Rapid processing of closure and viewpoint-invariant symmetry: Behavioral criteria for feedforward processing

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This is a post-peer-review, pre-copyedit version of an article published in ***Psychological Research.*** *The final authenticated version is available online at* https://doi.org/10.1007/s00426-013-0478-8

Abstract

To pin down the processing characteristics of symmetry and closure in contour processing, we investigated their ability to activate rapid motor responses in a primed flanker task. In three experiments, participants selected as quickly and accurately as possible the one of two target contours possessing symmetry or closure. Target pairs were preceded by prime pairs whose spatial arrangement was consistent or inconsistent with respect to the required response. We tested for the efficiency and automaticity of both cues' processing. For both closure and symmetry cues, priming effects were present in full magnitude in the fastest motor responses consistent with a simple feedforward model. Priming effects from symmetry cues were independent of skewing and the orientation of their symmetry axis but sometimes failed to increase with increasing prime-target interval. We conclude that closure and (possibly) viewpoint-independent symmetry cues are extracted rapidly during the first feedforward wave of neuronal processing.

Keywords: Symmetry, closure, viewpoint-invariance, feedforward processing, priming

Introduction

General

To make sense of the world before our eyes, the human visual system resorts to a number of strategies and heuristics. These include *grouping principles* that provide a basis for organizing the incoming stream of visual information into coherent units and perceiving separate objects. Two well-established principles are *symmetry* (e.g., Schumann, 1900) and *closure* (e.g., Wertheimer, 1923) which rely on the use of specific grouping cues: Perceived figures or shapes may be either symmetric or asymmetric (i.e., are reflected along their central axis or not),[1] and may possess contours that are either enclosed or open.

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* y[2] and secondly in the speed and effortlessness of their processing. The latter point is of importance for the current paper: Research suggests that symmetry as well as closure are primitives in early 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 & Patterson, 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.

Although there are successful computational models of symmetry and closure (Van der Helm & Leeuwenberg, 1996, 1999; Wagemans, Van Gool, Swinnen, & van Horebeek, 1993), the physiological mechanisms are still unclear. Symmetry processing can 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 neural processing (e.g., via horizontal connections in V1, see Bauer & Heinze, 2002; or feedback connections from areas higher in the visual hierarchy, see Zipser, Lamme, & Schiller, 1998; Roelfsema, 2006).

In this study, we are interested in the time-course of processing for symmetry and closure. We test the notion that symmetry as well as closure processing can be based on an early read-out during the first feedforward wave of neuronal processing (Lamme & Roelfsema, 2000). We do this by using a *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 et al., 2011; Schmidt, Niehaus, & Nagel, 2006). We show that symmetry and closure can be processed not only relatively

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[1] 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”.

[2] 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).

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. Testing the limits of feedforward processing, we apply the primed flanker method to test for view-point invariance in symmetry processing and also look at the role of the orientation of the symmetry axis. In the following sections, we will first review findings that describe common characteristics of symmetry and closure processing and then detail our experimental approach.

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 short 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 masked polygonal shapes with presentation times of 25 ms (Carmody et al., 1977) and in dot patterns with presentation times of 13 ms (Niimi et al., 2005).

Additionally, a number of studies suggest that the processing of symmetry may even be automatic (not relying on cognitive control) (Baylis & Driver, 1994; for a summary see Treder, 2010). For example, Koning and Wagemans (2009) presented participants with two three-dimensional objects and instructed them to judge whether or not their facing contours are symmetric. Interestingly, also task-irrelevant contours speeded responses when they were also symmetric. Because participants were not able to voluntarily preclude this influence, these findings suggest that processing of symmetry is independent of cognitive control. This notion is also supported by findings 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 their symmetry. This finding corresponds to that of healthy participants, suggests 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?

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 short stimulus presentation times of 150-160 ms (Kovács & Julesz, 1993; Saarinen & Levi, 1999). Also, 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 further 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.[3]

Symmetry and closure as non-accidental properties

The processing advantages of symmetry and closure are presumably due to their

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[3] 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). Also, there is no unequivocal evidence that the processing of closure is automatic.

significance in object recognition (e.g., Marino & Scholl, 2005; Treder, 2010). Effective object recognition must be viewpoint-invariant, that is, it must be possible to recognize an object 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 and colleagues demonstrated that symmetry detection in skewed stimuli – measured by sensitivity and speed – decreases with an increase in skewing angle (Wagemans, 1993; Wagemans, Van Gool, & d'Ydewalle, 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. Also, responses were speeded 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.

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 symmetry axis (e.g., Rock & Leaman, 1963; Palmer & Hemenway, 1978; 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, 1998a). 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 sum, both symmetry and closure are important features that are able to 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.

Visuomotor processing dynamics as a test of feedforward processing

We adopted a *primed flanker task* (Schmidt & Schmidt, submitted) 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. It is a variant of the response priming paradigm, which is especially useful to investigate early phases of visual processing (Schmidt, Haberkamp, & Schmidt, 2011, Schmidt et al., 2011; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). In response priming, participants react as quickly and accurately as possible to a target stimulus that is preceded by a prime stimulus either mapped to the same response as the target (consistent) or to the alternative response (inconsistent). Typically, in consistent configurations participants respond faster and make fewer errors than in inconsistent configurations. The response priming effect is defined as the difference between response speed or error rates in consistent and inconsistent cases and typically increases with the temporal interval between prime and target onset (stimulus onset asynchrony, *SOA*). Generally, response priming effects occur because the prime activates the response assigned to it (Eimer & Schlaghecken, 1998; Klotz, Heumann, Ansorge, & Neumann, 2007; Leuthold & Kopp, 1998; Schmidt, 2002; Vath & Schmidt, 2007). Specifically, their origin is detailed by the *rapid-chase theory of response priming* (Schmidt et al., 2006; Schmidt 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 (Lamme & Roelfsema, 2000; see Vorberg et al., 2003, for a formal model). 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 time has progressively more time to activate the wrong response. By using online motor measures such as pointing responses 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 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*).[4]

Response priming works irrespective of whether primes are presented at identical or separate positions from the targets, and whether they are masked or unmasked (Vorberg et al., 2003). We used a spatial arrangement where 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. 1A). This arrangement has several advantages. First, the response to the relevant stimulus dimension (e.g., symmetry) is based on the comparison of two stimuli (a 2AFC task). This makes the task easier and allows for faster responses. Second, targets do not cover the same positions as the primes. This precludes masking and temporal integration effects that would complicate the interpretation of the results.

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[4] Note that the rapid-chase criteria do not guarantee that the system is strictly feedback-free (e.g., VanRullen & Koch, 2003) but establish it to be indistinguishable from a pure feedforward system.

This task can be used to study response-time effects in a principled fashion provided by the framework of rapid-chase theory. Rapid-chase theory predicts that priming effects should increase with prime-target SOA (Vorberg et al., 2003). In addition, 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 increase in slower responses would contradict a rapid-chase account. 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 & Schmidt, 2009; Schmidt et al., 2011; 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 and closure processing, we expected that both cues can produce priming effects in fast visuomotor responses. However, only symmetry processing should show signs of automaticity. 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.

Experiment 1

General

In a primed flanker task, 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 in the center of the screen (Fig. 1A). 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).

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 suitable 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 were shown to be more robust against three-dimensional skewing (Wagemans, 1992, 1993; Sawada & Pizlo, 2008), 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 was 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 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.[5]

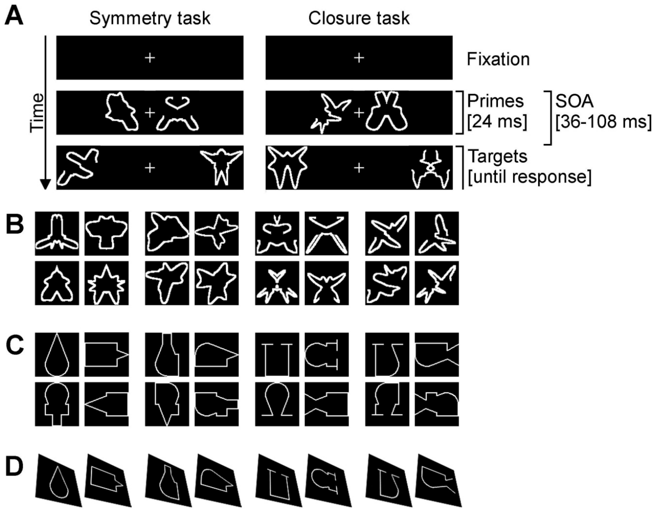

Figure 1. Procedure and stimuli in Experiments 1, 2, and 3. Two primes and two targets were presented in the sequence displayed (A). In the symmetry task, participants responded to either the symmetric or asymmetric target and in the closure task to either the closed or open target. The two primes (and 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 Experiment 1 (B), 2 (C), and 3 (D). Note that primes in Experiment 3 are presented on dark backgrounds that are skewed with the same angles as the primes (30° pitch, 30° yaw, projected onto the frontal plane).

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. Participants were debriefed after the final session and received an explanation of the experiment. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association.

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.

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. 1B). 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 1A. 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 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

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[5] While grouping strength can be easily matched for some grouping dimensions (e.g., similarity in brightness or size; Schmidt & Schmidt, submitted), 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.

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 1000 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 one-hour 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 1000 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. Repeated-measures analyses of variance (ANOVAs) were performed with Huynh-Feldt-corrected *p* values. ANOVAs were fully-factorial with factors of consistency (*C*) and prime-target SOA (*S*). We report *F* values 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.

Results and Discussion

Priming effects. Both tasks in Experiment 1 produced response priming effects in response times and error rates (Fig. 2A). Separate ANOVAs affirmed faster responses and lower error rates in consistent compared to inconsistent trials in the symmetry task [$F_C(1,7) = 37.70$, $p < .001$, and $F_C(1,7) = 32.89$, $p = .001$, for response times and error rates, respectively] and in the closure task [$F_C(1,7) = 38.32$, $p < .001$, and $F_C(1,7) = 18.54$, $p = .004$]. 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 [$F_{CxS}(3,21) = 7.70$, $p = .001$, and $F_{CxS}(3,21) = 7.19$, $p = .003$] and in the closure task [$F_{CxS}(3,21) = 9.80$, $p = .001$, and $F_{CxS}(3,21) = 11.02$, $p < .001$]. This corresponds to earlier findings in response priming experiments (cf., Schmidt et al., 2011; Vorberg et al., 2003).[6]

Finally, with increasing SOA, overall response times became faster and error rates increased in the symmetry task [$F_S(3,21) =$

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[6] Note that errors in inconsistent trials represent motor responses that were misled by the conflicting prime information. This follows from response priming experiments with pointing responses, in which primes initiate a response towards them and sometimes provoke a full-fledged movement to their position (cf. Schmidt et al., 2006), and experiments measuring lateralized readiness potentials (Leuthold & Kopp, 1998; Eimer & Schlaghecken, 1998; Vath & Schmidt, 2007). Priming effects in error rates, as in response times, increase with prime-target SOA because the prime signal has more time to influence the response before the target signal becomes effective (cf. Schmidt et al., 2011; Vorberg et al., 2003).

6.34, *p* = .006; $F_S(3,21) = 5.99$, *p* = .004] as well as the closure task [$F_S(3,21) = 5.55$, *p* = .028; $F_S(3,21) = 17.86$, *p* < .001].

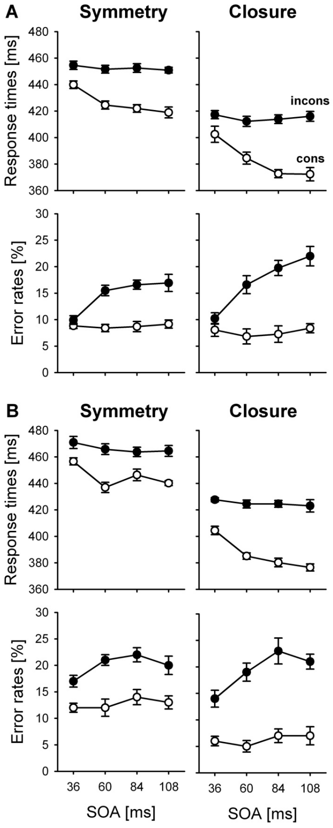


Figure 2. Results of the primed flanker task in Experiment 1 (A) and Experiment 2 (B). The results of the symmetry task are displayed in the left panels, of the closure task in the right panels. Mean response times and error rates in consistent (white) and inconsistent (black) trials are displayed as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

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 [$F_{CxTI}(1,7) = .01$, *p* = .922, and $F_{CxTI}(1,7) = .83$, *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 (Schmidt & Schmidt, submitted), these differences were not analyzed further.

Response time distributions. Our results imply that both grouping cues are analyzed quickly enough to affect speeded motor responses. To study their processing in more detail, we analyzed the response time functions in both tasks. These are obtained by sorting raw response times, separately for each participant and condition (defined by the levels of consistency and SOA in the symmetry and closure task), and then calculating mean response times for 10%-bins ranging from 0% to 100% (Fig. 3A, 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.

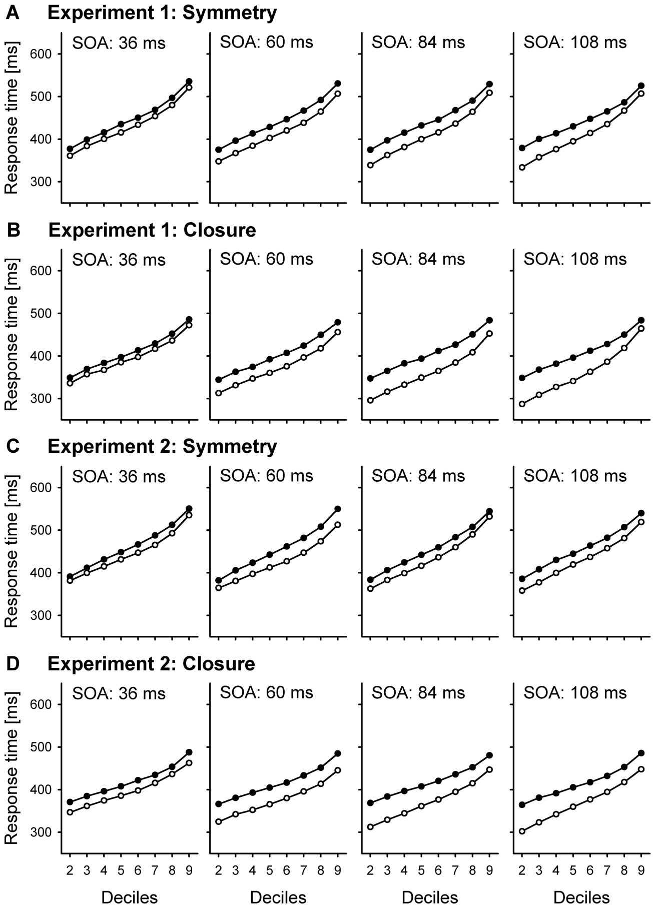


Figure 3. Response time functions for Experiment 1 (A, B) and Experiment 2 (C, D). Response times in consistent (white) and inconsistent trials (black) are displayed as a function of response speed (bins 2 to 9), separately for each task and SOA. It is a strong

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 to 9 in each task were subjected to a repeated-measures ANOVA with factors of consistency (*C*), prime-target SOA (*S*), and percentile (*P*). We will only report the interactions of consistency and percentile. The analysis in the symmetry task (Fig. 3A) revealed an interaction of factors of consistency and percentile [$F_{CxP}(7,49) = 4.49$, $p = .037$] and one of consistency, SOA and percentile [$F_{CxSxP}(21,147) = 2.38$, $p = .030$], showing a decrease of the priming effect in slower responses, particularly in SOAs of 84 ms and 108 ms. This result pattern was repeated in the closure task (Fig. 3B) with interactions of consistency and percentile [$F_{CxP}(7,49) = 4.57$, $p = .042$] as well as of consistency, SOA and percentile [$F_{CxSxP}(21,147) = 3.78$, $p = .007$].

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).

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, neither in the symmetry task [$F_C(1,7) = .81$, $p = .398$; $F_{CxS}(3,21) = .64$, $p = .600$] nor in the closure task [$F_C(1,7) = 1.45$, $p = .268$; $F_{CxS}(3,21) = .25$, $p = .854$]. Thus, in both tasks the respective irrelevant cue was efficiently ignored by the visual system (Seydell-Greenwald & Schmidt, 2012; Tapia, Breitmeyer, & Shooner, 2010).

Experiment 2

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 wanted to generalize and extend those findings by investigating the potential role of the symmetry axis. To this aim, 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.

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. Participants were debriefed after the final session and received an explanation of the experiment. All of them gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association.

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. 1C). 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. 1A). Again, participants performed the two tasks in two one-hour 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 1000 ms. Statistical methods correspond to those adopted in Experiment 1 with the further factor of symmetry axis (*SA*).

Results and Discussion

Priming effects. As in Experiment 1, we observed response priming effects in response times and error rates in the symmetry task [$F_C(1,7) = 18.85$, $p = .003$, and $F_C(1,7) = 25.37$, $p = .002$, for response times and errors, respectively] and the closure task [$F_C(1,7) = 107.84$, $p < .001$, and $F_C(1,7) = 49.73$, $p < .001$] (Fig. 2B). In the closure task, this effect increased with SOA in response times as well as error rates [$F_{CxS}(3,21) = 7.27$, $p = .002$, and $F_{CxS}(3,21) = 3.08$, $p = .050$]. However, in the symmetry task, the priming effects in response times or error rates did not depend on SOA [$F_{CxS}(3,21) = 1.78$, $p = .181$, and $F_{CxS}(3,21) = .74$, $p = .497$].

Finally, as in Experiment 1, with increasing SOA, overall response times became faster and error rates increased in the symmetry task [$F_S(3,21) = 5.45$, $p = .006$, and $F_S(3,21) = 3.59$, $p = .031$] as well as the closure task [$F_S(3,21) = 11.51$, $p < .001$, and $F_S(3,21) = 5.37$, $p = .007$]. Also, priming effects did not depend on task instruction (TI), neither in the symmetry nor in the closure task [$F_{CxTI}(1,7) = .13$, $p = .730$, and $F_{CxTI}(1,7) = .27$, $p = .619$]. Again, response times were about 50 ms slower in the symmetry than in the closure task.

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. 3C, D). We performed repeated-measures ANOVA with factors of consistency (*C*), prime-target SOA (*S*), and percentile (*P*) for response time bins 2 to 9, reporting only the interactions of consistency and percentile. The analysis in the symmetry task (Fig. 3C) revealed neither an interaction of factors of consistency and percentile nor one of consistency, SOA and percentile [$F_{CxP}(7,49) = 1.42$, $p = .276$; $F_{CxSxP}(21,147) = 1.77$, $p = .093$]. Thus, the priming effect was the same in the fastest responses as in the slower ones. In contrast, in the closure task (Fig. 3D) we observed an interaction of consistency and percentile [$F_{CxP}(7,49) = 6.19$, $p = .029$], 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 percentile [$F_{CxSxP}(21,147) = 5.25$, $p < .001$]. 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).

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 neither in the symmetry task [$F_C(1,7) =.59$, $p = .467$; $F_{CxS}(3,21) = .76$, $p = .517$] nor in the closure task [$F_C(1,7) = 2.31$, $p = .173$; $F_{CxS}(3,21) = .57$, $p = .572$], showing that the task irrelevant cue was efficiently ignored by the visual system (Seydell-Greenwald & Schmidt, 2012; Tapia, Breitmeyer, & Shooner, 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 [$F_{CxSA}(1,7) = 3.98$, $p = .086$; $F_{CxSA}(1,7) = .37$, $p = .562$]. Also, we observed no main effect of symmetry axis on response times [$F_{SA}(1,7) = .49$, $p = .831$]. However, participants made fewer errors when primes and targets were reflected horizontally compared to vertically [$F_{SA}(1,7) = 8.19$, $p = .024$]. We will discuss this finding later with reference to the results of Experiment 3.

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, 1998a), we observed no response-time difference between vertical and horizontal symmetry axes.

Experiment 3

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 Fig. 1C are seen from a non-orthogonal line of view, their actual projections on the retina are skewed, for example, as in Fig. 1D. 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. 1C and 1D).

In Experiment 3, we wanted to extend our findings on symmetry processing by investigating the role of viewing position in our paradigm. 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.

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 were debriefed after the final session and received an explanation of the experiment. They gave informed consent and were treated in accordance with the ethical guidelines of the American Psychological Association.

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 degrees about the vertical mid-line and the horizontal mid-line and calculated the resulting projections on the frontal plane (Fig. 1D). 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 Experiment 1 and 2 (cf. Fig. 1A), using the newly constructed prime stimuli. Participants performed the task in two one-hour 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 1000 ms in the first and second session, respectively. Statistical methods correspond to those adopted in Experiment 2 with the further factor of framing (*F*).

Results and Discussion

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

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

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 strong priming effects in response times as well as error rates [$F_{C}(1,7) = 102.42$, $p < .001$ and $F_{C}(1,7) = 51.02$, $p < .001$, respectively] that effect was neither modulated by SOA nor framing [response times: $F_{CxS}(3,21) = .31$, $p = .780$; F_{CxF} $(1,7) = 1.60$, $p = .247$; $F_{CxSxF}(3,21) = 2.04$, $p = .144$; error rates: $F_{CxS}(3,21) = 1.20$, $p = .329$; $F_{CxF}(1,7) = 1.30$, $p = .291$;

$F_{CxSxF}(3,21) = .62$, $p = .610$] (Fig. 4). In contrast to Experiment 2, we observed no main effect of SOA [$F_{S}(3,21) = 1.65$, $p = .209$; $F_{S}(3,21) = .61$, $p = .615$]; however, there were main effects of symmetry axis on error rates [$F_{C}(1,7) = 20.56$, $p = .003$] and response times [$F_{SA}(1,7) = 10.60$, $p = .014$] as well as an interaction effect of symmetry axis and framing on response times [$F_{SAxF}(1,7) = 8.47$, $p = .023$]. 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 (3.42 ms versus 11.13 ms). Error rates did not significantly differ between both sessions of Experiment 3 [$F_{F}(1,7) = .29$, $p = .606$] (session 1: 11.04% and session 2: 10.15%), making a speed-accuracy trade-off unlikely.

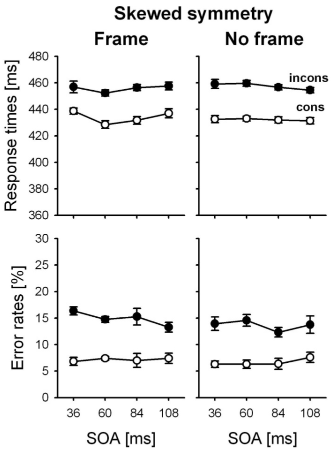
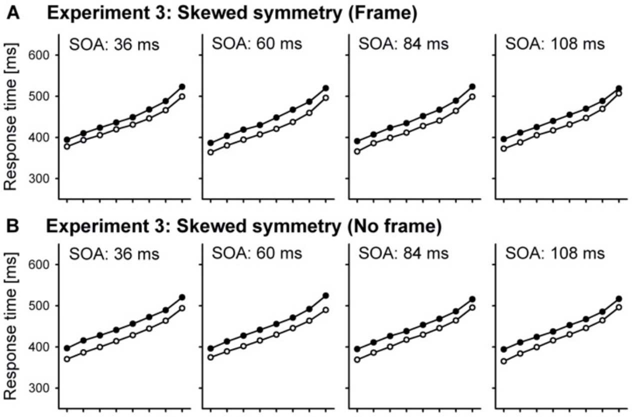


Figure 4. Results of the primed flanker task in Experiment 3. For specifications see Fig. 2.

The role of skewing. Finally, we compared the results in Experiment 2 and the two sessions of Experiment 3 for the six participants that participated 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: $F_{EXP}(2,10) = .30$, $p = .658$; $F_{CxEXP}(2,10) = .91$, $p = .435$; error rates: $F_{EXP}(2,10) = 4.74$, $p = .076$; $F_{CxEXP}(2,10) = .03$, $p = .901$] although the power with six participants was sufficient to discover the priming effects in response times [$F_{C}(1,5) = 29.45$, $p = .003$] and error rates [$F_{C}(1,5) = 78.36$, $p < .001$]. 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 [$F_{SAxEXP}(2,10) = 6.02$, $p = .048$]. Note, however, that this effect is small and only observed in plain error rates, not in priming effects or response speeds [response times: $F_{SAxEXP}(2,10) = .84$, $p = .440$; $F_{CxSAxEXP}(2,10) = 1.11$, $p = .368$; error rates: $F_{CxSAxEXP}(2,10) = .61$, $p = .519$]. Therefore, we refrain from a further interpretation of this interaction effect.


A Experiment 3: Skewed symmetry (Frame)

B Experiment 3: Skewed symmetry (No frame)

Figure 5. Response time functions for sessions 1 and 2 of Experiment 3 (A, B). For specifications see Fig. 3.

Response time distributions. Analyses of the response time functions revealed no significant interactions of the factors consistency and percentile neither in session 1 nor 2 (Fig. 5A, B) [$F_{CxP}(7,49) = .62$, $p = .528$, and $F_{CxP}(7,49) = .49$, $p = .670$, respectively]. 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 percentile [$F_{CxPxEXP}(14,70) = 1.52$, $p = .232$], meaning that skewing had no relevance for the early processing of the symmetry primes.

Conclusion

In sum, 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 will discuss this issue in the next section.

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 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 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 later 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 versus asymmetric or closed versus 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 will 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.

Temporally efficient processing of symmetry and closure

One measure of efficiency of 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 were shown to reliably discriminate between simple symmetric and asymmetric shapes with presentation times as short as 25 ms (Carmody et al., 1977), and in random dot patterns for presentation times as short 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 versus 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 short 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.

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, Fize, & Marlot, 1996; VanRullen & Koch, 2003) the theory does not preclude quick feedback between visual areas and local recurrent activity – 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; Schmidt et al., 2011). 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.

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 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 widespread 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 contrasted. From this contrast it is possible to determine the earliest point in time when symmetry-specific processing starts. While our data contrast with studies showing only late symmetry-specific activation between 500-1000 ms after stimulus presentation (with abstract geometric stimuli, Jacobsen & Höfel, 2003; Höfel & Jacobsen, 2007), 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.

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 the primary visual cortex (V1) (Bauer & Heinze, 2002) as well as by feedback from extrastriate areas higher in the visual hierarchy (Zipser, Lamme, & Schiller, 1996). Still, Houtkamp and Roelfsema (2010; 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).

Automaticity of symmetry and closure processing

Although our findings illustrate the speed of symmetry and closure processing, they do not argue for its automaticity. 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 irrelevant (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 and are thus in contrast to the notion 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 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 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.

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 (neither framed nor 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 will 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, 1998a). 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, 1981), or even reported that horizontally oriented stimuli were processed more easily (Jenkins, 1983; Pashler, 1990). Wagemans and colleagues (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 compared to contour stimuli (Sawada & Pizlo, 2008) and also lead to slower response times (Wagemans, 1993). Nevertheless, some studies found 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 will first describe the general role of the factors skewing and framing and after that we will discuss their interaction with the symmetry axis.

Viewpoint-invariance of symmetry processing

In contrast to evidence from earlier studies which showed a strong influence of skewing on symmetry detection performance and speed (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 shortly 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 also 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 were shown without a frame. Although several studies reported interacting effects of symmetry axis and skewing on output measures, the exact type of this interaction was complex (Wagemans, 1993; Wagemans et al., 1991, 1992).

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 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.

Acknowledgments

Filipp Schmidt, Thomas Schmidt, University of Kaiserslautern, Faculty of Social Sciences, Psychology I. Correspondence may be sent to either author (filipp.schmidt@sowi.uni-kl.de, thomas.schmidt@sowi.uni-kl.de). We thank Shanley Allen, Neiloufar Family, Kalliopi Katsika, Mark Calley, Andreas Weber, Alina Kholodova, and Anke Haberkamp for comments on an early version of the manuscript and Michael Herzog, Rob van Lier, Johan Wagemans, and Rufin VanRullen for helpful suggestions. This research was supported by Schm1671/1-5 of the German Research Foundation to T.S.

References

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

Barlow, H. B., & Reeves, B. C. (1979) The versatility and absolute efficiency of detecting mirror symmetry in random dot displays. *Vision Research, 19,* 783-93. doi:10.1016/0042-6989(79)90154-8

Bauer, R., & Heinze, S. (2002). Contour integration in striate cortex. Classic cell responses or cooperative selection? *Experimental Brain Research, 147,* 145–152. doi:10.1007/s00221-002-1178-6

Baylis, C. G., & Driver, J. (1994). Parallel computation of symmetry but not repetition within visual shapes. *Visual Cognition, 1,* 377–400. doi:10.1080/13506289408401715

Bertamini, M. (2010). Sensitivity to reflection and translation is modulated by objectness. *Perception, 39,* 27–40. doi:10.1068/p6393

Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews, 36,* 96-107. doi:10.1016/S0165-0173(01)00085-6

Carmody, D. P., Nodine, C. F., & Locher, P. J. (1977). Global detection of symmetry. *Perceptual and Motor Skills, 45,* 1267-1273. doi:10.2466/pms.1977.45.3f.1267

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. T*utorials in Quantitative Methods for Psychology, 1,* 42-45.

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.

Driver, J., Baylis, G. C., & Rafa, R. D. (1992). Preserved figure-ground segregation and symmetry perception in visual neglect. *Nature, 360,* 73-75. doi:10.1038/360073a0

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

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. doi:10.1016/0042-6989(93)90080-G

Elder, J. H., & Zucker, S. W. (1998). Evidence for boundary-specific grouping. *Vision Research, 38,* 143-152. doi:10.1016/S0042-6989(97)00138-7

Enns, J. (1986). Seeing textons in context. *Perception & Psychophysics, 39,* 143-147. doi:10.3758/BF03211496

Enquist, M., & Arak, A. (1994). Symmetry, beauty and evolution. *Nature, 372,* 169-172. doi:10.1038/372169a0

Friedenberg, J., & Bertamini, M. (2000). Contour symmetry detection: the influence of axis orientation and number of objects. *Acta Psychologica, 105,* 107-118. doi:10.1016/S0001-6918(00)00051-2

Garrigan, P., Fortunato, L., & LaSala, A. (2010). The Effects of Closure on Contour Shape Learning. *Journal of Vision, 10,* 1167. doi: 10.1167/10.7.1167

Höfel, L., & Jacobsen, T. (2007). Electrophysiological indices of processing aesthetics: Spontaneous or intentional processes? *International Journal of Psychophysiology,* 65, 20–31. doi:10.1016/j.ijpsycho.2007.02.007

Houtkamp, R., & Roelfsema, P. R. (2010). Parallel and serial grouping of image elements in visual perception. *Journal of Experimental Psychology: Human Perception and Performance, 36,* 1443-1459. doi: 10.1037/a0020248

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. doi:10.3758/CABN.3.4.289

Jenkins, B. (1983). Component processes in the perception of bilaterally symmetric dot textures. *Perception & Psychophysics, 34*, 433-440. doi:10.3758/BF03203058

Julesz, B. (2006). F*oundations of Cyclopean Perception.* Cambridge: MIT Press. (Original published in 1971).

Kanbe, F. (2008). Role of endpoints and closure in feature search. *Japanese Psychological Research, 50,* 145-151. doi:10.1111./j.1468-5884.2008.00371.x

Kiesel, A., Kunde, W., & Hoffmann, J (2007). Mechanisms of subliminal response priming. *Advances in Cognitive Psychology, 3,* 307-315. doi:10.2478/v10053-008-0032-1

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.

Koffka, K. (1935). *Principles of Gestalt psychology.* London: Routledge & Kegan Paul.

Koning, A., & Van Lier, R. (2006). No symmetry advantage when object matching involves accidental viewpoints. *Psychological Research, 70,* 52-58. doi:10.1007/s00426-004-0191-8

Koning, A., & Wagemans, J. (2009). Detection of symmetry and repetition in one and two objects: structures versus strategies. *Experimental Psychology, 56,* 5-17. doi:10.1027/1618-3169.56.1.5

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 of the United States of America, 90,* 7495-7497.

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. doi:10.1016/S0166-2236(00)01657-X

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

Locher, P. J., & Wagemans, J. (1993). The effects of element type and spatial grouping on symmetry detection. *Perception, 22,* 565-587. doi:10.1068/p220565

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. doi:10.1167/9.12.11

Marino, A. C., & Scholl, B. J. (2005). The role of closure in defining the “objects” of object-based attention. *Perception & Psychophysics, 67,* 1140-1149. doi:10.3758/BF03193547

Mathes, B., & Fahle, M. (2007). Closure facilitates contour integration. *Vision Research, 47,* 818-827. doi:10.1016/j.visres.2006.11.014

Mori, S. (1997). Effects of absolute and relative gap sizes in visual search for closure. *Canadian Journal of Experimental Psychology, 51,* 112-124. doi:10.1037/1196-1961.51.2.112

Niimi, R., Watanabe, K., & Yokosawa, K. (2005). The role of visible persistence for perception of visual bilateral symmetry. *Japanese Psychological Research, 47,* 262-270. doi:10.1111/j.1468-5884.2005.00295.x

Niimi, R., & Yokosawa, K. (2008). Determining the orientation of depth-rotated familiar objects. *Psychonomic Bulletin & Review, 15,* 208-214. doi:10.3758/PBR.15.1.208

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,* 132–139. doi:10.1167/2.2.1

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. doi:10.1016/j.visres.2007.03.020

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. doi:10.1037/0096-1523.4.4.691

Pashler, H. (1990). Coordinate Frame for Symmetry Detection and Object Recognition. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 150-163. doi:10.1037/0096-1523.16.1.150

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. doi:10.1016/S0042-6989(00)00110-3

Rock, I., & Leaman, R. (1963). An experimental analysis of visual symmetry. *Acta Psychologica, 21,* 171-183. doi:10.1016/0001-6918(63)90047-7

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

Roland, P. E. (2010). Six principles of visual cortical dynamics. *Frontiers in Systems Neuroscience, 4:28*. doi:10.3389/fnsys.2010.00028

Saarinen, J., & Levi, D. M. (1999). The effect of contour closure on shape perception. *Spatial vision, 2,* 227-238. doi:10.1163/156856899X00139

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. doi:10.1073/pnas.0500319102

Sawada, T., & Pizlo, Z. (2008). Detection of skewed symmetry. *Journal of Vision, 8(5): 14,* 1-18. doi:10.1167/8.5.14

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.* doi:10.3389/fpsyg.2011.00169.

Schmidt, F., Haberkamp, A., & Schmidt, T. (2011). Dos and Don'ts in Response Priming. *Advances in Cognitive Psychology, 7,* 120-131. doi:10.2478/v10053-008-0092-2

Schmidt, T., Niehaus, S., & Nagel, A. (2006). Primes and targets in rapid chases: Tracing sequential waves of motor activation. *Behavioural Neuroscience, 120,* 1005-1016. doi:10.1016/j.neuroscience.2006.11.044

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

Schmidt, F., & Schmidt, T. (submitted). *Grouping principles in direct competition.*

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.

Seydell-Greenwald, A., & Schmidt, T. (2012). Rapid activation of motor responses by illusory contours. *Journal of Experimental Psychology: Human Perception and Performance, 38*, 1168-1182.

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. J., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature, 381,* 520-522. doi: 10.1038/381520a0

Treder, M. S. (2010). Behind the looking glass: a review on human symmetry perception. *Symmetry, 2,* 1510-1543. doi:10.3390/sym2031510

Treisman, A., & Paterson, R. (1984). Emergent features, attention, and object perception. *Journal of Experimental Psychology: Human Perception and Performance, 10*, 12-31. doi:10.1037/0096-1523.10.1.12

Treisman, A., & Souther, J. (1985). Search asymmetry: A diagnostic for preattentive processing of separable features. *Journal of Experimental Psychology: General, 114,* 285-310. doi:10.1037/0096-3445.114.3.285

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. doi:10.1016/j.neuroimage.2004.09.018

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. doi:10.1016/j.visres.2009.08.015

VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? *Trends in Cognitive Sciences, 7,* 207-213. doi:10.1016/S1364-6613(03)00095-0

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. doi: 10.1068/p3029

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

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. doi:10.1037/0096-1523.19.2.364

Wagemans, J. (1995). Detection of visual symmetries. *Spatial Vision, 9,* 9-32. doi:10.1163/156856895X00098

Wagemans, J. (1997). Characteristics and models of human symmetry detection. *Trends in Cognitive Sciences, 1,* 346-352. doi:10.1016/S1364-6613(97)01105-4

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. doi:10.3758/BF03205058

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. doi:10.1080/14640749208401295

Wagemans, J., Van Gool, L., Swinnen, V., & Van Horebeek, J. (1993). Higher-order structure in regularity detection. *Vision Research, 33,* 1067–1088. doi:10.1016/0042-6989(93)90241-N

Wenderoth, P. (1994). The salience of vertical symmetry. *Perception, 23,* 221-236. doi:10.1068/p230221

Wenderoth, P. (1997). The effects on bilateral symmetry detection of multiple symmetry, near symmetry, and axis orientation. *Perception, 26,* 891-904. doi:10.1068/p260891

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 Section A: Human Experimental Psychology, 53,* 165-190.

Wenderoth, P., & Welsh, S. (1998a). Effects of pattern orientation and number of symmetry axes on the detection of mirror symmetry in dot and solid patterns. *Perception, 27,* 965-976. doi:10.1068/p270965

Wenderoth, P., & Welsh, S. (1998b). The effects of cuing on the detection of bilateral symmetry. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology, 51,* 883-903. doi:10.1080/027249898391431

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

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