes from the primes.

By analyzing the temporally early phases of the motor responses, we link the results to neuronal feedforward activation. Specifically, a fully developed priming effect in the fastest responses is predicted by rapid-chase theory and is consistent with feedforward processing of self-splitting objects.

Finally, the number of shapes in the primes was varied to obtain different amounts of occlusion. Previous psychophysical experiments with occluded shapes (e.g., Guttman et al., 2003) as well as with illusory shapes (e.g., Gegenfurtner, Brown, & Rieger, 1997) led us to expect that priming effects would be smaller with more superimposed shapes (cf. *Temporal Variation Hypothesis*). In the same line of argument, outline contours were expected to produce priming effects more easily, because the interruptions in their contours are smaller.

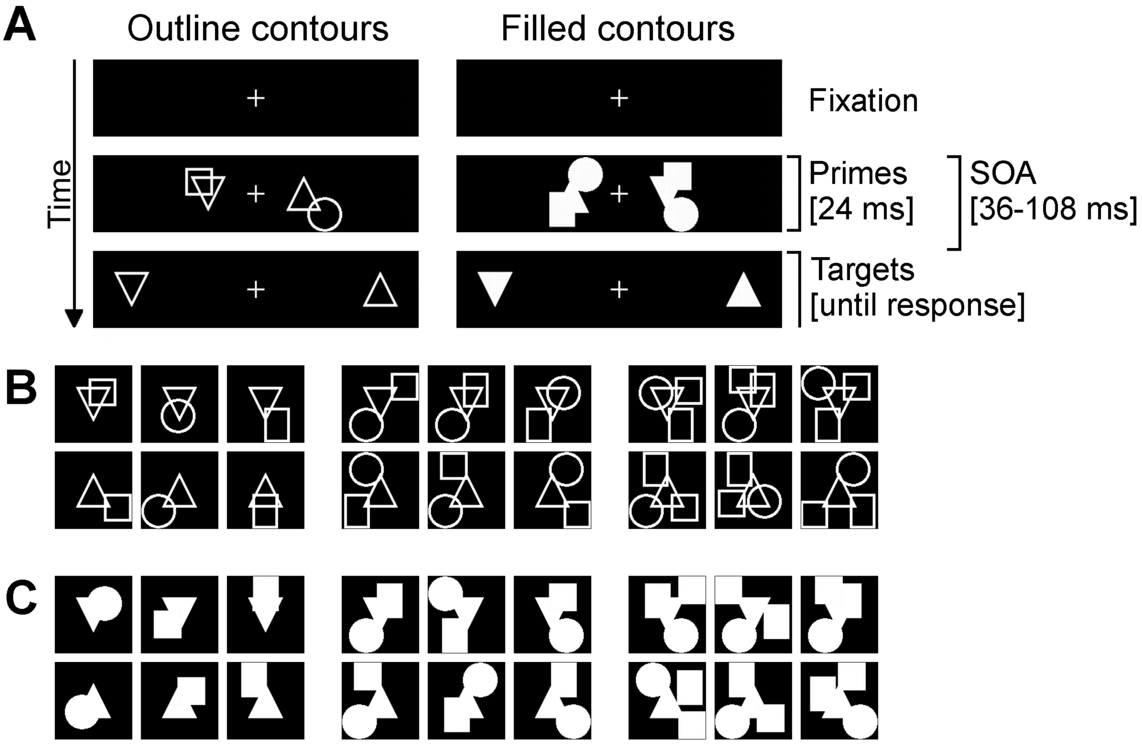

Figure 20. Procedure and stimuli. Two primes and two flanking targets were presented in the sequences displayed (**a**). Participants were asked to respond to the position of either the upward or downward pointing target triangle. Primes were self-splitting objects containing triangles that were either mapped to the same responses (consistent) or opposite responses (inconsistent) as the targets. Examples of the outline contour stimuli (**b**) and filled contour stimuli (**c**) with an increasing number of occluders (panels from left to right).

4.2.2 Methods

Participants. Eight right-handed students from the University of Kaiserslautern, Germany (3 female, 5 male, ages 22-24), with normal or corrected vision participated in the experiment for payment of € 6 per hour. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association. They were debriefed after the final session.

Apparatus and Stimuli. The participants were seated in a dimly lit room in front of a CRT color monitor (1280 x 1024 pixels) with a monitor retrace rate of 85 Hz at a viewing distance of approximately 70 cm. Stimulus presentation and timing was controlled by using Presentation® software (www.neurobs.com).

The stimuli (primes and targets) were either outline contour stimuli (line width of 0.09° of visual angle, 1 cm ≈ 0.82° of visual angle; Fig. 20B) or filled contour stimuli (Fig. 20C). Primes and targets in a respective session were always either outline contours or filled contours. Targets were isosceles triangles (with a base and height of 1.56°) that pointed upward or downward and were presented in white (60.00 cd/m^2) on a dark background (0.13 cd/m^2). Primes were designed by superimposing one, two, or three occluder shapes (square: 0.90° x 0.90°; rectangle: 0.82° x 1.15°; circle: diameter of 1.15°) on an upward target triangle such that each shape overlapped with the triangle (Fig. 20B, C). Every class of primes (one, two or three occluders) contained 30 stimuli. In the filled-prime contours, the number of occluders determined the number of visible edges (2.13, 1.07, and 0.47, respectively) and the amount of visible contours (66%, 58%, and 42%, respectively) of the prime triangle.

All primes in every class were flipped horizontally to obtain stimuli with downward triangles. Primes and targets were arranged on the left and right of the fixation cross (diameter of 0.41°; 60.00 cd/m^2) in the center of the screen. The center-to-center distance between fixation cross and prime triangles was about 1.89°, that between fixation cross and target triangles about 3.69°.

Procedure. Typical trials are depicted in Figure 20A. In the beginning a fixation cross was presented. After a variable delay, two primes were presented for 24 ms simultaneously to the left and right of fixation. After an SOA of either 36, 60, 84, or 108 ms, targets appeared to the left and right of the prime positions. The participants had to decide as quickly and accurately as possible on which side of the fixation cross the upward target triangle (half of the participants: downward triangle) was presented. They were instructed to ignore the primes. The two primes and targets were always opposed to each other in the orientation of the triangle. The number of occluders varied randomly on a trial-by-trial basis between one to three. The two primes in a particular trial always had the same number of occluders. Targets remained on screen until participants gave their response.

The time interval from trial start to target onset was constant at 1000 ms to allow for an optimal preparation for each response to the target. After each block, summary feedback on response times and error rates was provided. All stimulus combinations of consistency, prime-target SOA and number of occluders occurred equiprobably and pseudo-randomly in a completely crossed repeated-measures design.

Participants responded in six half-hour sessions alternately to either outline contours or filled contours (always two sessions in a row). Each of these consisted of one practice block of 32 trials followed by 27 blocks of 32 trials, accumulating to a total of 5,184 trials per participant.

Data treatment and statistical methods. Practice blocks were not analyzed. For the analysis of response times and error rates, we eliminated trials with response times shorter than 100 ms or longer than 1000 ms (0.13% of trials with outline contours and filled contours, respectively). Then, we performed repeated-measures ANOVAs with Huynh-Feldt-corrected p values.

ANOVAs for analyzing response times and error rates were fully-factorial with factors of consistency (C), prime-target SOA (S), and number of occluders (O). All error rates were arcsine-transformed to comply with ANOVA requirements.

ANOVAs for analyzing response time functions were fully-factorial with factors of consistency (C), prime-target SOA (S), number of occluders (O), and decile (D). Deciles were obtained by sorting response times, separately for each participant and condition (defined by the levels of consistency and SOA for the outline and filled contours) into multiple ordinal bins of data. Each bin summarizes 10% of the cumulative distribution (note that the first and last bins are excluded because they are likely to be distorted by outliers). As a result, the priming effect can be examined as a function of response speed and SOA. We will only report the interactions of consistency and decile.

F values are reported with subscripts indicating the respective effect (e.g., F_{CxS} for the interaction of consistency and prime-target SOA).

4.2.3 Results and Discussion

Response times and error rates: General. The results are depicted in Figure 21. An overall ANOVA including the factor stimuli (outline contours vs. filled contours, ST) showed response priming effects in response times and error rates [$F_{\mathrm{C}}(1,7) = 54.44$, $p < .001$; $F_{\mathrm{C}}(1,7) = 42.76$, $p < .001$]: participants responded faster and made fewer errors when prime and target triangles on the same side of fixation had the same orientation. In both measures, this effect increased with prime-target SOA [$F_{\mathrm{CxS}}(3,21) = 9.03$, $p = .001$; $F_{\mathrm{CxS}}(3,21) = 8.12$, $p = .001$] and decreased with the number of occluders [$F_{\mathrm{CxO}}(2,14) = 5.88$, $p = .019$; $F_{\mathrm{CxO}}(2,14) = 17.04$, $p < .001$]. Overall response times also slowed down with the number of occluders [$F_{\mathrm{O}}(2,14) = 12.64$, $p = .001$] while error rates were the same [$F_{\mathrm{O}}(2,14) = .01$, $p = .992$]. In general, response times and error rates were not different for outline and filled contours [$F_{\mathrm{ST}}(1,7) = 0.11$, $p = .750$; $F_{\mathrm{ST}}(2,14) = 0.35$, $p = .572$]. To investigate these results in more detail, we performed separate analyses for each class of stimuli.

Response times and error rates: Outline contours. With outline contours (Fig. 21A), we obtained reliable priming effects in response times and error rates [$F_{\mathrm{C}}(1,7) = 43.31$, $p < .001$; $F_{\mathrm{C}}(1,7) = 27.66$, $p = .001$] that increased with SOA [$F_{\mathrm{CxS}}(2,14) = 9.03$, $p = .001$; $F_{\mathrm{CxS}}(2,14) = 8.12$, $p = .001$]. The number of occluders modulated priming effects in error rates [$F_{\mathrm{CxO}}(2,14) = 4.52$, $p = .052$; $F_{\mathrm{CxSxO}}(6,42) = 2.55$, $p = .034$] but not in response times [$F_{\mathrm{CxO}}(2,14) = 2.14$, $p = .156$; $F_{\mathrm{CxSxO}}(6,42) = 0.98$, $p = .433$]. Specifically, the net priming effect was larger with one occluder (7.79%) compared to two or three occluders (5.46% and 4.79%). Finally, responses slowed down if the number of occluders increased [FO(2,14) = 8.81, p = .006]. The total error rate was 10.30% of all trials.

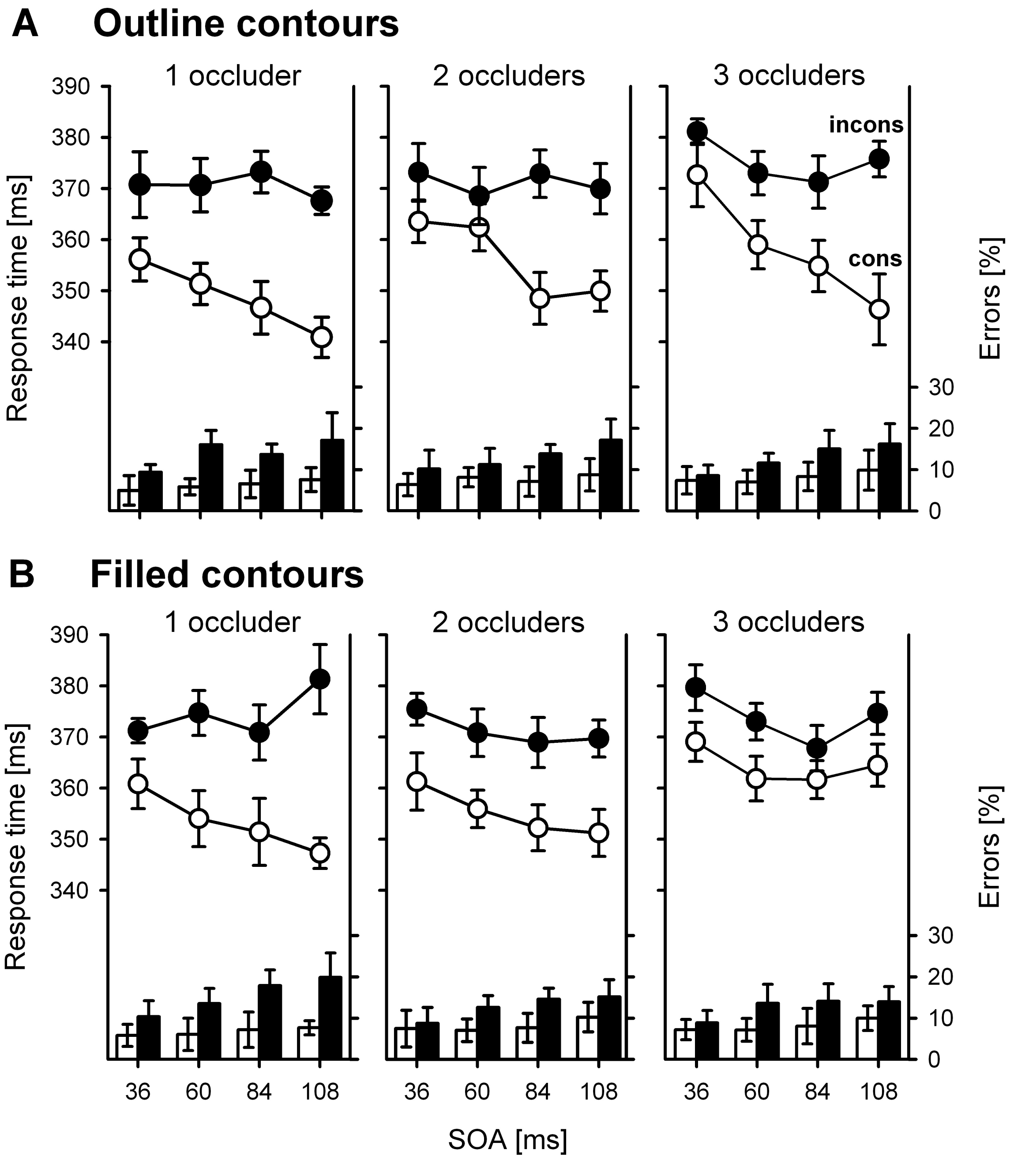

Figure 21. Results of the primed flanker task for outline contours (**a**) and filled contours (**b**). Mean response times (line plots) and error rates (bar plots) in consistent (white) and inconsistent (black) trials are displayed as a function of prime-target SOA. Error bars denote the standard error of the mean corrected for between-subjects variance (Cousineau, 2005; Loftus & Masson, 1994).

Response time distributions: Outline contours. The analysis of the response time functions for outline contours revealed priming effects [FC(1,6) = 36.45, p = .001] that were not modulated by the factor decile [$F_{\mathrm{CxD}}(7,42) = 0.62$, $p = .499$; $F_{\mathrm{CxSxD}}(42,252) = 0.76$, $p = .800$; $F_{\mathrm{CxOxD}}(14,84) = 0.18$, $p = .997$; $F_{\mathrm{CxSxOxD}}(42,252) = 0.84$, $p = .681$]. In other words, the priming effect was fully developed in the earliest responses and did not change in later ones (Fig. 22A).

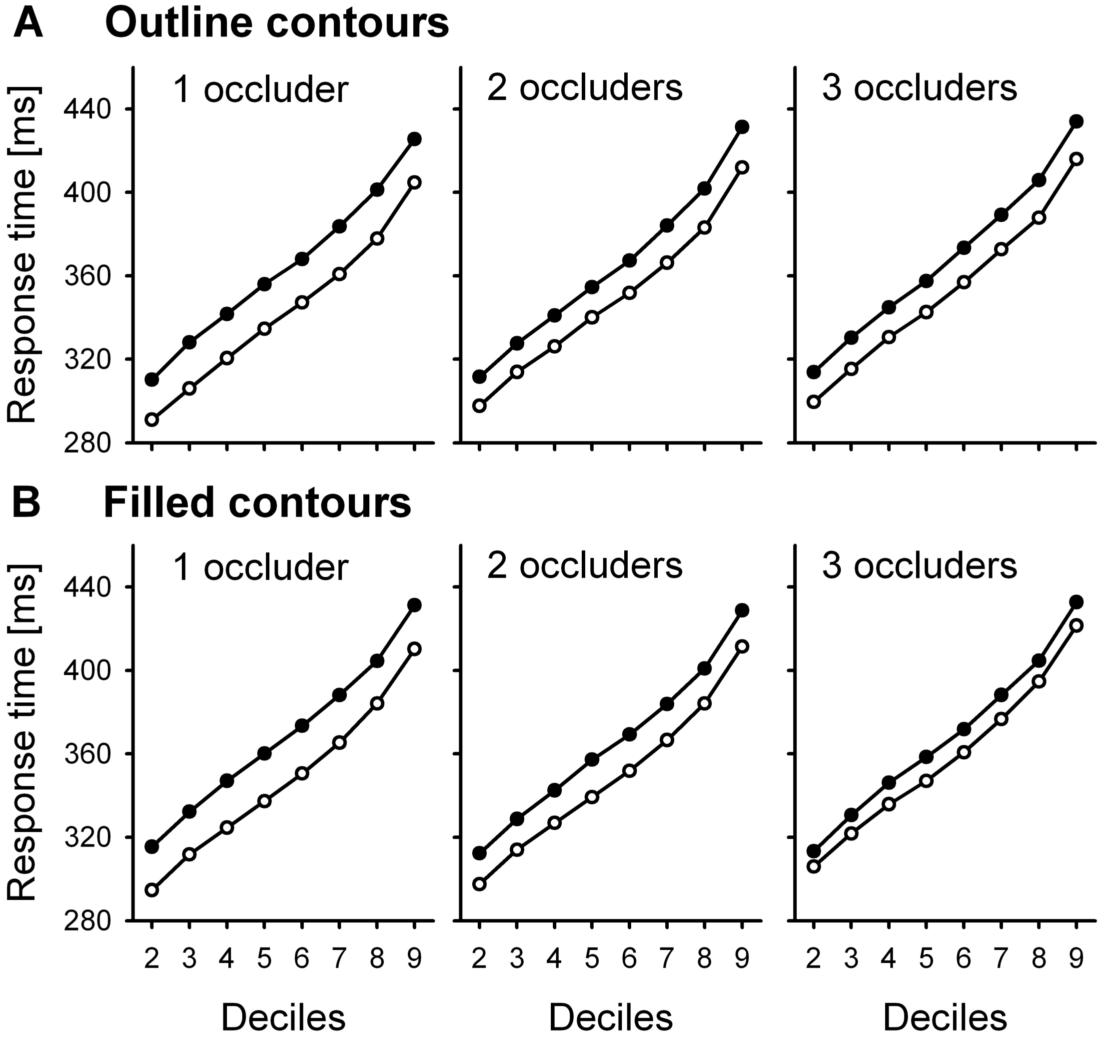

Figure 22. Response time functions for outline contours (**a**) and filled contours (**b**). Response times in consistent (white) and inconsistent trials (black) are displayed as a function of response speed (deciles 2 to 9), separately for the different numbers of occluders. It is a strong prediction of rapid-chase theory that priming effects should be fully present in the fastest responses and not increase any further in slower responses. Data were collapsed across SOA because that factor did not interact with the factor decile.

Response times and error rates: Filled contours. With filled contours (Fig. 21B), we obtained priming effects in response times and error rates [$F_{\mathrm{C}}(1,7) = 50.11$, $p < .001$; $F_{\mathrm{C}}(1,7) = 33.96$, $p = .001$] that increased with SOA in error rates [$F_{\mathrm{CxS}}(2,14) = 9.80$, $p = .001$] and by trend in response times [$F_{\mathrm{CxS}}(2,14) = 2.88$,

p = .068]. The number of occluders strongly modulated priming effects in response times as well as error rates [$F_{\mathrm{CxO}}(2,14) = 9.12$, p = .003; $F_{\mathrm{CxO}}(2,14) = 8.18$, p = .004]. Specifically, in error rates the net priming effect was larger with one occluder (8.74%) compared to two or three occluders (4.62% and 4.55%) – exactly as with outline contours – but in response times it linearly decreased with the number of occluders (20.87 ms, 16.25 ms, and 9.68 ms). Finally, overall responses also slowed down with the number of occluders [$F_{\mathrm{O}}(2,14) = 13.31$, p = .001]. The total error rate was 10.58% of all trials.

Response time distributions: Filled contours. Just as with outline contours, we obtained priming effects [$F_{\mathrm{C}}(1,7) = 51.67$, $p < .001$] with filled contours that were not modulated by the factor decile [$F_{\mathrm{CxD}}(7,49) = 0.73$, p = .504; $F_{\mathrm{CxSxD}}(21,147) = 1.37$, p = .232; $F_{\mathrm{CxOxD}}(14,98) = 0.20$, p = .944; $F_{\mathrm{CxSxOxD}}(42,294) = 0.68$, p = .810]. Thus, the effect was again fully developed in the earliest responses and did not change in later ones (Fig. 22B).

4.3 General Discussion

We determined the processing dynamics and time course of Good Gestalt to draw conclusions about the type of neuronal processing underlying it (feedforward vs. recurrent). In addition, we investigated whether the amount of occlusion would modulate this processing.

Because the law of Good Gestalt plays a major role in the perception of self-splitting objects, we tested the influence of triangles that were part of self-splitting objects (Petter, 1956) on rapid visuomotor responses. The primed flanker task (Chapter 2) provides information not only about the absolute speed of processing but also about the type of processing (based on assumptions of the rapid-chase theory, Schmidt et al., 2006). Generally, we wanted to know whether the primes led to response priming effects in response times and error rates, indicating fast processing of self-splitting objects. Specifically, we were interested in whether these effects (1) would be different for outline and filled contours, (2) would depend on the number of occluders, and (3) would be fully developed in the fastest motor responses, indicating feedforward processes.

Indeed, we obtained priming effects in response times and error rates for outline and filled contours that increased with SOA (exceptions discussed below), corresponding to earlier findings in response priming experiments (cf. Schmidt, Haberkamp, Veltkamp et al., 2011). In the current study, these effects demonstrate the capability of the visual system to extract and process the orientation of a triangle from briefly presented (24 ms) overlapping contours even if they were merged into one single shape. Notably, these effects were fully present in the fastest responses and did not increase any further in slower responses. Together, these findings suggest that self-splitting objects were “split” into their components by the visual system rapidly enough to not only influence visuomotor processing of the targets, but also to influence the fastest responses in particular.[19]

When analyzing and comparing the results for the outline contours with those for the filled contours, we can draw several conclusions. On the level of overall response times and error rates, results were similar for the two stimulus classes. Differences emerged mainly with respect to the influence of the number of occluders and with respect to the indicators of feedforward processing. We will discuss these differences in detail in the following sections.

4.3.1 The Role of the Number of Occluders

With respect to overall response times, the number of occluders had a similar effect for outline and filled contours. More occluders slowed down response times which most probably reflected the higher complexity of the respective primes. Specifically, with more occluders the primes contained more potentially task-relevant information (i.e., more edges and contours). This information was automatically analyzed by the visual system which increased the overall processing time.

However, with respect to priming effects, the number of occluders had different effects depending on the stimulus class. With outline contours, occluders played no role for the magnitude of the priming effects, at least in response times. Even with three occluders (i.e., a total of four overlapping contours) the visual system was still able to extract the task-relevant triangle from the briefly presented tangle of lines. For error rates, however, priming effects were largest with one occluder, and smaller in trials with two or three occluders (which did not differ from each other). With filled contours, occluders had a greater role in shaping the priming effects. Most importantly, priming effects in response times decreased with an increasing number of occluders. In addition, even though the priming effects were still present with two and even three occluders, they no longer increased with increasing SOA. This is important because it represents a violation of a prediction from rapid-chase theory. With regard to the priming effects in error rates, the result pattern was the same for filled contours as for outline contours.

4.3.2 Indicators of Feedforward Processing

When analyzing the response time functions, we observed priming effects for outline and filled contours in all phases of the participants' responses. The effects were fully present in the earliest responses and did not decrease in slower ones. According to the rapid-chase theory, this pattern is consistent with a feedforward

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[19] As described in Section 1.4, there are differences between the processing of self-splitting objects and visual completion. Still, when comparing our findings to earlier ones on the time course of visual completion, our results are indicating a process that can be completed in a relatively short time (i.e., within 24 ms compared to 46-114 ms for masked visual completion stimuli in Murray et al., 2001).

system where prime and target signals traverse the visuomotor system in strict sequence, without mixing or overlapping (Schmidt et al., 2006; Vath & Schmidt, 2007).

Results for outline contour primes show that the visuomotor system is able to process the features that are relevant for its response in a feedforward fashion, namely, the non-occluded edges and contours of the triangles in the two prime stimuli.

A similar pattern of results for filled contour primes (i.e., self-splitting objects) would imply that the prime configurations can be broken down into their components without the necessity of extensive recurrent processing. However, only with one occluder the priming effects were showing the typical pattern of an increase with SOA. Thus, the results for two and three occluders were somewhat mixed (i.e., the shape of the response time functions argues in favor of feedforward processing while the lack of the typical SOA effect calls feedforward processing into question, cf. Chapter 3). We conclude that although the processing of objects that are part of self-splitting objects is implemented early on in visuomotor processing, the amount of occlusion (i.e., the number of occluders) determines whether it occurs in a feedforward fashion or whether recurrent processing is necessary.

With regard to our stimulus set, only self-splitting objects comprised of two objects were processed in a feedforward manner, as indicated by the increasing priming effects with increasing SOA and the fully present effects in earliest visuomotor responses. This implies that the visual system completes two tasks within this temporally early phase of processing of self-splitting objects with one occluder. First, a sufficient number of key features are extracted to identify the task-relevant object, that is, all relevant angles and sides to distinguish between an upward and a downward pointing triangle.[20] Second, these features are processed in a feedforward manner without extensive recurrent processing, and activate a rapid motor response.

As such, our results suggest that the processing of self-splitting objects with one occluder is more similar to the processing of illusory contours than to that of visual completion with occluded objects. The former was shown to be generated by relatively local integration of signals implemented by feedforward signals (e.g., Heitger, von der Heydt, Peterhans, Rosenthaler, & Kübler, 1998; Seydell-Greenwald & Schmidt, 2012) while the latter is most probably implemented by feedback activation from higher levels (Sugihara, Qiu, & von der Heydt, 2011; Zhang & von der Heydt, 2010). Only when the amount of occlusion is increased does the processing resemble that of occluded objects.

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[20] This is easier the more features are visible, a fact that was described earlier in terms of the *support ratio*: the ratio of physically specified (visible) length to total edge length in occluded shapes. An increasing support ratio increases the perceived connectedness of two contour segments separated by an occluder as well as the illusory contour strength (e.g., Shipley & Kellman, 1992).

4.3.3 Implementation of Feedforward Processing

How is the rapid feedforward processing of self-splitting objects with one occluder implemented in the visuomotor system? The visual system has stored a vast number of Gestalt templates as a result of previous visual experience (cf. Wagemans, Feldman et al., 2012). In terms of neural architecture, these templates correspond to feature detectors that are tuned to specific conjunctions of lower-level features including a large number of simple but also a number of complex shapes (e.g., Barlow, 1972; Tanaka, Saito, Fukada, & Moriya, 1991; cf. base groupings, Roelfsema, 2006). The templates are constantly matched with the incoming visual information. This process of template matching or searching for a set of key features to recognize an occluded object or shape (establish *analogies*, Bar, 2007) can be described in terms of computational modeling (e.g., Ullmann, 1992; Ying & Castañon, 2002) and does also apply to self-splitting objects.

Specifically with respect to response priming, participants generally establish *action triggers* depending on task instructions (e.g., "respond to the upward oriented triangle") that tie specific stimuli or features to specific responses (*action trigger account,* Kiesel et al., 2007). As a result, the template of a task-relevant stimulus is directly linked to the execution of the visuomotor task. If one of the stored templates is task-relevant and a sufficient number of its key features matches the visual input, that input is used immediately to guide visuomotor processing (i.e., within the first feedforward processing phase).

For a more general discussion on the extent and limits of grouping in fast visuomotor processing see Sections 5.3.3. and 5.3.4.

4.3.4 Implications for Good Gestalt

But what do our results tell us about the law of Good Gestalt? We are convinced that our findings provide evidence that the implementation of Good Gestalt is not based on feedforward processing. The criteria of the rapid-chase theory are fulfilled only for self-splitting objects with one occluder, a case in which the visuomotor response can be based on activation of groups of specific feature detectors. The law of Good Gestalt is more general and implies that all self-splitting objects "split" into shapes that are as simple, regular, and as well-structured as possible. Therefore, it should also apply to primes with more than one occluder. As the pattern of priming effects show, these primes indeed are "split" into their components within the phase of rapid visuomotor processing but this occurs more slowly compared to primes with one occluder and is not consistent with a feedforward account. Thus, with two or three occluders recurrent processing is necessary to "split" the self-splitting objects into their components. Note that this is the case although our experimental paradigm is relatively restricted (e.g., by presenting primes at fixed spatial positions). Our findings therefore suggest that Good Gestalt is based on recurrent processing.

4.3.5 Conclusion

By employing outline contour stimuli and filled contour stimuli (self-splitting objects) in a primed flanker task, we showed that both are processed rapidly in accord with a simple feedforward processing account (i.e., with the rapid-chase theory, Schmidt et al., 2006). In the case of self-splitting objects, the feedforward processing was limited to configurations with only one occluder – more occluders eliminated the typical increase of response priming effects with SOA, therefore violating an important prediction from rapid-chase theory. We conclude that the implementation of the law of Good Gestalt is relatively fast (given that the Good Gestalten are task relevant, cf. Kiesel et al., 2007) but based on recurrent processing.

5. General Discussion

5.1 Thesis: Aims and Scope

Perceptual grouping is one of the fundamental processes in visual perception. Because grouping determines which elements of the visual field are perceived as belonging together, it is an integral part of object recognition. Although the field of perceptual grouping has a long tradition of research (e.g., Koffka, 1935; Wagemans, 1923), a number of basic questions are remaining unsolved (for a review see Wagemans, Elder et al., 2012). Most prominently, the grouping principles that describe the heuristics according to which elements are grouped are still the focus of intense research and debate.

In my thesis, I used a new behavioral method to investigate and compare a number of grouping principles and to draw conclusions about their processing characteristics and physiological mechanisms. Because our visual percept changes rapidly over time, it is essential to consider the time course of any perceptual process when investigating it (Hegdé, 2008). The changes that occur in time provide valuable information: for example, by comparing temporally early and late phases of visual processing it is possible to draw conclusions about which type of neuronal processing is involved (Schmidt, Haberkamp, Veltkamp et al., 2011; van Zoest, Hunt, & Kingstone, 2010). I investigated these changes by establishing the primed flanker task as an objective measure of perceptual grouping. Specifically, I identified and compared the temporal processing dynamics of a number of grouping cues (i.e., similarity by brightness, shape, and size; symmetry and closure; Good Gestalt).

In the primed flanker task, a participant reacts to one of two simultaneously presented targets as quickly and accurately as possible. The two targets are presented in the left and right periphery and the participant presses a left or right button depending on the position of the target with a predefined characteristic. Targets are preceded by two primes to the left and right of the central fixation that are either consistent or inconsistent with respect to the task-relevant characteristic.

The task is designed against the background of two theoretical accounts: the incremental grouping theory (e.g., Roelfsema, 2006) and the rapid-chase theory (e.g., Schmidt et al., 2006), that complement each other. Both theories are based on the concept of two radically different phases of visual processing: a rapid feedforward process where visual activation proceeds in bottom-up direction through the visual system, and a slower, recurrent process developing in the immediate wake of this fast feedforward sweep (Lamme & Roelfsema, 2000; Schmidt, Haberkamp, Veltkamp et al., 2011). The incremental grouping theory uses this concept to further explain and understand processes of perceptual grouping while the rapid-chase theory defines behavioral criteria to distinguish between the two phases of processing.

The incremental grouping theory introduces a distinction between parallel, local (base) grouping implemented by feedforward processing and serial (incremental) grouping implemented by recurrent processing. This distinction has led to an improved understanding of the processes underlying perceptual grouping. It makes the claim that it might be as important to know *when* grouping principles are implemented (e.g., by feedforward or recurrent processing, cf. Roelfsema, 2006) as *where* they are implemented (e.g., in what areas of the visual cortex, cf. Sasaki, 2007). This *when* of visual processing can be investigated by behavioral methods through application of the rapid-chase theory. The theory provides stringent behavioral (rapid-chase) criteria for pointing or keypress responses to decide whether two successive visuomotor stimuli are processed strictly sequentially or not: (1) prime rather than target signals should determine the onset and initial direction of the response (*initiation criterion*); (2) target signals should influence the response before it is completed (*takeover criterion*); (3) movement kinematics should initially depend only on prime characteristics and be independent of all target characteristics (*independence criterion*). In keypress responses, priming effects should increase with SOA (Vorberg et al., 2003) and should be at least as large in fast responses as in slower responses (Seydell-Greenwald & Schmidt, 2012). Importantly, strictly sequential processing in terms of the theory would be expected if the two stimulus signals are implemented by feedforward activation. Thus, the rapid-chase theory can be used to decide on the basis of behavioral findings whether a visual process (e.g., perceptual grouping) is in accordance with neuronal feedforward or recurrent processing.

I combined both theories by testing whether the visuomotor processing dynamics of different grouping principles as measured in the primed flanker task comply with the rapid-chase criteria. In other words, I applied the rapid-chase theory to perceptual grouping. This allows to draw conclusions about whether the grouping principles are implemented by base or incremental grouping processes.[21] In the following section, I summarize the experiments and major results of my thesis. Then, I discuss the implications of our results for the primed flanker task as a method, for the role of grouping strength, and for the understanding of base and incremental grouping. I link the incremental grouping theory to the related research field on fast categorization of natural and familiar objects. Then, I discuss the possibly intricate relationship between rapid-chase processes and base grouping, and evaluate two classical theories of grouping with respect to a temporally dynamic view of vision. Finally, I provide a glimpse into potential future studies and close by a conclusion.

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[21] Note that we studied different grouping principles, and that the research field of perceptual grouping is multifaceted. Thus, we decided not only to investigate processing dynamics of the grouping cues, but also other factors that, based on earlier studies, were assumed to modulate the processing of the cues (e.g., grouping strength).

5.2 Experiments: Results and Conclusions

5.2.1 Grouping by Brightness, Shape, and Size

In our first two experiments, we used the primed flanker task to compare different types of base groupings (Chapter 2). While the incremental grouping theory (Roelfsema & Houtkamp, 2011) makes a strong distinction between base grouping (parallel processing) and incremental grouping (serial processing), it does not provide a way to distinguish different grouping principles within these two categories. However, it has been shown that grouping principles are different. Namely some forms of grouping and segmentation take place early, rapidly, and effortlessly, whereas others occur later, consume time, and require controlled attentional processing (cf. Section 1.4). This should also be true for different principles within the base grouping category.

In the first experiment (Section 2.2), we asked participants to respond to the orientation of targets that were grouped horizontally or vertically by brightness or shape. Targets were preceded by primes with consistent or inconsistent orientation and primes and targets were grouped by either cue. A preceding scaling task measured the grouping strength of the cues in terms of each other (i.e., weaker brightness grouping, equal grouping strengths, stronger brightness grouping) for each participant. We found that while the grouping strength of the primes mainly determined the magnitude of the priming effects, grouping strength of the targets mainly determined the overall response times. In addition, shape primes produced larger priming effects even when the subjective grouping strength of both cues was equalized. Only when the grouping strength of the brightness primes was further increased did they lead to priming effects of similar magnitude as those induced by shape primes.

In the second experiment (Section 2.3), we contrasted the grouping cues of brightness and size and replicated the role of prime and target grouping strength on priming effects and response times, respectively. However, there was no difference between priming effects based on whether the prime stimuli were grouped by size or by brightness.

We used these two experiments to establish the primed flanker task as a new objective measure to compare base grouping cues in terms of their impact on fast visuomotor processing. Two conclusions can be drawn from these experiments. First, grouping strength strongly modulates the extent to which a grouping cue influences speeded visuomotor processing. Second, even with the subjective grouping strength equalized, grouping by shape still has a stronger impact on rapid visuomotor processes than grouping by brightness. This suggests that different base groupings show some variation in their processing characteristics although they all are supposed to rely on feedforward activation (Roelfsema & Houtkamp, 2011). In a next step, we investigated more complex grouping principles that may be implemented by incremental grouping processes (i.e., by recurrent processing).

5.2.2 Grouping by Symmetry and Closure

In the next three experiments, we used the primed flanker task to investigate the processing of symmetry and closure (Chapter 3). These cues are remarkable because they are relatively complex, that is, they are defined by the spatial relationships between their multiple stimulus components. For example, to decide whether a shape is symmetric, the shape has to be transformed geometrically, (i.e., reflected along the virtual mirror axis). In contrast, grouping by brightness, shape, and size can be obtained without the exhaustive processing of all components. Because of their complexity, the processing of symmetry and closure supposably involves recurrent activation. However, both cues also are readily available and do not seem to require a time-costly computation or recombination of stimulus components which is evidence for feedforward processing. In terms of the incremental grouping theory, it is therefore unclear whether symmetry and closure are base groupings or incremental groupings. Our primary aim was to collect data to resolve this inconsistency.[22] We also varied characteristics of the symmetry stimuli (i.e., the perceived line of view and the orientation of the symmetry axis) that have been shown to modulate symmetry processing, because we assumed that they would also play an important role in rapid visuomotor processing. Finally, by investigating the influence that the irrelevant cue had on the processing of the relevant cue, the task allowed us to make claims about the automaticity of symmetry and closure processing.

In the first experiment (Section 3.2), we asked participants in two primed flanker tasks to respond to the symmetry or closure of simple contour targets. Targets were preceded by primes that were consistent or inconsistent with respect to their symmetry or closure. We observed priming effects in response times and error rates for both grouping cues. By analyzing the response time distributions, we showed that these priming effects were fully developed in the earliest phases of visuomotor processing and did not increase in later phases. This pattern is consistent with a simple feedforward processing model as described by the rapid-chase theory.

In the second experiment (Section 3.3), we used the same task to investigate the role of axis orientation in symmetry processing and replicate the findings of the first experiment with a new stimulus set. We constructed stimuli with either a horizontal or a vertical axis. As in the first experiment, we observed priming effects for symmetry and closure and response time functions that were consistent with a

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[22] We refrained from directly comparing the two cues due to the difficulties in measuring the strength of grouping by symmetry and closure in terms of each other.

feedforward processing account. However, priming effects in the symmetry task did not increase with SOA, violating an important prediction of rapid-chase theory. The orientation of the symmetry axis had no influence on any of these results or on overall response times. Generally, overall response times were slower than in the first experiment.

In the third experiment (Section 3.4), we investigated whether there are any effects of the line of view on symmetry perception. To this end, we used as primes skewed stimuli based on the stimulus set of the second experiment. As in the second experiment, we varied the axis orientation though we did not include a closure task. In line with our previous findings, we observed priming effects that were fully developed in the earliest phases of visuomotor processing but did not increase with SOA. Neither the orientation of the symmetry axis nor the skewing had any influence on the size of the priming effects. Response times were also slower than in the first experiment.

Overall, we showed that closure processing is rapid and consistent with a simple feedforward model while symmetry processing only seems to fit that model if the task allows for fast responding (as in our first experiment). In contrast to a number of earlier studies (e.g., Wenderoth, 1994; Wenderoth & Welsh, 1998), the orientation of the axis did not affect symmetry processing. Furthermore, skewing of the primes did not modulate priming effects, suggesting some degree of viewpoint-invariance in the temporally early processing of symmetry. This finding is also in contrast to earlier studies that suggested skewing as detrimental to visual processing of symmetry (e.g., Wagemans, 1993). Finally, when participants responded to one of the two grouping cues, the other cue had no effect on the visuomotor response (i.e., neither cue was processed in an automatic fashion; for symmetry this result is at odds with those of previous studies). Based on these findings, we conclude that closure and possibly viewpoint-independent symmetry is processed in a feedforward fashion within a primed flanker task. This is relevant because it implies that both cues are processed by specialized neuronal pathways and can be extracted from images by the visual system early on as simple or primitive properties. In a final step, we decided to study a grouping principle that is most likely based on recurrent processing (i.e., incremental grouping).

5.2.3 Grouping by Good Gestalt

Finally, we used the primed flanker task to investigate the processing of Good Gestalt (Chapter 4). This cue is at the core of the ideas of the Gestalt school and subsumes a number of basic grouping principles. As symmetry and closure, the cue is relatively complex. Specifically, it requires the visual system to identify the most "simple" shape in the visual field. This task is especially challenging when other shapes occlude relevant features of that shape and as a consequence visual completion processes are thought to rely on feedback activation. Nevertheless, the visual system seems to manage this task well. Even when observers are confronted with shapes that are combined into a single object by superimposition, they typically promptly perceive a configuration of several distinct shapes.

In the experiment (Section 4.2), participants responded in a primed flanker task to the orientation of an upward or downward pointing triangle. Targets were preceded by primes that were consistent or inconsistent with respect to this orientation. We measured Good Gestalt by using as primes superimposed shapes that were either outline or filled contours each containing the target shapes. We also varied the number of occluding shapes (and, thereby, the amount of occlusion) to investigate the role of this factor in rapid visuomotor processing of Good Gestalt. We observed priming effects in both response times and error rates, suggesting that the visual system can separate superimposed shapes early on. These priming effects did not depend on the number of occluders when the primes and targets were outline contours, but decreased with the number of occluders when primes and targets were filled contours. In both cases priming effects were fully developed in the earliest phases of visuomotor processing, consistent with a simple feedforward processing account. However, priming effects with filled contours increased with SOA only with one occluder (but not with two or three occluders), violating a prediction of rapid-chase theory. It should be noted that at the same time responses were not slower compared to those with outline contours.

These results suggest that feedforward processing of occluded shapes is restricted to cases when the amount of occlusion is small (as a consequence of presenting outline contours or only one occluder). Thus, the implementation of Good Gestalt seems to be relatively fast but based on recurrent processing.

5.3 Primed Flanker Task: Scope and Implications

All our findings serve to establish the primed flanker task as a new objective measure for investigating processes of perceptual grouping. The task is designed against the background of the incremental grouping theory (e.g., Houtkamp & Roelfsema, 2010; Roelfsema & Houtkamp, 2011) and the rapid-chase theory (e.g., Schmidt et al., 2006). Specifically, it combines the focus on temporal processing dynamics of grouping principles that is provided by the incremental grouping theory with a behavioral approach to investigate these dynamics. Thus, it can be used to compare the temporal processing dynamics of different grouping principles and classify the principles based on the distinction between base and incremental grouping.

Earlier studies have tried to discover the processing mechanisms of different grouping cues by focusing on processing speed (e.g., for detection of symmetry, Barlow & Reeves, 1979; for detection of closure, Elder & Zucker, 1993). However, when distinguishing between feedforward and feedback processing, analyzing raw response times might not always be sufficient. Feedback activity as well as interactions between visual signals during processing can be rapid (Bullier, 2001, 2004; Roland, 2010; Sillito et al., 2006). For example, the visual ventral pathway (from the occipital cortex along the temporal lobe) that contains cells sensitive to information pertaining to object identity is divided into at least two sub-pathways: a fast magnocellular pathway for rapid analysis of motion and low frequency spatial information and a slow parvocellular pathway that conveys high frequency information (e.g., Nowak & Bullier, 1997). Because the waves of the feedforward activation in these two paths proceed with different speed, the first-arriving less detailed information might modulate the processing of the later-arriving detailed information through fast and local feedback loops (Fabre-Thorpe, 2011).[23] In addition, identifying processes that are mainly driven by feedforward processes based on raw response speed requires the comparison of the observed processing speed to the maximum processing speed of the system (Lamme & Roelfsema, 2000; e.g., by EEG methods, cf. Thorpe et al., 1996). Therefore, this approach can only identify feedforward processes that proceed with maximum or close to maximum speed. Feedforward processing in neuronal pathways with slower signal transmission is probably mistaken with recurrent processing. Finally, the grouping of similar features that is part of incremental grouping might be faster than suggested by the incremental grouping theory (e.g., as a result of neuronal synchronization, van der Helm, 2012).

The limitations of interpreting raw speed are also evident in our results. I interpreted priming effects in the fastest responses as clear indicators of rapid processing. Because these effects did not decrease in slower responses, the findings are also corresponding with the behavioral criteria of the rapid-chase theory (Section 1.6; Schmidt et al., 2006). However, in some instances we found that although the response speed was consistent with feedforward processing, the priming effects failed to increase with prime-target SOA (Sections 3.3., 3.4, and 4.2). This violates the prediction of rapid-chase theory that the influence of the prime signal on motor responses should increase with increasing time before the arrival of the target signal (i.e., increasing SOA). Only by considering both criteria (response speed and modulation of priming effects by SOA) can the visual processing, for example, of a grouping cue, be said to be indistinguishable from pure feedforward processing.

But why do we need a task that helps to classify grouping principles into base and incremental groupings? The classification proposed by the incremental grouping theory has the following main advantages. First, it links different grouping principles

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[23] However, these local feedback loops can most probably not account for integration of information over a large area because local connections within a visual area are much slower than feedforward or feedback connections between areas (Girard, Hupé, & Bullier, 2001).

to specific types of neuronal processing and, thereby, links the descriptive findings of the Gestalt School to those of contemporary neuroscience. Second, it reduces the complexity in the field of perceptual grouping research by providing a common framework for the plethora of empirical findings. For example, by tying incremental grouping to attentive processing and base grouping to preattentive processing, it provides a new approach to whether grouping depends on visual attention or not (cf. Kimchi & Razpurker-Apfeld, 2004). The primed flanker task is useful for distinguishing between base and incremental grouping on the grounds of easy-to-collect behavioral data (Chapters 3 and 4). Furthermore, the results of the task provide insights beyond that simple distinction in at least two ways. These will be detailed in the following two sections.

5.3.1 Comparing Different Base Groupings

The primed flanker task allows to contrast different grouping principles even when they are all base groupings. Thus, the results of the task are able to shed light on the relative efficiencies of the neuronal feedforward pathways by which different base groupings are implemented. This is important because base groupings occur at the earliest stages of object perception; together they specify the perceptual units for subsequent visual processing. The incremental grouping theory emphasized the dichotomy of base and incremental grouping at the cost of potentially overlooking these important differences between base groupings.

Indeed, we found that grouping by shape and by brightness differ in the efficiency with which they drive response priming effects (Chapter 2). Both are base groupings which, according to the incremental grouping theory, are implemented by multi-feature detectors during an initial feedforward sweep. The speed and efficiency of these feature detectors, as well as that of the processing pathways within the visual system, is different for different features. There is a large number of neurons tuned to different features or feature conjunctions (e.g., Hegdé & van Essen, 2007; Tanaka, 1996) as well as different visual processing pathways (e.g., Chen et al., 2007; Merigan & Maunsell, 1993) whose speeds are determined by neurophysiological constraints (cf. Nowak & Bullier, 1997). As a consequence, there is no single feedforward sweep but multiple parallel sweeps that operate at different speeds (Lamme & Roelfsema, 2000). While they all proceed rapidly and are mainly determined by feedforward connections, they can still be discerned through behavioral measures. In other words, while all base grouping cues are processed with remarkable speed, they still can be distinguished on the basis of results obtained in paradigms such as the primed flanker task.

5.3.2 Defining the Role of Grouping Strength

The primed flanker task can also be used to test whether there are factors that alter the processing mode of a specific grouping principle. For example, based on previous studies we expected that a change in the orientation of the symmetry axis might preclude feedforward processing of symmetry. Indeed, we found that one dominant factor modulated the processing dynamics of all the investigated cues, namely, grouping strength. This is most obvious in our results on grouping by brightness, shape, and size (Chapter 2). The relative grouping strengths of primes and targets strongly influenced objective measures (response times, error rates, and priming effects), in support of earlier studies (e.g., Han & Humphreys, 1999; Kimchi, 2000). Likewise, the implementation of Good Gestalt was dependent on that factor (Chapter 4). When we presented filled contours and added occluders, we effectively reduced grouping strength by reducing the available features that the law of Good Gestalt is based on. This precluded feedforward processing, again implying that grouping was only in accordance with a feedforward processing account when the grouping strength was strong enough. In our experiments on closure and symmetry processing, the role of grouping strength is somewhat difficult to evaluate because we did not manipulate it directly (Chapter 3). However, we found that the processing of closure was generally in accord with a feedforward account while symmetry processing was consistent with such an account only in the first but not in the two follow-up experiments.

These latter findings illustrate an important characteristic of grouping strength. Specifically, the perceptual strength of a stimulus depend on its similarity with its neighbors. For example, in visual search experiments, the speed of participants in locating a target within a group of distractors strongly decreases with increasing similarity of target and distractor features (e.g., Duncan & Humphreys, 1989). Similarly, in experiments on perceptual grouping the factor grouping strength is a relative measure that depends on stimulus features in interaction with the stimulus context (cf. Experiment 2 in Houtkamp & Roelfsema, 2010). In line with this, the irregular stimuli in the first symmetry experiment shared less features than the regular stimuli in the two follow-up experiments.

Note that our principal results on grouping strength (i.e., the boosting effects of grouping strength on response times and priming effects) are in accordance with predictions of the accumulator model by Vorberg et al. (2003). As described before, the model assumes that a prime consistent with a subsequent target activates the correct response ahead of the target. An inconsistent prime, on the other hand, leads to an activation of the incorrect response that needs to be counteracted by the target. The actual motor response results from an integration of information by two mutually inhibiting accumulators that each vote for one of the two motor responses (e.g., "right button" vs. "left button") which are fed by the prime and the target. The stronger prime and target signals are, the stronger they are driving the respective accumulator. Thus, the model makes specific predictions for the role of perceptual strength of primes and targets: stronger prime signals augment priming effects by deepening the response conflict, while stronger target signals speed the overall response times. Although there are some examples for successful applications of the model when primes and targets were of equal perceptual strength (Krüger, Klapötke, Bode, & Mattler, 2013; Mattler & Palmer, 2012; Vorberg et al., 2003), studies seldomly varied both prime and target strength directly. In one exemplary response priming study, Vath and Schmidt (2007) used primes and targets with low and high color saturation, respectively. In line with the predictions of the accumulator model, they found that priming effects increased with prime saturation and response times sped up with target saturation.[24] In sum, these findings and the model predictions correspond to our experimental findings.

Another implication of our findings is that the strong dichotomy of base and incremental grouping is called into question (this concern is shared by other scholars, e.g., Peter van der Helm, personal communication). In the following section, I will further discuss this issue.

5.3.3 Base and Incremental Grouping on a Continuum

First, on grounds of our observations regarding grouping strength I propose (in addition to the model predictions by Vorberg et al., 2003) that strong prime and target signals are likely to be transmitted by feedforward sweeps while weaker signals may elicit additional feedback activation. Thus, it might not only be the speed of the feedforward sweep that depends on stimulus variables such as contrast (Lamme & Roelfsema, 2000) but these variables might also change the type of processing itself. For example, it might not be possible to discern the relevant stimulus from the background or other stimuli in the visual field based on feedforward activation only. In a more general sense this indicates that a base grouping process might turn into something more like an incremental grouping process and vice versa depending on stimulus and context factors.

Second, the strict dichotomy between base and incremental grouping can be challenged on other grounds. Namely, incremental grouping might turn into base grouping through processes of perceptual learning (this is also acknowledged by Houtkamp & Roelfsema, 2011). Baker, Behrmann, and Olson (2002) found that after training, neurons in monkey inferotemporal cortex became selective for specific shape conjunctions (while before training they were selective only for the single shapes; also

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[24] Note that the authors observed the strongest priming effects with a high saturation of both prime and target, a finding that we will not further discuss because this condition is not comparable to any in our experiments.

see Li, Piech, & Gilbert, 2009). This finding suggests that incremental grouping might become base grouping given sufficient perceptual experience with a grouping constellation. This idea is consistent with those of other scholars which assume that grouping principles in general are not innate (as suggested by the Gestalt psychologists) but arise “from repeated experiences with environmental regularities and physical laws” (DiLollo, 2011, p. 37; Todorovic, 2011; for a review on perceptual grouping in infants see Bhatt & Quinn, 2011; for the role of selective attention in perceptual learning see Roelfsema, van Ooyen, & Watanabe, 2010; for a review on the related Bayesian approach to perceptual grouping see Wagemans, Feldman et al., 2012).

This perceptual learning approach to grouping is also validated by base grouping of complex stimuli which is possible only in cases when observers had long-term experience with those stimuli (e.g., human faces, Tsao & Livingstone, 2008; Crouzet, Kirchner, & Thorpe, 2010; animals in natural scenes, Thorpe et al., 1996). For example, Thorpe et al. (1996) measured lateralized readiness potentials in participants that distinguished between natural scenes with and without animals. Importantly, the authors reported differential potentials between both types of scenes that developed from 150 ms after stimulus onset. These rapid categorization processes are typically explained in terms of feedforward processing within a hierarchy of increasingly complex feature detectors (e.g., VanRullen & Thorpe, 2001). This is supported by findings that these processes are independent of the position of the animal in the visual field (Drewes, Trommershäuser, & Gegenfurtner, 2011) and are not abolished by controlling for low-level differences in the images (New, Cosmides, & Tooby, 2007).

5.3.4 Lessons from Hardwired Binding: Feedforward Pathways and Context Dependency

With respect to the recognition of natural and familiar objects (or scenes), VanRullen (2009) proposed a distinction between two possible processing modes that has striking similarity to that between base and incremental grouping. The author distinguishes between two types of binding (i.e., of the process that is part of perceptual grouping and determines which particular elements of the visual field will be perceived together): (1) *hardwired binding* of frequently encountered, natural objects that is feedforward and not relying on attention, and (2) *on-demand binding* for more arbitrary or meaningless feature conjunctions that depends on feedback and is mediated by attention (VanRullen, 2009). Thus, hardwired and on-demand binding on one side and base and incremental grouping on the other side are different conceptualizations of the same basic processes in visual cognition. Combining the insights from both these theoretical frameworks can contribute to the understanding of the flexible nature of perceptual grouping.

First, the incremental grouping theory states that base grouping is implemented by the activation of cardinal cells or multi-feature detectors but does not take a strong position on how this activation is achieved. There are different notions about the type of *neural coding* by which the information is transmitted in visual processing hierarchies. However, because the first feedforward wave is based on neurons that fire at most a single *spike* (i.e., an action potential) before the next level of the hierarchy is activated (Lamme & Roelfsema, 2000), rapid processing can for example not be based on coding of neuronal firing rates (cf. Gautrais & Thorpe, 1998). In the context of hardwired binding, different modes of neural coding were compared in modeling studies in artificial networks. Interestingly, it was shown that most of the stimulus-relevant information could be extracted from the temporal distribution of the very first spikes in the feedforward wavefront (e.g., Gollisch & Meister, 2008; Guyonneau, VanRullen, & Thorpe, 2004; Serre, Oliva, & Poggio, 2007) and that this *spike-timing-dependent plasticity* (STDP) can be shaped by learning processes (Guyonneau, VanRullen, & Thorpe, 2005; Masquelier, Guyonneau, & Thorpe, 2009). This richness in information in STDP and its susceptibility to perceptual learning makes it a likely candidate for the neural coding involved in base grouping.

Second, the incremental grouping theory does not detail the characteristics of the feedforward pathways that are activated in base grouping. For example, Schmidt and Schmidt (2009) presented natural images of animals and objects in a response priming paradigm. In one task, participants were instructed to identify the target image containing an animal (or object). In another task, participants were instructed to identify the target containing a small (or large) animal/object. Only in the first task, the time course of the priming effects in pointing responses was in accordance with a feedforward processing account (Schmidt & Schmidt, 2009). This suggests that the multi-feature detectors that categorize animals and objects are part of a feedforward visuomotor processing pathway but those that categorize large and small are not. The research on processing of natural images in categorization tasks offers some background for this finding (for a review see Fabre-Thorpe, 2011). Generally, stimuli can be categorized on a superordinate level (an animal, a vehicle), a basic level (a bird, a farm vehicle), or on a subordinate level (a robin, a tractor). Interestingly, research on the rapid categorization of natural images (i.e., on hardwired binding) shows that superordinate object or scene categories are rapidly available, suggesting feedforward processing, and are faster than the more detailed basic representations (Grill-Spector & Kanwisher, 2005; Macé, Joubert, Nespoulous, & Fabre-Thorpe, 2009). At the same time, basic representations can be activated without the need of focused attention (Poncet, Reddy, & Fabre-Thorpe, 2012), suggesting that they are also coded as base groupings but using feedforward pathways that are slower than that for superordinate categorizations. However, on the subordinate level, feedforward processing is normally not found any more.[25] In other words, while base grouping can rapidly group together all stimuli that are identified by specialized multi-feature detectors (i.e., a robin or a tractor), the speed of their visuomotor processing depends on the task: Rapid motor responses only occur in those tasks where base grouping meets an established visuomotor feedforward response pathway (cf. Haberkamp, Schmidt, & Schmidt, 2013).

Indeed, it is likely that superordinate categorizations are so fast because they can be based on the coarse magnocellular information of the fast ventral pathway (Fei-Fei, Iyer, Koch, & Perona, 2007).[26] Because the resulting stimulus representations are relatively coarse, the knowledge about the object is critical. The more detailed and substantial it is, the faster the categorizations. In neurophysiological terms, this might be achieved by facilitation of low-level feature grouping by feedback projections from higher, object-selective visual cortex (Jeurissen, Self, & Roelfsema, 2013). The critical defining object features that enable rapid categorizations can be discovered experimentally: the performance in categorization tasks with animals in natural images depends on whether the animal is in a canonical posture, on its relative size within the image, and on the presence of diagnostic animal features (Delorme, Richard, & Fabre-Thorpe, 2010). In terms of the incremental grouping theory, that means that a task has to rely on incremental grouping given two conditions. First, it has to depend on successful parsing of natural images into different objects (by combining low-level and high-level features that belong to one perceptual object, Korjoukov et al., 2012). Second, it cannot be solved by a correspondence of existing object knowledge and coarse stimulus representations (Korjoukov et al., 2012). With respect to the findings by Schmidt and Schmidt (2009) this suggests that the categorization of large vs. small does rely on high-level information (e.g., because the decision boundary is inherently relative) that is not part of a specific object template and thus not part of a feedforward processing pathway.[27]

Another relevant finding with respect to the processing of natural images is the dependency of even the earliest motor responses on high-level context. Joubert, Fize,

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[25] However, these effects are also subject to influences of perceptual learning. For example, car experts show an early availability of subordinate categorizations of cars (Curby & Gauthier, 2009). From this follows that even categorizations on subordinate levels can be implemented by feedforward processing when the respective pathways are established by experience.

[26] Though note that these categorizations are not based on the analysis of simple image statistics (i.e., the relative amount of high spatial-frequency energy in the vertical and horizontal orientation, Wichmann, Drewes, Roas, & Gegenfurtner, 2010).

[27] Interestingly, Bacon-Macé, Kirchner, Fabre-Thorpe, and Thorpe (2007) found that the earliest phase of motor responses do not depend on whether participants answer to natural images in a categorization task or in a discrimination task (i.e., deciding which of two simultaneously presented images contains an animal). This indicates that both tasks are based on feedforward processing.

Rousselet, and Fabre-Thorpe (2008) asked their participants in a categorization task to respond to the presence of animals in natural (congruent) or urban (incongruent) contexts. They found that even in the earliest phase of the behavioral responses, performance depended on context congruency. The authors argue for a model in which the neuronal populations of the ventral stream that respond selectively to animals co-activate other neuronal populations. Specifically, these other populations are those that are activated by stimuli usually occurring together with animals in our visual environment (i.e., neurons specific for natural contexts). This co-activation should facilitate responses. In contrast, when an animal is presented within an incongruent urban context, the respective neuronal populations of animal and context would compete for the motor response. This would result in an impediment of responses. This conflict might be present all along the visual stream due to bidirectional interactions between neuronal populations and could thus be part of the first feedforward phase of processing (Joubert et al., 2008). In terms of the incremental grouping theory this would imply that base grouping does not only depend on the object and the low-level features of its context but also on the information on a class of contexts irrespective of their different low-level features (e.g., the class of natural contexts).[28]

In sum, feedforward transmission of visuomotor responses does not only depend on base vs. incremental grouping of the respective stimuli but also on the available processing pathways. The type of neural coding in base grouping feedforward pathways is most probably temporal rather than rate coding (i.e., based on the temporal distribution of the first spikes in the wavefront and not on firing rates). Finally, incremental grouping and base grouping are not dichotomous classes of grouping but the high-ends of one continuum that can be transformed into another by processes of perceptual learning as well as stimulus and context factors.

Based on the latter insight that base and incremental grouping are located on a continuum, I discuss why the primed flanker task is particularly suited to study perceptual grouping in the framework of the incremental grouping theory.

5.4 Linking Rapid-Chase Theory and Base Grouping

In my thesis I argue for the primed flanker task as a new objective measure of perceptual grouping. A main feature of the task is its theoretical foundation in response priming and the rapid-chase theory. As a result, the task can be used to evaluate the role of feedforward and feedback activation in the processing of different grouping cues. But why is the fulfillment of the rapid-chase criteria a good indicator of base grouping? The evaluation of the criteria is based on behavioral output which

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[28] A related finding is the dependency of performance in categorization tasks on the type and number of distractor images (cf. Fabre-Thorpe, 2011).

is necessarily an indirect indicator for assessing the types of neuronal activation. In addition, even the fulfillment of the rapid-chase criteria does not guarantee that visual processing is strictly feedback-free (cf. Schmidt et al., 2006).

These objections can be met by considering the link between rapid-chase theory and base grouping more closely. Conceptually, rapid-chase processing is not necessarily equivalent to pure feedforward processing, but rather allows for feedback activity as long as prime and target signals are processed in strict sequence (Schmidt et al., 2006). There are two reasons why this does not limit the interpretation of our findings but rather highlight the primed flanker task as a useful method to investigate base and incremental grouping.

First, base and incremental grouping are not dichotomous but should instead be seen as located on a continuum (see Section 5.4.3). The primed flanker task which is designed against the background of the rapid-chase theory can identify the relative positions of different grouping cues on this continuum by identifying their speed of processing as well as the level of feedback involvement. In other words, grouping cues can be compared regarding the necessity of feedback during visual processing without artificially categorizing the cues into base and incremental groupings.

Second, there is no conclusive evidence that base grouping is implemented by pure feedforward activation. Although there are many studies supporting the view of a temporally efficient process which is based mainly on feedforward activation, evidence for the total lack of feedback in this process is hard to obtain. This is true even for the most up-to-date methods that have been used to investigate neural responses to pathfinder tasks in monkeys. On the one hand, single-cell recordings are temporally very accurate but cannot be used to measure interactions between neurons or to map complete feedforward pathways (e.g., Roelfsema et al., 2004). On the other hand, blocking the different neurotransmitters that are supposedly involved in the transmission of feedforward and feedback signals to selectively suppress feedforward or feedback signals (Self et al., 2012; van Kerkoerle et al., 2009) is limited as well by (1) the area investigated, typically V1 only, (2) the selectivity of the laminar structure and (3) the selectivity of the blockers used. Thus, given the speed of some feedback processes, rapid-chase systems with their possibility of minimal feedback might be a more realistic model for base grouping than the implementation of base grouping by pure feedforward activation.

5.5 Reevaluating Classical Theories of Perceptual Grouping

The focus on temporal processing dynamics that also provided the theoretical framework for my thesis is adopted by an increasing number of scholars in visual neuroscience (e.g., Hegdé, 2008; Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000; Schmidt, Haberkamp, Veltkamp et al., 2011; van Zoest et al., 2010). In the following, I illustrate the implications of this change in focus by contrasting the incremental grouping theory with two classical theories of perceptual grouping. Both, Palmer and Rock's (1994a, b) *process theory of perceptual organization* (Palmer, 2003) and the feature-integration theory (Treisman, 2006; Treisman & Gelade, 1980), have been influential approaches to explain perceptual grouping.

The process theory of perceptual organization (Palmer & Rock, 1994a, b) assumes that grouping is achieved by a sequence of processing steps. On a first level, the retinal image is partitioned into a number of non-overlapping regions, each defined by the uniformity of its features (e.g., color, luminance, or motion) (the so-called grouping principle of *uniform connectedness*). On a second level, contours are assigned to these regions, leading to figure-ground segregation. On a third level, the resulting *entry-level units* are subjected to grouping (*larger superordinate units*, wholes) and parsing operations (*smaller subordinate units*, parts). Thus, perceptual grouping principles act upon entry-level units resulting from preceding processes of uniform connectedness and figure-ground segregation. The order of the three levels was assumed to be stable, however, any level might activate the next level before its own completion. Also, higher levels might influence processing on lower levels through feedback (Palmer, 2003). As a consequence, the predictive power of the theory for empirical investigations has always been limited because processes in cascade with feedback "can only be used to predict the order in which processes begin, not necessarily the order in which they end" (Palmer & Rock, 1994b, p. 516). Additionally, later studies have been casting doubt on the exact order of the levels (especially with respect to figure-ground segregation, e.g., Palmer & Brooks, 2008; Peterson, 1994), culminating in the realization that grouping might occur at many different levels of visual processing (Palmer, 2003; Palmer et al., 2003). Also, the claim that uniform connectedness precedes any other grouping process turned out to be inconsistent with more recent findings (Han et al., 1999b; Kimchi, 1998, 2000). However, the most fundamental flaw in the theory is its indifference to the feedforward and feedback architecture of the visual system (i.e., to the temporal dynamics of processing). Indeed, any grouping process might either be related to the first, second, or third level of the theory depending on whether it relies on feedforward or feedback activation. This has also been acknowledged by the authors of the theory, although, they rather euphemistically frame this fundamental problem as "a difficult, but important, area for future research" (Palmer et al., 2003, p. 329). In sum, the process theory of perceptual organization is incompatible with recent findings and theoretical progress in perceptual grouping and is therefore no useful framework for the interpretation of our results.

The feature-integration theory (see Section 1.5; Treisman, 2006; Treisman & Gelade, 1980) assumes that grouping of low-level features in a visual scene occurs in parallel and without the need for attentional resources. In contrast, binding of feature conjunctions does not occur in parallel but is a serially working, attention-requiring, process. By this classification, the feature-integration theory much resembles the incremental grouping theory with its distinction between base and incremental grouping. However, there are also discrepancies between both theories that arise from their different perspectives on visual processing and the different empirical findings they are based on (Roelfsema & Houtkamp, 2011). According to the feature-integration theory, the metaphorical spotlight of spatial attention shifts between different locations and between object representations to bind object features. In contrast, the incremental grouping theory assumes that attention might adopt the shape of the relevant object (Duncan, 1984) and that this object-based attention might also spread within object representations. The latter is the case in our first set of experiments in which different elements within a single object are grouped together by similarity. Also, according to the original feature-integration theory, feature conjunctions can never be processed in parallel (but see Treisman, 2006). In contrast, the incremental grouping theory states that feature conjunctions at a single spatial location can be processed in parallel (Tanaka et al., 1991). This is illustrated in our experiments on symmetry and closure because both groupings arise from conjunctions of different object parts. Finally, the incremental grouping theory extends the feature-integration theory by linking the spread of attention to the spread of enhanced neuronal activity, thereby implicitly shifting the focus to the temporal aspects of visual processing. In sum, the feature-integration theory has been laying the foundations for modern theories on perceptual grouping; it has been extended and refined by the incremental grouping theory mainly by reconciling it with conflicting findings and linking it to neurophysiology.

As a next step, I point out future experiments that arise from my thesis and other implementations of the primed flanker task.

5.6 Future Studies

All of the experiments discussed in my thesis lend themselves to follow-up studies. Most straightforward, the experiments might be replicated by using pointing trajectories or force responses, or by additionally collecting electrophysiological measures, to link the results even more strongly to underlying motor processes (cf. Schmidt et al., 2006). However, more interesting would be controlled variations in experimental parameters to further illuminate the processing mechanisms of the investigated grouping cues. While the experiments on grouping by similarity (brightness, shape, and size) may be refined mainly with respect to methodology, our findings on grouping by symmetry, closure, and Good Gestalt are an excellent starting point for further empirical investigations.

First, our experiments on symmetry and closure processing paved the way for more extensive investigations with the primed flanker paradigm. Infinite stimulus sets of random polygonal shapes (e.g., Wagemans, 1993) as well as controlled changes in grouping strength and other stimulus parameters can further elucidate the characteristics of feedforward processing of both cues. For example, grouping strength might be varied by directly varying the amount of closure (by changes in the size of gap in the closed contour, e.g., Elder & Zucker, 1993) or symmetry (e.g., Barlow & Reeves, 1979). In closure processing, futures studies might investigate the role of curvature (Mathes & Fahle, 2007) while in symmetry processing they might focus on other types of symmetry (e.g., translational symmetry, Treder & van der Helm, 2007) or on a wider range of symmetry axes and skewing angles (e.g., Wagemans et al., 1991). Our experiments were a first attempt to specify the extent and limits of early symmetry and closure processing; by detailing these, it will be possible to extend current (specifically symmetry) models by this early processing component.

Second, our experiments on the processing of Good Gestalt with self-splitting objects established a new objective measure for this grouping principle. This might allow for a stricter formalization of the principle. Also, by varying the strength of different grouping cues within self-splitting objects (e.g., connectedness or good continuation of edges and contours) it might be possible to identify the cues' respective weights in the emergence of Good Gestalt.

Finally and more generally, the primed flanker task can be employed to investigate the temporal processing dynamics of other visual phenomena. For example, we already obtained promising results in the field of visual illusions. When participants respond to targets of different size that are preceded by primes rendered smaller or larger by a visual illusion, the obtained priming effects are changing qualitatively over the time course of processing (e.g., Weber, Noé, Hoffmann, Schmidt, & Schmidt, 2012). These findings are challenging a number of current explanations on the source of this visual illusion. Generally, there is an increasing awareness that many visual phenomena, including fundamental ones, may be inadequately understood because their processing time course is not known (e.g., stimulus saliency, Donk & van Zoest, 2008). Response priming, and specifically the primed flanker paradigm, provides an experimental approach to address this problem (Schmidt, Haberkamp, Veltkamp et al., 2011).

5.7 Summary and Conclusion

Perceptual grouping is an integral part of visual object recognition. In my thesis, I investigated the mechanisms of different principles of perceptual grouping. Based on recent studies and theoretical considerations, I argue that the research on perceptual grouping can strongly benefit from a focus on the temporal dynamics of the grouping processes. I presented the primed flanker task that is based on the incremental grouping theory (e.g., Houtkamp & Roelfsema, 2010; Roelfsema & Houtkamp, 2011) and the rapid-chase theory (e.g., Schmidt et al., 2006) to specifically investigate and compare the temporal processing dynamics of different grouping principles. The findings of my thesis show that the task produces valuable insights into the mechanisms of different principles of perceptual grouping, thereby contributing to our better understanding of these integral components of visual perception.

While the primed flanker task turned out to be suited to disclose the processing dynamics of the investigated grouping principles, our results provide only equivocal evidence for a strict dichotomy of base and incremental grouping. I argue that any grouping principle might be a base grouping given that the initial feedforward sweep of activation carries information that is rich enough to meet the perceptual demands of the task at hand. Only if this first representation of the visual scene is not detailed or specific enough to complete the task, the response has to rely on more elaborate, recurrent, top-down processes (cf. Ahissar & Hochstein, 2004; Bar, 2007; Hochstein & Ahissar, 2002). This suggests that the distinction between base and incremental grouping is not necessarily a distinction between different classes of grouping principles but merely between different types of processing across principles.

Although we found that some grouping principles might be too complex in general to be implemented by base groupings (i.e., Good Gestalt, see Section 4.3), our findings also illustrate that feedforward vs. feedback processes did depend less on the investigated principle than on grouping strength or other factors.[29] This implies that it might not be possible to define a grouping principle per se as base or incremental grouping but the necessity of attentional or recurrent processing follows from these factors together with the grouping cue at hand. By the way, these results also cast serious doubt on research that is investigating differences between grouping principles without any extensive control of grouping strength (e.g., Ben-Av & Sagi, 1995; Razpurker-Apfeld & Kimchi, 2007; Quinlan & Wilton, 1998). With respect to the incremental grouping theory, our findings suggest that the theory does not acknowledge all major factors playing a role in the grouping process (although perceptual learning has recently been integrated in the framework, Roelfsema & Houtkamp, 2011). At the same time, the theory is a major accomplishment with respect to the neurophysiology of grouping and to the awareness for temporal processing dynamics in grouping.

This latter change in focus on temporal aspects might have even more implications than considered by the incremental grouping theory. The theory refers to a macro level of description by identifying classes of grouping cues that are either processed in a feedforward or feedback manner. However, on a micro level of description, as a consequence of temporal processing dynamics the representation of a

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[29] This is even true for pathfinder tasks that were used to investigate incremental grouping (e.g., Houtkamp & Roelfsema, 2010; Roelfsema & Houtkamp, 2011): when the target elements in those tasks are aligned collinearly, they can appear to pop-out of the background elements (which suggests base grouping, Field, Hayes, & Hess, 1993).

visual stimulus changes over time. Thus, the behavioral response towards a stimulus does not only depend on its physical properties, the current task, or attributes of the participant, but also on the time at which the stimulus representation is accessed. In other words, performance depends on the particular point in time behavior is measured (van Zoest et al., 2010). For example, faster responses might be based on different stimulus representations than slower ones. Thus, to obtain a complete picture of the grouping process it might not be enough to differentiate between grouping cues that are processed mostly in a feedforward or feedback manner. Rather, the effectiveness of a grouping cue has to be evaluated over time (e.g., by analyzing response time functions). This is especially important when comparing different grouping cues.

Thus, the insights provided by a change in focus on temporal processing dynamics might imply that the field of perceptual grouping research has to be restructured around the question *when* perceptual grouping happens. This puts a number of classical theories into peril. The incremental grouping theory is a first step to a new understanding of grouping, however, not the end of it (for more generalized approaches to visual perception focusing on temporal processing dynamics see Ahissar & Hochstein, 2004; Bar, 2007; Hochstein & Ahissar, 2002). In every task designed to measure any visual phenomenon, it has to be acknowledged that time is a critical variable. Time may change the visual percept and, consequently, the obtained behavior quantitatively and qualitatively even when the stimulus is physically the same. Because of these far-reaching implications, the new focus on temporal processing dynamics has the potential to lead to a revolution in the study of visual processing. It might turn out, that it is much more important to know *when* something happens (and based on which type of neuronal processing) than *where* in the brain it happens. Importantly, this would be true not only for visual epiphenomena but for the fundamentals of visual processing such as perceptual grouping.

References

Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in cognitive sciences*, *8*, 457–464.

Alais, D., Blake, R., & Lee, S. H. (1998). Visual features that vary together over time group together over space. Nature Neuroscience, 1, 160–164.

Anderson, B. L. (2007a). The demise of the identity hypothesis, and the insufficiency and non-necessity of contour relatability in predicting object interpolation: Comment on Kellman, Garrigan, & Shipley (2005). *Psychological Review, 144,* 470–487.

Anderson, B. L. (2007b). Filling-in theories of completion: Rejoinder to Kellman, Garrigan, Shipley, and Keane (2007) and Albert (2007). *Psychological Review, 114,* 509–527.

Anderson, B. L. (2007c). Postscript: Filling in models of completion. *Psychological Review, 117,* 525–527.

Arrington, K. F. (1994). The temporal dynamics of brightness filling-in. *Vision Research, 34,* 3371–3387.

Ash, M. G. (1995). *Gestalt psychology in German culture, 1890–1967: Holism and the quest for objectivity.* Cambridge, MA: Cambridge University Press.

Attneave, F. (1954). Some informational aspects of visual perception. *Psychological Review, 61,* 183–193.

Bacon-Macé, N., Kirchner, H., Fabre-Thorpe, M., & Thorpe, S. J. (2007). Effects of task requirements on rapid natural scene processing: from common sensory encoding to distinct decisional mechanisms. *Journal of Experimental Psychology: Human Perception and Performance*, *33*(5), 1013–1026.

Bahnsen, P. (1928). Eine Untersuchung über Symmetrie und Asymmetrie bei visuellen Wahrnehmungen. *Zeitschrift für Psychologie, 108,* 129–154.

Baker, C. I., Behrmann, M., & Olson, C. R. (2002). Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Nature Neuroscience, 5,* 1210–1216.

Bar, M. (2007). The proactive brain: using analogies and associations to generate predictions. *Trends in cognitive sciences*, *11*, 280–289.

Barlow, H. B. (1972). Single units and sensation: a neuron doctrine for perceptual psychology. *Perception, 1,* 371–394.

Barlow, H. B., & Reeves, B. C. (1979). The versatility and absolute efficiency of detecting mirror symmetry in random dot displays. *Vision Research, 19,* 783–79.

Bauer, R., & Heinze, S. (2002). Contour integration in striate cortex. Classic cell responses or cooperative selection? *Experimental Brain Research, 147,* 145–152.

Baylis, C. G., & Driver, J. (1994). Parallel computation of symmetry but not repetition within visual shapes. *Visual Cognition, 1,* 377–400.

Beck, D. M., & Palmer, S. E. (2002). Top-down influences on perceptual grouping. *Journal of Experimental Psychology: Human Perception & Performance, 28,* 1071–1084.

Behrmann, M., & Kimchi, R. (2003). What does visual agnosia tell us about perceptual organization and its relationship to object perception? *Journal of Experimental Psychology: Human Perception & Performance, 29,* 19–42.

Ben-Av, M. B., & Sagi, D. (1995). Perceptual grouping by similarity and proximity: Experimental results can be predicted by intensity autocorrelations. *Vision Research, 35,* 853–866.

Bertamini, M. (2010). Sensitivity to reflection and translation is modulated by objectness. *Perception, 39,* 27–40.

Bhatt, R. S., & Quinn, P. C. (2011). How does learning impact development in infancy? The case of perceptual organization. *Infancy, 16,* 2–38.

Breitmeyer, B. G., Kafalıgönül, H., Öğmen, H., Mardon, L., Todd, S., & Ziegler, R. (2006). Meta- and paracontrast reveal differences between contour and brightness-processing mechanisms. *Vision Research, 46,* 2645–2658.

Bruno, N., Bertamini, M., & Domini, F. (1997). Amodal completion of partly occluded surfaces: Is there a mosaic stage? *Journal of Experimental Psychology: Human Perception & Performance, 23,* 1412–1426.

Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews, 36,* 96–107.

Bullier, J. (2004). Communications between cortical areas of the visual system. In L. M. Chalupa, & J. S. Werner (Eds.), *The Visual Neurosciences, Vol. 1* (pp. 522–540). Cambridge, MA: MIT Press.

Carmody, D. P., Nodine, C. F., & Locher, P. J. (1977). Global detection of symmetry. *Perceptual and Motor Skills, 45,* 1267–1273.

Cavanagh, P. (2011). Visual cognition. *Vision Research, 51,* 1538–1551.

Chen, C. M., Lakatos, P., Shah, A. S., Mehta, A. D., Givre, S. J., Javitt, D. C., & Schroeder, C. E. (2007). Functional anatomy and interaction of fast and slow visual pathways in macaque monkeys. *Cerebral Cortex*, *17*, 1561–1569.

Claessens, P. M., & Wagemans, J. (2008). A Bayesian framework for cue integration in multistable grouping: Proximity, collinearity, and orientation priors in zig-zag lattices. *Journal of Vision, 8(7):33,* 1–23.

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology, 1,* 42–45.

Crouzet, S. M., Kirchner, H., & Thorpe, S. J. (2010). Fast saccades toward faces: Face detection in just 100 ms. *Journal of Vision*, *10(4):16*, 1–17.

Curby, K. M., & Gauthier, I. (2009). The temporal advantage for individuating objects of expertise: perceptual expertise is an early riser. *Journal of Vision, 9(6):7*, 1–13.

Dakin, S. C., & Herbert, A. M. (1998). The spatial region of integration for visual symmetry detection. *Proceedings of the Royal Society B: Biological Sciences, 265,* 659–664.

Delorme, A., Richard, G., & Fabre-Thorpe, M. (2010). Key visual features for rapid categorization of animals in natural scenes. *Frontiers in Psychology, 1:21.*

DeYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience, 11,* 219–226.

DiLollo, V. (2011). Iterative reentrant processing. In V. Coltheart (Ed.), *Tutorials in Visual Cognition* (pp. 9–42). London: Taylor & Francis.

Dinnerstein, D., & Wertheimer, M. (1957). Some determinants of phenomenal overlapping. *The American Journal of Psychology, 70,* 21–37.

Donk, M., & van Zoest, W. (2008). Effects of salience are short-lived. *Psychological Science*, *19*, 733–739.

Drewes, J., Trommershäuser, J. & Gegenfurtner, K.R. (2011) Parallel visual search and rapid animal detection in natural scenes. *Journal of Vision, 11(2):2,* 1–21.

Driver, J., Baylis, G. C., & Rafa, R. D. (1992). Preserved figure-ground segregation and symmetry perception in visual neglect. *Nature, 360,* 73–75.

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General, 113,* 501–517.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96,* 433–458.

Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology: Human Perception & Performance*, *24*, 1737–1747.

Eimer, M., & Schlaghecken, F. (2003). Response facilitation and inhibition in subliminal priming. *Biological Psychology*, *64*, 7–26.

Ekstrom, L. B., Roelfsema, P. R., Arsenault, J. T., Bonmassar, G., & Vanduffel, W. (2008). Bottom-up dependent gating of frontal signals in early visual cortex. *Science*, *321*, 414–417.

Elder, J. H., & Zucker, S. W. (1993). The effect of contour closure on the rapid discrimination of two-dimensional shapes. *Vision Research, 33,* 981–991.

Elder, J. H., & Zucker, S. W. (1998). Evidence for boundary-specific grouping. *Vision Research, 38,* 143–152.

Engel, A. K., König, P., Kreiter, A. K., Schillen, T. B., & Singer, W. (1992). Temporal coding in the visual cortex: new vistas on integration in the nervous system. *Trends in Neurosciences*, *15*, 218–226.

Enns, J. (1986). Seeing textons in context. *Perception & Psychophysics, 39,* 143–147.

Enquist, M., & Arak, A. (1994). Symmetry, beauty and evolution. *Nature, 372,* 169–172.

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics, 16*, 143–149.

Fabre-Thorpe, M. (2011). The characteristics and limits of rapid visual categorization. *Frontiers in psychology, 2:243.*

Fei-Fei, L., Iyer, A., Koch, C., & Perona, P. (2007). What do we perceive in a glance of a real-world scene? *Journal of Vision, 7(1):10,* 1–29.

Felleman D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1,* 1–47.

Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local "association field". *Vision Research, 33,* 173–193.

Field, G. D., Sampath, A. P., & Rieke, F. (2005). Retinal processing near absolute threshold: From Behavior to Mechanism. of *of Physiology, 67,* 491–514.

Fisher, C. B., & Bornstein, M. H. (1982). Identification of symmetry: effects of stimulus orientation and head position. *Perception & Psychophysics, 32,* 443–448.

Friedenberg, J., & Bertamini, M. (2000). Contour symmetry detection: the influence of axis orientation and number of objects. *Acta Psychologica, 105,* 107–118.

Gallace, A., & Spence, C. (2011). To what extent do Gestalt grouping principles influence tactile perception? *Psychological Bulletin, 137,* 538–561.

Garner, W. R. (1974). *The processing of information and structure.* Hillsdale, NJ: Erlbaum Associates.

Garrigan, P., Fortunato, L., & LaSala, A. (2010). The effects of closure on contour shape learning. *Journal of Vision, 10,* 1167.

Gautrais, J., & Thorpe, S. (1998). Rate coding versus temporal order coding: a theoretical approach. *BioSystems, 48,* 57–65.

Gegenfurtner, K. R., Brown, J. E., & Rieger, J. (1997). Interpolation processes in the perception of real and illusory contours. *Perception, 26,* 1445–1458.

Gepshtein, S., & Kubovy, M. (2000). The emergence of visual objects in space-time. *Proceedings of the National Academy of Science (USA), 97,* 8186–8191.

Gilbert, C. D., & Sigman, M. (2007). Brain states: top-down influences in sensory processing. *Neuron, 54,* 677–696.

Girard, P., Hupé, J. M., & Bullier, J. (2001) Feedforward and feedback connections between areas V1 and V2 of the monkey have similar rapid conduction velocities. *Journal of Neurophysiology, 85,* 1328–1331.

Gollisch, T., & Meister, M. (2008). Rapid neural coding in the retina with relative spike latencies. *Science*, *319*, 1108–1111.

Grill-Spector, K., & Kanwisher, N. (2005). Visual recognition. *Psychological Science, 16,* 152–160.

Grossberg, S., & Mingolla, E. (1985). Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading. *Psychological Review, 92,* 173–211.

Guttman, S. E., Sekuler, A. B., & Kellman, P. J. (2003). Temporal variations in visual completion: A reflection of spatial limits?. *Journal of Experimental Psychology Human Perception and Performance*, *29*, 1211–1227.

Guyonneau, R., VanRullen, R., & Thorpe, S. J. (2004). Temporal codes and sparse representations: a key to understanding rapid processing in the visual system. *Journal of Physiology-Paris*, *98*, 487–497.

Guyonneau, R., VanRullen, R., & Thorpe, S. J. (2005). Neurons tune to the earliest spikes through STDP. *Neural Computation*, *17*, 859–879.

Haberkamp, A., Schmidt, F., & Schmidt, T. (2013). Rapid visuomotor processing of phobic images in spider- and snake-fearful participants. *Acta Psychologica, 144,* 232–242.

Han, S., Ding, Y., & Song, Y. (2002). Neural mechanisms of perceptual grouping in humans as revealed by high density event related potentials. *Neuroscience Letters, 319,* 29–32.

Han, S., & Humphreys, G. W. (1999). Interactions between perceptual organization based on Gestalt laws and those based on hierarchical processing. *Perception & Psychophysics, 61,* 1287–1298.

Han, S., Humphreys, G. W., & Chen, L. (1999a). Parallel and Competitive Processes in Hierarchical Analysis. *Journal of Experimental Psychology: Human Perception & Performance, 25,* 1411–1412.

Han, S., Humphreys, G. W., & Chen, L. (1999b). Uniform connectedness and classical Gestalt principles of perceptual grouping. *Perception & Psychophysics, 61,* 661–674.

Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Gu, H. (2005). Attentional modulation of perceptual grouping in human visual cortex: fMRI studies. *Human Brain Mapping, 25,* 424–432.

Hegdé, J. (2008). Time course of visual perception: coarse-to-fine processing and beyond. *Progress in Neurobiology, 84,* 405–439.

Hegdé, J., & Felleman, D. J. (2007). Reappraising the Functional Implications of the Primate Visual Anatomical Hierarchy. *Neuroscientist, 13,* 416–421.

Hegdé, J., & Van Essen, D. C. (2007). A comparative study of shape representation in macaque visual areas V2 and V4. *Cerebral Cortex, 17,* 1100–1116.

Heitger, F., von der Heydt, R., Peterhans, E., Rosenthaler, L., & Kübler, O. (1998). Simulation of neural contour mechanisms: Representing anomalous contours. *Image and Vision Computing, 16,* 407–421.

Henderson, J. M., & Hollingworth, A. (1999). High-level scene perception. *Annual review of psychology*, *50*, 243–271.

Hochberg, J. E., & Hardy, D. (1960). Brightness and proximity factors in grouping. *Perceptual and Motor Skills,* 10, 22.

Hochberg, J. E., & McAlister, E. (1953). A quantitative approach to figural “goodness.” *Journal of Experimental Psychology, 46,* 361–364.

Hochberg, J. E., & Silverstein, A. (1956). A quantitative index of stimulus-similarity: Proximity versus differences in brightness. *American Journal of Psychology, 69,* 456–458.

Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, *36*, 791–804.

Höfel, L., & Jacobsen, T. (2007). Electrophysiological indices of processing aesthetics: Spontaneous or intentional processes? *International Journal of Psychophysiology, 65,* 20–31.

Houtkamp, R., & Roelfsema, P. R. (2010). Parallel and serial grouping of image elements in visual perception. *Journal of Experimental Psychology: Human Perception & Performance, 36,* 1443–1459.

Houtkamp, R., Spekreijse, H., & Roelfsema, P. R. (2003). A gradual spread of attention during mental curve tracing. *Perception & Psychophysics, 65,* 1136–1144.

Jacobsen, T., & Höfel, L. (2003). Descriptive and evaluative judgment processes: Behavioral and electrophysiological indices of processing symmetry and aesthetics. *Cognitive, Affective, & Behavioral Neuroscience, 3,* 289–299.

Jaśkowski, P. (2008). The negative compatibility effect with nonmasking flankers: a case for mask-triggered inhibition hypothesis. *Consciousness and Cognition*, *17*, 765–777.

Jenkins, B. (1983). Component processes in the perception of bilaterally symmetric dot textures. *Perception & Psychophysics, 34,* 433–440.

Jeurissen, D., Self, M. W., & Roelfsema, P. R. (2013). Surface reconstruction, figure-ground modulation, and border-ownership. *Cognitive Neuroscience*, *4*, 50–52.

Jolicœur, P., Ullman, S., & MacKay, M. (1986). Curve tracing: A possible basic operation in the perception of spatial relations. *Memory & Cognition, 14,* 129–140.

Joubert, O. R., Fize, D., Rousselet, G. A., & Fabre-Thorpe, M. (2008). Early interference of context congruence on object processing in rapid visual categorization of natural scenes. *Journal of Vision, 8:11,* 1–18,

Julesz, B. (2006). *Foundations of cyclopean perception.* Cambridge, MA: MIT Press. (Original published in 1971).

Kanbe, F. (2008). Role of endpoints and closure in feature search. *Japanese Psychological Research, 50,* 145–151.

Kellman, P. J., Garrigan, P., & Shipley, T. F. (2005). Object interpolation in three dimensions. *Psychological Review, 112,* 586–609.

Kellman, P. J., Garrigan, P., Shipley, T. F., & Keane, B. (2007). Interpolation processes in object perception: A reply to Anderson. *Psychological Review, 114,* 488–502.

Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology, 23,* 141–221.

Kiesel, A., Kunde, W., & Hoffmann, J. (2007). Mechanisms of subliminal response priming. *Advances in Cognitive Psychology, 3,* 307–315.

Kimchi, R. (1998). Uniform connectedness and grouping in the perceptual organization of hierarchical patterns. *Journal of Experimental Psychology: Human Perception & Performance, 24,* 1105–1118.

Kimchi, R. (2000). The perceptual organization of visual objects: A microgenetic analysis. *Vision Research, 40,* 1333–1347.

Kimchi, R., & Razpurker-Apfeld, I. (2004). Perceptual grouping and attention: Not all groupings are equal. *Psychonomic Bulletin & Review, 11,* 687–696.

Klotz, W., Heumann, M., Ansorge, U., & Neumann, O. (2007). Electrophysiological activation by masked primes: Independence of prime-related and target-related activities. *Advances in Cognitive Psychology*, *3*, 449–465.

Klotz, W., & Neumann, O. (1999). Motor activation without conscious discrimination in metacontrast masking. *Journal of Experimental Psychology: Human Perception & Performance, 25,* 976–992.

Klotz, W., & Wolff, P. (1995). The effect of a masked stimulus on the response to the masking stimulus. *Psychological Research, 58,* 92–101.

Köhler, W. (1920). *Die physischen Gestalten in Ruhe und im stationären Zustand. Eine naturphilosophische Untersuchung.* Braunschweig, Germany: Friedrich Vieweg und Sohn.

Kohl, P., Schmidt, F., & Schmidt, T. (2010). Response Priming (English Launch Version). http://en.wikipedia.org/wiki/Response_Priming.

Koffka, K. (1935). *Principles of Gestalt psychology.* London, UK: Lund Humphries.

Kogo, N., & Wagemans, J. (2013). The emergent property of border-ownership and the perception of illusory surfaces in a dynamic hierarchical system. *Cognitive Neuroscience*, *4*, 54–61.

Koning, A., & van Lier, R. (2006). No symmetry advantage when object matching involves accidental viewpoints. *Psychological Research, 70,* 52–58.

Koning, A., & Wagemans, J. (2009). Detection of symmetry and repetition in one and two objects: Structures versus strategies. *Experimental Psychology, 56,* 5–17.

Korjoukov, I., Jeurissen, D., Kloosterman, N. A., Verhoeven, J. E., Scholte, H. S., & Roelfsema, P. R. (2012). The time course of perceptual grouping in natural scenes. *Psychological Science*, *23*, 1482–1489.

Korjoukov, I., & Roelfsema, P. R. (2012). A neurodynamical model for contrast-invariant and scale-invariant contour grouping. *Perception ECVP Abstract Supplement, 41,* 142.

Kovács, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Sciences (USA), 90,* 7495–7497

Krüger, D., Klapötke, S., Bode, S., & Mattler, U. (2013). Neural correlates of control operations in inverse priming with relevant and irrelevant masks. *NeuroImage, 64,* 197–208.

Kubovy, M., Holcombe, A. O., & Wagemans, J. (1998). On the lawfulness of grouping by proximity. Cognitive Psychology, 35, 71–98.

Kubovy, M., & van den Berg, M. (2008). The Whole Is Equal to the Sum of Its Parts: A Probabilistic Model of Grouping by Proximity and Similarity in Regular Patterns. *Psychological Review, 115,* 131–154.

Lachmann, T., & van Leeuwen, C. (2005). Task-invariant aspects of goodness in perceptual representation. *The Quarterly Journal of Experimental Psychology, 58,* 1295–1310.

Lachmann, T., & van Leeuwen, C. (2008). Goodness is central: Task-invariance of perceptual organization in a dual-task setting. *Japanese Psychological Research, 50,* 193–203.

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience, 1,* 204–240.

Lamme, V. A. F., Rodriguez-Rodriguez, V., & Spekreijse, H. (1999). Separate processing dynamics for texture elements, boundaries and surfaces in primary visual cortex of the macaque monkey. *Cerebral Cortex, 9,* 406–413.

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences,* 23, 571–579.

Leeuwenberg, E. L. J. (1969). Quantitative specification of information in sequential patterns. *Psychological Review, 76,* 216–220.

Lefebvre, C., Dell'acqua, R., Roelfsema, P. R., & Jolicœur, P. (2011). Surfing the attentional waves during visual curve tracing: Evidence from the sustained posterior contralateral negativity. *Psychophysiology*, *48*, 1510–1516.

Lerner, Y., Hendler, T., & Malach, R. (2002). Object-completion effects in the human lateral occipital complex. *Cerebral Cortex, 12,* 163–177.

Leuthold, H., & Kopp, B. (1998). Mechanisms of priming by masked stimuli: Inferences from event-related brain potentials. *Psychological Science*, *9*, 263–269.

Li, W., Piech, V., & Gilbert, C. D. (2009). Learning to link visual contours. *Neuron, 57,* 442–451.

Lingnau, A., & Vorberg, D. (2005). The time course of response inhibition in masked priming. *Perception & Psychophysics*, *67,* 545–557.

Locher, P. J., & Wagemans, J. (1993). The effects of element type and spatial grouping on symmetry detection. *Perception, 22,* 565–587.

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review, 1,* 476-490.

Logothetis, N. K. & Sheinberg, D. L. (1996). Visual object recognition. *Annual Review of Neuroscience, 19,* 577–621.

Macé, M. J.-M., Joubert, O. R., Nespoulous, J.-L., & Fabre-Thorpe, M. (2009). Time-course of visual categorizations: you spot the animal faster than the bird. *PLoS ONE, 4,* e5927.

Machilsen, B., Pauwels, M., & Wagemans, J. (2009). The role of vertical mirror symmetry in visual shape detection. *Journal of Vision, 9(12):11*, 1–11.

Manassi, M., Sayim, B., & Herzog, M. H. (2012). Grouping, pooling, and when bigger is better in visual crowding. *Journal of Vision, 12(10):13,* 1–14.

Marino, A. C., & Scholl, B. J. (2005). The role of closure in defining the "objects" of object-based attention. *Perception & Psychophysics, 67,* 1140–1149.

Marr, D. (1982). *Vision.* San Francisco: Freeman.

Masquelier, T., Guyonneau, R., & Thorpe, S. J. (2009). Competitive STDP-based spike pattern learning. *Neural computation*, *21*, 1259–1276.

Mathes, B., & Fahle, M. (2007). Closure facilitates contour integration. *Vision Research, 47,* 818–827.

Mattler, U. (2003). Delayed flanker effects on lateralized readiness potentials. *Experimental Brain Research*, *151*, 272–288.

Mattler, U. (2005). Inhibition and decay of motor and nonmotor priming. *Perception & Psychophysics*, *67*, 285–300.

Mattler, U., & Palmer, S. (2012). Time course of free-choice priming effects explained by a simple accumulator model. *Cognition*, *123*, 347–360.

Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.

Mori, S. (1997). Effects of absolute and relative gap sizes in visual search for closure. *Canadian Journal of Experimental Psychology, 51,* 112–124.

Müller, G. E. (1903). Die Gesichtspunkte und die Tatsachen der psychophysischen Methodik. In L. Asher, & K. Spiro (Eds.), *Ergebnisse der Physiologie, II. Abteilung, II. Jahrgang* (pp. 267–516). Wiesbaden: J. F. Bergmann.

Murray, R. F., Sekuler, A. B., & Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin & Review*, *8*, 713–720.

New, J., Cosmides, L., & Tooby, J. (2007). Categoryspecific attention for animals reflects ancestral priorities, not expertise. *Proceedings of the National Academy of Sciences (USA), 104,* 16598–16603.

Niimi, R., Watanabe, K., & Yokosawa, K. (2005). The role of visible persistence for perception of visual bilateral symmetry. *Japanese Psychological Research, 47,* 262–270.

Niimi, R., & Yokosawa, K. (2008). Determining the orientation of depth-rotated familiar objects. *Psychonomic Bulletin & Review, 15,* 208–214.

Norcia, A. M., Candy, T. R., Pettet, M. W., Vildavski, V. Y., & Tyler, C. W. (2002). Temporal dynamics of the human response to symmetry. *Journal of Vision, 2(2):1,* 132–139.

Nowak, L. G., & Bullier, J. (1997) The timing of information transfer in the visual system. In K. S. Rockland, J. H. Kaas, & A. Peters (Eds.), *Cerebral Cortex (Volume 12 Extrastriate Cortex in Primates)* (pp. 205–241). Plenum Press.

Oka, S., Victor, J. D., Conte, M. M., & Yanagida, T. (2007). VEPs elicited by local correlations and global symmetry: characteristics and interactions. *Vision Research, 47,* 2212–2222.

Overvliet, K. E., Krampe, R. T., & Wagemans, J. (2012). Perceptual grouping in haptic search: The influence of proximity, similarity, and good continuation. *Journal of Experimental Psychology: Human Perception and Performance, 38,* 817–821.

Palmer, S. E. (1992). Common region: a new principle of perceptual grouping. *Cognitive Psychology, 24,* 436–447.

Palmer, S. E. (1999). *Vision science: Photons to phenomenology.* Cambridge, MA: MIT Press.

Palmer, S. E. (2002). Perceptual grouping: It is later than you think. *Current Directions in Psychological Science, 11,* 101–106.

Palmer, S. E. (2003). Perceptual organization and grouping. In R. Kimchi, M. Behrmann, & C. R. Olson (Eds.), *Perceptual Organization in Vision: Behavioral and Neural Perspectives* (pp. 3–43). Hillsdale, NJ: Lawrence Erlbaum Associates

Palmer, S. E., & Beck, D. (2007). The repetition discrimination task: An objective method for studying perceptual grouping. *Attention, Perception, & Psychophysics, 69,* 68–78.

Palmer, S. E., & Brooks, J. L. (2008). Edge-region grouping in figure-ground organization and depth perception. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 1353.

Palmer, S. E., Brooks, J. L., & Nelson, R. (2003). When does grouping happen? *Acta Psychologica, 114,* 311–330.

Palmer, S. E., & Ghose, T. (2008). Extremal edges: A powerful cue to depth perception and figure-ground organization. *Psychological Science, 19,* 77–84.

Palmer, S. E., & Hemenway, K. (1978). Orientation and symmetry: Effects of multiple, rotational, and near symmetries. *Journal of Experimental Psychology: Human Perception and Performance, 4,* 691–702.

Palmer, S. E., Neff, J., & Beck, D. (1996). Late influences on perceptual grouping: Amodal completion. *Psychonomic Bulletin & Review, 3,* 75–80.

Palmer, S. E., & Rock, I. (1994a). Rethinking perceptual organization: the role of uniform connectedness. *Psychonomic Bulletin & Review, 1,* 29–55.

Palmer, S. E., & Rock, I. (1994b). On the nature and order of organizational processing: A reply to Peterson. *Psychonomic Bulletin & Review*, *1*, 515–519.

Pashler, H. (1990). Coordinate frame for symmetry detection and object recognition. *Journal of Experimental Psychology: Human Perception and Performance, 16,* 150–163.

Pashler, H. (1999). *The psychology of attention.* Cambridge, MA: MIT Press.

Peterson, M. A. (1994). The proper placement of uniform connectedness. *Psychonomic Bulletin & Review*, *1*, 509–514.

Petter, G. (1956). Nuove richerche sperimentali sulla totalizzazione percettiva. *Revista di Psicologia, 50,* 213–227.

Pomerantz, J. R., & Garner, W. R. (1973). Stimulus configuration in selective attention tasks. *Perception & Psychophysics, 14,* 565–569.

Pomerantz, J. R., & Kubovy, M. (1986). *Theoretical approaches to perceptual organization: Simplicity and likelihood principles.* In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), Handbook of perception and human performance (pp. 36-1–36-46). New York, NY: Wiley.

Pomerantz, J. R. & Portillo, M. C. (2011). Grouping and emergent features in vision: Toward a theory of basic Gestalts. J*ournal of Experimental Psychology: Human Perception & Performance, 37,* 1331–1349.

Pomerantz, J. R., Sager, L. C., & Stoever, R. J. (1977). Perception of wholes and their component parts: Some configurational superiority effects. *Journal of Experimental Psychology: Human Perception & Performance, 3,* 422–435.

Poncet, M., Reddy, L., & Fabre-Thorpe, M. (2012). A need for more information uptake but not focused attention to access basic-level representations. *Journal of Vision*, *12(1): 18*, 1–16.

Quinlan, P. T., & Wilton, R. N. (1998). Grouping by proximity or similarity? Competition between the Gestalt principles in vision. Perception, 27, 417–430.

Raab, D. H. (1962). Magnitude estimation of the brightness of brief foveal stimuli. *Science*, *135*, 42–44.

Rainville, S. J. M., & Kingdom, F. A. A. (2000). The functional role of oriented spatial filters in the perception of mirror symmetry–psychophysics and modeling. *Vision Research, 40,* 2621–2644.

Ratcliff R. (1979). Group reaction time distributions and an analysis of distribution statistics. *Psychological Bulletin, 86*, 446–461.

Razpurker-Apfeld, I., & Kimchi, R. (2007). The time course of perceptual grouping: The role of segregation and shape formation. *Perception & Psychophysics*, *69*, 732–743.

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience, 2,* 1019–1025.

Ringach, D. L., & Shapley, R. (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research, 36,* 3037–3050.

Rock, I., & Brosgole, L. (1964). Grouping based on phenomenal proximity. *Journal of Experimental Psychology, 67,* 531–538.

Rock, I., & Leaman, R. (1963). An experimental analysis of visual symmetry. *Acta Psychologica, 21,* 171–183.

Rock, I., Nijhawan, R., Palmer, S. E., & Tudor, L. (1992). Grouping based on phenomenal similarity of achromatic color. *Perception, 21,* 779–789.

Rockland, K. S., & Pandya, D. N. (1979) Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus-monkey. *Brain Research,* 179, 3–20

Roelfsema, P. R. (2006). Cortical algorithms for perceptual grouping. *Annual Reviews of Neuroscience, 29,* 203–227.

Roelfsema, P. R., & Houtkamp, R. (2011). Incremental grouping of image elements in vision. *Attention, Perception, & Psychophysics, 73,* 2542–2572.

Roelfsema, P. R., Houtkamp, R., & Korjoukov, I. (2010). Further evidence for the spread of attention during contour grouping: A reply to Crundall, Dewhurst, and Underwood (2008). *Attention, Perception, & Psychophysics, 72,* 849–862.

Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature, 395,* 376–381.

Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. (2004). Synchrony and covariation of firing rates in the primary visual cortex during contour grouping. *Nature Neuroscience, 7,* 982–991.

Roelfsema, P. R., Tolboom, M., & Khayat, P. S. (2007). Different processing phases for features, figures, and selective attention in the primary visual cortex. *Neuron*, *56*, 785–792.

Roelfsema, P. R., van Ooyen, A., & Watanabe, T. (2010). Perceptual learning rules based on reinforcers and attention. *Trends in Cognitive Sciences*, *14*, 64–71.

Roland, P. E. (2010). Six principles of visual cortical dynamics. *Frontiers in systems neuroscience*, *4:28.*

Rubin, E. (1915). *Visuell wahrgenommene Figuren. Studien in psychologischer Analyse.* Copenhagen, Denmark/Berlin, Germany: Gyldendalske Boghandel.

Rubin, E. (1922). Zur Psychophysik der Geradheit. *Zeitschrift für Psychologie, 90,* 67–105.

Saarinen, J., & Levi, D. M. (1999). The effect of contour closure on shape perception. *Spatial Vision, 2,* 227–238.

Sasaki, Y. (2007). Processing local signals into global patterns. C*urrent Opinion in Neurobiology, 17,* 1–8.

Sasaki, Y., Vanduffel, W., Knutsen, T., Tyler, C., & Tootell, R. (2005). Symmetry activates extrastriate visual cortex in human and nonhuman primates. *Proceedings of the National Academy of Sciences (USA),* 102, 3159–3163.

Sawada, T., & Pizlo, Z. (2008). Detection of skewed symmetry. *Journal of Vision, 8(5):14,* 1–18.

Schmidt, F., Haberkamp, A., & Schmidt, T. (2011). Dos and don'ts in response priming research. *Advances in Cognitive Psychology, 7(2),* 120–131.

Schmidt, F., & Schmidt, T. (2010). Feature-based attention to unconscious shapes and colors. *Attention, Perception, & Psychophysics*, *72*, 1480–1494.

Schmidt, F., & Schmidt, T. (2013). Grouping principles in direct competition. *Vision Research, 88,* 9–21.

Schmidt, F., & Schmidt, T. (2014). Rapid processing of closure and viewpoint-invariant symmetry: Behavioral criteria for feedforward processing. *Psychological Research, 78,* 37-54.

Schmidt, T. (2002). The finger in flight: Real-Time Motor Control by Visually Masked Color Stimuli. *Psychological Science, 13,* 112–118.

Schmidt, T. (2013). Invisible stimuli, implicit thresholds: Why "not seen" judgments cannot be interpreted in isolation. *arXiv:1306.0756* [q-bio.NC]

Schmidt, T., Haberkamp, A., Veltkamp, G. M., Weber, A., Seydell-Greenwald, A., & Schmidt, F. (2011). Visual processing in rapid-chase systems: Image processing, attention, and awareness. *Frontiers in Psychology, 2:169.*

Schmidt, T., Niehaus, S., & Nagel, A. (2006). Primes and targets in rapid chases: Tracing sequential waves of motor activation. *Behavioural Neuroscience, 120,* 1005–1016.

Schmidt, T., & Schmidt, F. (2009). Processing of natural images is feedforward: A simple behavioral test. *Attention, Perception, & Psychophysics, 71,* 594–606.

Schulz, M. F., & Sanocki, T. (2003). Time course of perceptual grouping by color. *Psychological Science, 14,* 26–30.

Schumann, F. (1900). Beiträge zur Analyse der Gesichtswahrnehmungen. Erste Abhandlung. Einige Beobachtungen über die Zusammenfassung von Gesichtseindrücken zu Einheiten. *Zeitschrift für Psychologie und Physiologie der Sinnesorgane, 23,* 1–32.

Schwarz, W., & Mecklinger, A. (1995). Relationship between flanker identifiability and compatibility effect. *Perception & Psychophysics*, *57*, 1045–1052.

Sekuler, A. B., & Palmer, S. E. (1992). Perception of partly occluded objects: A microgenetic analysis. *Journal of Experimental Psychology: General, 121,* 95–111.

Self, M. W., Kooijmans, R. N., Supèr, H., Lamme, V. A., & Roelfsema, P. R. (2012). Different glutamate receptors convey feedforward and recurrent processing in macaque V1. *Proceedings of the National Academy of Sciences (USA)*, *109*, 11031–11036.

Self, M. W., van Kerkoerle, T., Supèr, H., & Roelfsema, P. R. (2013). Distinct roles of the cortical layers of area V1 in figure-ground segregation. *Current Biology, 23*, 2121–2129.

Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. *Proceedings of the National Academy of Sciences (USA), 104,* 6424–6429.

Seydell-Greenwald, A., & Schmidt, T. (2012). Rapid activation of motor responses by illusory contours. *Journal of Experimental Psychology: Human Perception & Performance, 28,* 1168–1182.

Shadlen, M. N., & Movshon, J. A. (1999). Synchrony unbound: A critical evaluation of the temporal binding hypothesis. *Neuron, 24,* 67–77.

Shipley, T. F., & Kellman, P. J. (1992). Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Perception & Psychophysics, 52,* 97–106.

Shore, D. I., & Enns, J. T. (1997). Shape completion time depends on the size of the occluded region. *Journal of Experimental Psychology: Human Perception & Performance, 23,* 980–998.

Sillito, A. M., Cudeiro, J., & Jones, H. E. (2006). Always returning: feedback and sensory processing in visual cortex and thalamus. *Trends in Neurosciences*, *29*, 307–316.

Singer, W. & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual Review of Neuroscience, 18,* 555–586.

Stevens, S. (1957). On the psychophysical law. *Psychological Review, 64,* 153–181.

Sugihara, T., Qiu, F. T., & von der Heydt, R. (2011). The speed of context integration in the visual cortex. *Journal of Neurophysiology, 106,* 374–385.

Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature*, *401*, 269–272.

Sumner, P. (2007). Negative and positive masked-priming–implications for motor inhibition. *Advances in Cognitive Psychology*, *3*, 317–326.

Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience, 19,* 109–139 (1996).

Tanaka, K., Saito, H. A., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology, 66,* 170–189.

Tapia, E., Breitmeyer, B. G., & Shooner, C. R. (2010). Role of task-directed attention in nonconscious and conscious response priming by form and color.

Journal of Experimental Psychology: Human Perception and Performance, 36, 74–87.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*, 520–522.

Todorovic, D. (2011). What is the origin of the Gestalt Principles? *Humana.Mente Journal of Philosophical Studies, 2011,* 17, 1–20.

Treder, M. S. (2010). Behind the looking glass: a review on human symmetry perception. *Symmetry, 2,* 1510–1543.

Treder, M. S., & van der Helm, P. A. (2007). Symmetry versus repetition in cyclopean vision: a microgenetic analysis. *Vision Research, 47,* 2956–2967.

Treisman, A. (1996). The binding problem. *Current Opinion in Neurobiology, 6,* 171–178.

Treisman, A. (2006). How the deployment of attention determines what we see. *Visual Cognition, 14,* 411–443.

Treisman, A., & Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology, 12,* 97–136.

Treisman, A., & Paterson, R. (1984). Emergent features, attention, and object perception. *Journal of Experimental Psychology: Human Perception and Performance, 10,* 12–31.

Treisman, A., & Souther, J. (1985). Search asymmetry: A diagnostic for preattentive processing of separable features. *Journal of Experimental Psychology: General, 114,* 285–310.

Troscianko, T., Benton, C. P., Lovell, P. G., Tolhurst, D. J., & Pizlo, Z. (2009). Camouflage and visual perception. *Philosophical Transactions of the Royal Society B, 364,* 449–461.

Tsao, D. Y. & Livingstone, M. (2008). Mechanisms of face perception. *Annual Review of Neuroscience, 31,* 411–437.

Tyler, C. W., Baseler, H. A., Kontsevich, L. L., Likova, L. T., Wade, A. R., & Wandell, B. A. (2005). Predominantly extra-retinotopic cortical response to pattern symmetry. *Neuroimage, 24,* 306–314.

Ullman, S. (1984). Visual routines. *Cognition, 18,* 97–159.

Ullman, J. R. (1992). Analysis of 2-D occlusion by subtracting out. *IEEE Transactions* on *Pattern Analysis* and Machine *Intelligence, 14,* 485–489.

van den Berg, M., Kubovy, M., & Schirillo, J. A. (2011). Grouping by regularity and the perception of illumination. *Vision Research, 51,* 1360–1371.

van der Helm (2012). Cognitive architecture of perceptual organization: from neurons to gnosons. *Cognitive Processing, 13,* 13–40.

van der Helm, P. A., & Leeuwenberg, E. L. J. (1996). Goodness of visual regularities: A nontransformational approach. *Psychological Review, 103,* 429–456.

van der Helm, P. A., & Leeuwenberg, E. L. J. (1999). A better approach to goodness: Reply to Wagemans (1999). *Psychological Review, 106,* 622–630.

van der Helm, P. A., & Treder, M. S. (2009). Detection of (anti)symmetry and (anti)repetition: Perceptual mechanisms versus cognitive strategies. *Vision Research, 49,* 2754–2763.

van Kerkoerle, T. J., Self, M. W., & Roelfsema, P. R. (2009). Multiple short-term memory signals in monkey primary visual cortex. Program No. 652.18. *Neuroscience Meeting Planner. Chicago, IL: Society for Neuroscience, 2009. Online.*

van Zoest, W., Hunt, A. R., & Kingstone, A. (2010). Representations in Visual Cognition: It's About Time. *Current Directions in Psychological Science, 19,* 116–120.

VanRullen, R. (2009). Binding hardwired versus on-demand feature. *Visual Cognition, 17,* 103–119.

VanRullen, R., & Koch, C. (2003). Visual selective behaviour can be triggered by a feed-forward process. *Journal of Cognitive Neuroscience, 15,* 209–217.

VanRullen, R., & Thorpe, S. J. (2001). Is it a bird? Is it a plane? Ultra-rapid visual categorization of natural and artifactual objects. *Perception, 30,* 655–668.

Vath, N., & Schmidt, T. (2007). Tracing sequential waves of rapid visuomotor activation in lateralized readiness potentials. *Neuroscience, 145,* 197–208.

Vezzani, S., Marino, B. F. M., & Giora, E. (2012). An early history of the Gestalt factors of organization. *Perception, 41,* 148–167.

Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proceedings of the National Academy of Sciences (USA), 100,* 6275–6280.

Wagemans, J. (1993). Skewed symmetry: A nonaccidental property used to perceive visual forms. *Journal of Experimental Psychology: Human Perception and Performance, 19,* 364–380.

Wagemans, J. (1995). Detection of visual symmetries. *Spatial Vision, 9,* 9–32.

Wagemans, J. (1997). Characteristics and models of human symmetry detection. *Trends in Cognitive Sciences, 1,* 346–352.

Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., & von der Heydt, R. (2012). A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure-ground organization. *Psychological Bulletin, 138,* 1172–1217.

Wagemans, J., Feldman, J., Gepshtein, S., Kimchi, R., Pomerantz, J. R., van der Helm, P., & van Leeuwen, C. (2012). A century of Gestalt psychology in visual perception: II. Conceptual and theoretical foundations. *Psychological Bulletin, 138,* 1218–1252.

Wagemans, J., van Gool, L., & d'Ydewalle, G. (1991). Detection of symmetry in tachistoscopically presented dot patterns: Effects of multiple axes and skewing. *Perception & Psychophysics, 50,* 413–427.

Wagemans, J., van Gool, L., & d'Ydewalle, G. (1992). Orientational effects and component processes in symmetry detection. *Quarterly Journal of Experimental Psychology A, 44,* 475–508.

Wagemans, J., van Gool, L., Swinnen, V., & van Horebeek, J. (1993). Higher-order structure in regularity detection. *Vision Research, 33,* 1067–1088.

Wannig, A., Stanisor, L., & Roelfsema, P. R. (2011). Automatic spread of attentional response modulation along Gestalt criteria in primary visual cortex. *Nature Neuroscience, 14,* 1243–1244.

Weber, A., Noé, L., Hoffmann, L., Schmidt, T., & Schmidt, F. (2012). From physical to perceptual stimulus representations: Exploiting the Ebbinghaus illusion in a response priming paradigm. *Perception, 41*, ECVP Abstract Supplement.

Wenderoth, P. (1994). The salience of vertical symmetry. *Perception, 23,* 221–236.

Wenderoth, P. (1997). The effects on bilateral symmetry detection of multiple symmetry, near symmetry, and axis orientation. *Perception, 26,* 891–904.

Wenderoth, P. (2000). The differential effects of simultaneous and successive cueing on the detection of bilateral symmetry in dot patterns. *The Quarterly Journal of Experimental Psychology A, 53,* 165–190.

Wenderoth, P., & Welsh, S. (1998). Effects of pattern orientation and number of symmetry axes on the detection of mirror symmetry in dot and solid patterns. *Perception, 27,* 965–976.

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt, II. *Psychologische Forschung, 4,* 301–350.

Wichmann, F.A., Drewes, J., Rosas, P. & Gegenfurtner, K.R. (2010) Animal detection in natural scenes: critical features revisited. *Journal of Vision, 10(4):6,* 1–27.

Wolfe, J. M., & Horowitz, T. S. (2004). What attributes guide the deployment of visual attention and how do they do it? *Nature Reviews Neuroscience, 5,* 495–501.

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception & Performance, 16,* 121–134.

Ying, Z., & Castañon, D. (2002). Partially occluded object recognition using statistical models. *International Journal of Computer Vision, 49,* 57–78.

Zhang, N. R., & von der Heydt, R. (2010). Analysis of the context integration mechanisms underlying figure-ground organization in the visual cortex. *Journal of Neuroscience, 30,* 6482–6496.

Zipser, K., Lamme, V. A. F., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *The Journal of Neuroscience, 16,* 7376–7389.

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