

Time window(s) of cued visual selection

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The time course of cued target identification was measured in different feature dimensions. Spatially cued targets were generally identified in short time windows which varied between features and observers, but attention could also be held for later targets if the cued location was empty or the requested information not yet available. For orientation, color, and luminance polarity, but not for motion, target properties were faster seen than cues detected; instead of reporting the properties of the physically cued target observers reported the properties of a later target at the cued location. That is, the effective cuing windows were delayed. Different directions of target movement, however, were identified about in synchrony with the cue. These differences confirm earlier reports of an asynchronous perception of color, orientation, and motion. In the context of cued visual selection (CVS), the experiments confirm that cuing and cued target selection provide a spatially and temporally relatively precise access to the dynamics of neural processes in visual perception. © Author

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INTRODUCTION

Cued visual selection (CVS) describes the phenomenon that a single item in an ensemble of many items is cued and thus selected. Observers can then quickly identify this target without having it memorized from the previous presentation (for a demo, see www.vpl-goettingen.de/cvs/). Earlier experiments (Nothdurft, 2017a, b) had suggested that the speed of target identification may be closely related to the ongoing dynamics of neural representations; the larger the response, the shorter the accumulation time needed to identify the target. This raised questions about the exact timing of cued perception in these experiments. Are cues and targets perceived at the same time, or is there a delay between cue presentation and target perception? And if so, does the delay depend on what the target looks like and which of its properties have to be identified? I have addressed these questions in a number of experiments some of which were intermingled with other, already published tests.

My original approach had been straight forward; I measured target identification rates, at various cue delays

and for various target durations, and compared them with the dynamics of neural activity patterns reported in other studies. But were cues and targets indeed independent parameters in these tests? In the classical cuing experiments by Posner and colleagues (e.g., Posner, 1980; Posner, Snyder, & Davidson, 1980) cues and targets were considered as unconnected stimuli that can be separately manipulated. Cues were literally applied as hints or pointers to the probable location of a later presented target. With certain delays this has led to faster reactions and better target visibility, such as if the neural resources for these processes were attracted and concentrated at the location of the cue—a phenomenon metaphorically described as shifting the "spotlight of attention" (Posner, 1980). However, such attention shifts may include several distinct sub-processes, like preparation, guidance, selection, and identification (Eimer, 2014), which all may take their time to become effective. Should CVS then not suffer from various operational delays before the target is selected and identified?

The dynamics of attentional cuing have challenged vision researchers for several decades. Already Posner and

colleagues (Posner, 1980) had shown that valid cues may *shorten* the reaction times to a test stimulus presented 150-200 ms after the cue but *prolong* reaction times when the test stimulus was presented a little later (>300 ms; Posner and Cohen, 1984), a phenomenon later referred to as "inhibition of return" (cf. Klein, 2000). Numerous subsequent studies have reported that attentional cuing may follow different time courses and delays, depending on (i) how the cues were presented, (ii) which target properties had to be detected or discriminated, and (iii) which reactions observers should make in the response to the attended stimulus. Many studies compared the reaction times of observers with cued and non-cued targets (e.g., Posner, 1980; Posner & Cohen, 1984; Folk, Remington, & Johnston, 1992; Benso, Turatto, Mascetti, & Umiltà, 1998; Huang *et al.*, 2017), but quite a few studies have also reported perceptual variations, e.g. differences in the number of correctly identified targets when these were briefly presented and eventually masked (e.g., Kröse & Julesz, 1989; Müller & Rabbitt, 1989; Chastain, 1992; Chastain & Cheal, 1998; Gottlob, Cheal, & Lyon, 1999; Wilschut, Theeuwes, & Olivers, 2011). Also saccades and saccadic reaction times were found to reflect attentional variations (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Hickey, van Zoest, & Theeuwes, 2010; van Zoest, Donk, & Van der Stigchel, 2012; van Zoest, Van der Stigchel, & Donk, 2017; Weaver, van Zoest, & Hickey, 2017), but because of the strong top-down control of eye movements these effects were often hidden and only visible in very fast saccades after stimulus onset; they are generally considered as less reliable than manual reaction times (Wermer, Lincoln, & Helbig-Lang, 2017). Since already the speed of purely sensory target identification may vary in time (Moutoussis and Zeki, 1997a,b; Viviani & Aymoz, 2001; McIntyre & Arnold, 2018), without any cuing, it should not be surprising if additional attention effects might also generate large variations in the detection and discrimination of different features and targets.

Different modes of attentional cuing. Particularly large variations should be expected with the different modes of attentional cuing. There is general agreement in the literature that time courses differ between endogenous and exogenous spatial cuing, i.e., when cues are either symbolic pointers (often delivered at a central position near the fixation point) or local markers applied at the expected target location. Exogenous ("reflexive", "involuntary") cuing is fast (50-500 ms); cuing effects

become visible almost immediately after the cue and reach their maximum at delays of 100-300 ms (Kröse & Julesz, 1989; Benso, Turatto, Mascetti, & Umiltà, 1998; Chastain & Cheal, 1998; Gottlob, Cheal, & Lyon, 1999; Wilschut, Theeuwes, & Olivers, 2011; Huang *et al.*, 2017). Endogenous ("directed", "voluntary") cuing is notably slower (150-1000 ms); cuing effects need more time to develop and reach their maximum later (Müller & Rabbitt, 1989; Chastain & Cheal, 1998; Carlson, Hogendoorn, & Verstraten, 2006; Chakravarthi & VanRullen, 2011; Huang *et al.*, 2017). Other attractors of attention, like faces (vs. other objects; Bindemann, Burton, Langton, Schweinberger, & Doherty, 2007) and emotional cues (e.g., fearful or threatening faces; Müller, Andersen, & Attar, 2011; Jiang, Wu, Saab, Xiao, & Gao, 2018; see also Silvert & Funes, 2016), need generally longer (>300-1000 ms) to show measurable effects. Also feature-based attention shifts seem to be slow (Valdes-Sosa, Bobes, Rodriguey, & Pinilla, 1998; Liu, Stevens, & Carrasco, 2007; Andersen & Müller, 2010; Jenkins, Grubert, & Eimer, 2018) and certainly slower than exogenously cued attention shifts to spatial locations. In standard CVS experiments, the cuing is exogenous and should thus be particularly fast.

Attentional windows in visual search. Beyond the delay until an attentional process begins to work, also the time windows needed to identify a target are important parameters in CVS. The model that cues may attract, guide, and control the limited resources of *spatial attention* was supported and extensively studied in experiments on visual search (e.g., Treisman and Gelade, 1980; see, e.g., Wolfe, 1998), although the cuing aspect itself was perhaps not quite obvious to the first researchers. Targets with certain properties were quickly found such as if attention was either not necessary ("pre-attentive" search; Treisman, 1985; cf. Braun & Sagi, 1990; but see Joseph & Optican, 1996; Joseph, Chun, & Nakayama, 1997; Nothdurft, 1999) or was immediately attracted by accompanying stimulus properties (e.g., salience; Nothdurft, 2006). Other targets needed more time to be found and identified; it was assumed that they had to undergo a different and longer lasting search process that would include many serial attention shifts between items until the target was eventually found. In this model of "serial, attentive" search, the time to find the target (or to finish the search if the target was absent) should be proportional to the number of items; search

times divided by the number of inspected items should then reveal the mean duration of the attentional identification process repeatedly spent on individual items. These calculations, however, varied between observers and test conditions and did not lead to consistent results. Apparently, observers did not always shift their attention between individual items but sometimes inspected several items *en bloc*, which should then have led to an underestimate of the individual target's inspection times and of attentional time courses. In various attempts to measure the "attentional dwell time" in human vision with other experimental techniques, much longer durations were found (Duncan, Ward, Shapiro, 1994; Ward, Duncan, Shapiro, 1996; see also Hogendoorn, Carlson, & Verstraten, 2007; Longman, Lavrie, Munteanu, & Monsell, 2014).

While numerous studies have investigated which items are detected fast or not, it took researchers quite a while to notice that fast visual search may, in fact, be based on a similar cuing process as finding a salient target (Nothdurft, 2002; but see already Nakayama & Mackeben, 1989). Target salience is achieved from various stimulus properties, including feature contrast, that are not necessarily identical but often associated with target features in the tested patterns (Nothdurft, 2006). Targets that appeared salient from the target context, were faster found than the same targets arranged so that they were not salient from the target context (Nothdurft, 1992). Beyond of that, salient targets may attract attention in a similar way as cues do, and both lead to a similarly fast target selection and identification (Nothdurft, 2002).

The time course of cued visual selection. It appeared difficult to combine all the various measures of attention effects in different conditions and make an exact prediction of time courses and delays in the cued target identification of CVS. However, since cue and target properties in these experiments were standardized and since the temporal accuracy of cued selection is important for conclusions on the data, I decided to perform the measurements directly in the CVS paradigm. In the present study I tried to measure the attentional cuing windows and the relative delays of cues and perceived targets. It turned out that the *selection* process evoked by the cue could remain valid for rather long delays and still helped to identify late targets when there was no other information to be reported. This is comparable to the classical cuing condition, in which the (early) cue

indicates the probable target location; the cuing dynamics themselves varied, however, showing faster and slower reactions times at different delays (Posner, 1980; Posner & Cohen, 1984). In this condition in CVS, the cued selection could be held for several seconds but performance was found to slowly deteriorate over time (Nothdurft, 2017a, Exp.1). But when the cuing was applied to rivaling, withdrawn or masked target information, the cued evaluation of target properties was better timed. Such an exact timing should be necessary if cues were used to look at the underlying neural activity in perceptual processes, as is attempted with CVS (Nothdurft, 2017a, b, 2018).

Overview of the present study. I have measured the dynamics of cues and cued target identification in three series of experiments with different experimental approaches. In a mechanistic model, cuing can be seen as opening a temporally limited access to the neural representation of cued information. Target information presented during that window should be extracted best. This has two consequences. Since cues themselves must first be encoded in receptors and neurons to become effective, there should be a principal delay between the physical onset of a cue on the retina and its efficiency in the brain. This delay is not necessarily identical to the delay at which other target properties are encoded (like a bright stimulus might be faster encoded than a dim stimulus). In addition, target evaluation may require time both for the accumulation of neural signals and for the processing of certain properties before the target is reliably identified (cf. Nothdurft, 2017a). Both temporal processes may affect the perception and identification of cued targets in various ways. (i) A cued target might already be seen even when it was presented after the cue. This was tested in Experiment 1. (ii) Cues presented in dynamic patterns may perceptually extract the target properties (e.g., their orientation or color) at the moment of the cue, or perhaps a little earlier or later. This was tested in Experiment 2. (iii) The dynamics of cued visual perception may become particularly obvious when cues are presented in synchrony with a single visual event. Depending on when the cue is shown, that event may be seen or not. This was tested in Experiment 3. While it seems plausible to assume that the timing of cuing itself is constant for a given form and location of the cue, it would be particularly interesting to see if cuing effects might vary between different target features. Therefore, Experiments 2 and 3 were performed on target variations in different feature dimensions.

Altogether, the experiments showed that the timing of cues and targets plays an important role in CVS, revealing systematic differences between feature dimensions and considerable variations between observers. Within these variations, however, cuing is generally precise enough to allow for a timed analysis of the cued information.

GENERAL METHODS

Overview

The experiments were designed to measure the time course of exogenously cued visual selection. Observers saw regular arrangements of lines or squares, in which one item (the target) was briefly marked by a local cue; this target had then to be identified. By dynamic variations of target properties before and after the cue, the delay of cue efficiency and the necessary integration time for target analysis were measured.

In three series of experiments, different patterns and presentation dynamics were used. In Experiment 1, cues were applied, with various delays, around the target onset and offset to measure the speed at which target properties are analyzed. In Experiment 2, target features alternated in time, and cues were applied at various delays within the stimulus cycle to measure which information was actually seen. In Experiment 3, finally, cues were applied at various delays around a single event and it was measured at which delays this event could be detected and identified. In all experiments, observers had to report certain properties of the cued target by pressing different buttons on a computer keyboard. To compare the cuing dynamics for different features, the following stimulus dimensions were tested: orientation (Exp.1-3), color (Exp.2-3), luminance polarity (Exp.3), and motion direction (Exp.3).

Stimuli

All stimuli were generated with DOS VGA techniques on a 15" *ultra-high resolution* monitor (Ergo-View 15; Sigma Designs). The viewing distance was 67 ± 1.5 cm. Distance variations were due to head size differences between observers who had their heads conveniently leaned against the wall (cf. Nothdurft, 2017b); for each observer the viewing distance was constant in all experiments. Refreshing rate was 100 Hz resulting in a temporal resolution of 10 ms between subsequent display frames on the monitor. In one experiment (mentioned

there) a refreshing rate of 60 Hz (temporal resolution 16.7 ms) was used with one observer.

Patterns (cf. Figs 1, 3, and 10) displayed either lines or squares (rhomboids) arranged in a 9 x 9 rectangular raster (raster width 1.8 deg); the entire stimulus covered an area of approximately 15 deg x 15 deg. The center element of the raster was spared and a fixation point (0.1 deg x 0.1 deg, usually green) was shown instead. Three different item patterns were used. (A) In patterns used to measure the cuing window for *orientation* discrimination, items were lines at one of two oblique orientations ($\pm 45^\circ$). In Experiment 1 these lines were briefly presented and afterwards masked by the superimposition of both (orthogonal) line orientations at an increased contrast (Fig.1). In Experiments 2 and 3 (Figs.3 and 10) the lines alternated with their orthogonal counterparts. Lines were 0.8 deg x 0.2 deg and were shown in a regular raster with no positional jitter. (B) In patterns used for cuing *color* or *luminance* discrimination, items were red vs. green or dark vs. bright rhomboids (0.6 deg x 0.6 deg; cf. Figs.3 and 10). The red and green color patches were individually matched for equal luminance with each observer. (C) In patterns used to measure the timing of cued *movement direction* sensitivity, items were vertical lines (0.7 deg x 0.2 deg) that jumped randomly to the left or right ($4' = 0.07$ deg; cf. Fig.10a). To avoid conclusions from alignment variations, a random positional jitter of up to ± 0.15 deg was applied to raster cells in this stimulus. In all patterns, the chosen orientation, color, or movement direction was randomly assigned to each item; the assignments were refreshed in every new trial. All dynamic variations, i.e., changes in line orientation, item color, and single-step movements, were simultaneously applied to *all* items in the pattern; the report of target properties however, was restricted to the target, i.e. the single item in the raster that was randomly cued and thus selected.

Cues were arrangements of four little squares around the target (*four-dot cues*), each 0.2 deg x 0.2 deg, which were located 0.6 deg from the target center in the four oblique directions (cf. Fig. 1). For moving targets, cues were centered around the midpoint of movement. To reduce the large performance variations from crowding in such patterns (Nothdurft, 2017a) but nevertheless keep the uncertainty of cuing locations large enough to evoke *cued* visual selection, possible *target locations* were restricted to certain raster positions (indicated in the Mask pattern in Fig.1). These restrictions were the same in all experiments. Subjects were not informed about the restraints.

All stimuli except the fixation point (usually green) and the items in patterns with color or luminance variations were white (gray) on dark background. *Luminance settings* were 10.5 cd/m² for lines, 32 cd/m² for masking lines, 62 cd/m² for cues, and 47 cd/m² for the central fixation point (green), all presented on a screen background of about 3 cd/m². In patterns with red and green rhomboids (about 22 cd/m²), color settings were individually adjusted for best *equal luminance* by minimizing the apparent flicker in heterochromatic flicker photometry. In these patterns, the fixation point was white (20 cd/m²). Patterns in which targets had to be distinguished for their contrast polarity to the background (Fig.10), white (40 cd/m²) and dark (0.5 cd/m²) rhomboids were presented on an intermediate background of about 20 cd/m² which generated a similar Weber contrast for dark and bright targets.

Timing of cues

In all experiments, test patterns underwent dynamic changes during presentation. Lines were switched on and off, changed their orientation, or moved (jumped) to the left or right, and items changed their color or contrast polarity. Cues were shown (one per trial) at various delays in the dynamic process; they were always presented for 20 ms (33 ms in the one case with a 60 Hz frame rate). This short time was sufficient to let all observers detect and locate the cue. Subjects were asked to indicate the target properties they saw when the cue occurred; percepts depended on the cue delay and its occurrence in the actual pattern dynamics. Identification was high in certain conditions but could fall down to chance level (50% performance) in others.

Procedures

All stimuli were viewed binocularly. Trials started with a 500 ms presentation of the fixation point before any stimulus pattern or cue was shown. In most experiments, cues were superimposed on the current pattern about 500-800 ms later. When the test pattern was masked (Exp.1), also the mask was shown for 500 ms. In tests with alternating patterns (Exp.2), stimulus patterns flickered for at least 500 ms before the cue was presented; measurements then began with the first new cycle after this period. For slow flicker rates (long cycle times) the initial cue-free flickering period could thus be notably longer than 500 ms. Flickering continued until a response was made (maximally 10 s). The exact presentation time varied between runs and will be given below. After each

trial the screen was blanked and only the fixation point remained visible. Subjects could enter their responses without time pressure. About one second after the response, a new trial began.

Responses were made in a modified 2AFC task (Nothdurft, 2017b) by pressing certain keys on a computer keyboard. The modifications were: Subjects could reject, and later repeat, a trial if they felt they had been inattentive during presentation (very rarely used), and they could change their response immediately after a trial if they noticed they had pressed the wrong key (occasionally used, mainly in the first runs of a new test series). In some tests, the selection of response keys was intuitively clear, like those for targets tilted to or moving to the left (left-hand "<" key) or to the right (right-hand ">" key; German keyboard layout). For other targets the selections ("<" for red or dark, ">" for green or bright) had to be learned and memorized; the valid assignments were also sketched below the monitor screen. All observers became immediately familiar with the tasks and quickly with the keys to use; 1-2 initial training runs were sufficient to reach constant and reliable performance levels. All tests were blocked for same target features and response categories; tests with different target features were never intermingled in such a block.

Trials were grouped into runs, which usually covered all test conditions (cue delays) of one particular test series. Within each run, test conditions were randomly intermixed, each with 10-20 repetitions. In the course of an experiment, different runs were repeated in an interleaved sequence, to generate a final data base with usually 100 repetitions of every test condition. Experiments were carried out in sessions of 2h, each covering several tested runs. Subjects could pause whenever they wanted.

All tasks in the present study were performed *under fixation* which was controlled for with a video camera focused upon the subject's eyes. Controls were frequently made during the first sessions of every subject and regularly repeated in later sessions. All subjects quickly learned to perform the task without moving the gaze. Since subjects were asked to report what they saw with the (briefly presented) cue, there was no benefit from moving the eyes (cf. Fischer *et al.*, 1993).

Subjects

Analysis in this paper is based on the data from eight subjects (four female, four male), most of them students at

the Göttingen University. Seven subjects in the age of 20-24 years were paid for the time they spent in experiment. The eighth subject was the author who was 55 years old when the measurements began. All subjects had normal or corrected-to normal visual acuity on both eyes and, except the author, were naive as to the aim of the experiments. All subjects had carried out other experiments with cued target identification before.

RESULTS

The time windows of cued visual selection were studied in three series of experiments.

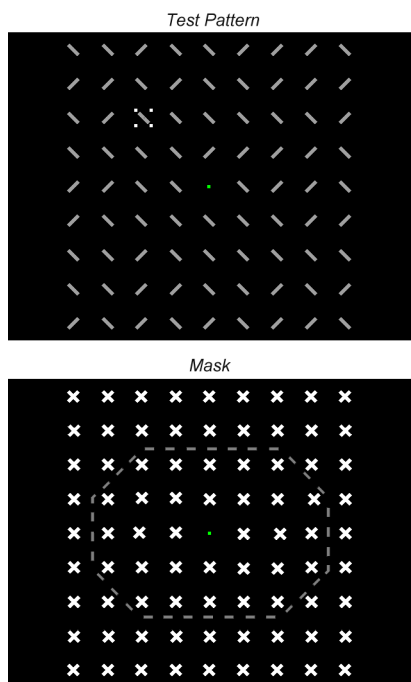


Figure 1. Test patterns in Experiment 1. Like in other CVS experiments, the test pattern was switched on and later masked, while one item was briefly marked with a four-dot cue. Observers had to indicate the orientation of the cued target. In the present Experiment 1, cues were given around pattern or mask onsets to measure the dynamics of cued target identification. Possible target locations were restricted to fovea-near regions as indicated by dashed lines in the lower pattern; these lines are only drawn for illustration and were not visible in the experiment. The fixation point in these patterns was green.

Experiment 1:

Target visibility around stimulus onset and offset

The first experiment was a modification of an experiment from the original CVS study (Nothdurft, 2017a). Patterns were made of 80 lines randomly tilted to the left or right; one of these lines was briefly cued and observers had to report the orientation of the cued target. Cue delays and target presentation times were systematically varied; thereafter all lines were masked. In the original experiment, data had revealed strong variations of the required target presentation time for reliable ratings; the modulation occurred in synchrony with target onset, not the cue, and appeared to reflect the response dynamics of neurons representing the target properties to be identified (for details, see Nothdurft, 2017a). This suggested that cuing might have opened access to the neural representation of target properties at the time when the cue was applied. To find out how exact that timing was, Experiment 1 of the present study was designed to measure target identification at target onset and offset (when line patterns were replaced by the mask). I used test patterns with short presentation times and delivered the cues shortly before and after the occurrence of the target. As the original study had already shown, targets were often not immediately recognized when the cue was presented but had to be shown for quite a while during which the neural responses might have been accumulated to reach a sufficient signal-to-noise ratio.

Method

Test patterns (Fig.1, upper stimulus) were shown for various durations (10-100 ms) and then masked (lower stimulus; cues (20 ms) were presented at various delays before, during, and after the test stimulus. A preliminary test covering four very short durations was performed by the author (HCN); additional tests with longer durations (50 ms and 100 ms) were later added. Three other subjects (one female) were also tested with these durations.

Tests were blocked for target duration; all cue delays with a given target duration were randomly intermixed in the same run, delays with different target durations were tested in different runs. Runs were repeated in intermingled sequence until each delay at a given target duration had been tested in 100-120 repetitions.

Results

The dynamics of test pattern and mask presentations are illustrated in Figure 2a, data from subject HCN and three other subjects are shown underneath (Fig.2b-d). The onsets and offsets of the line patterns are aligned (vertical lines), and rating performances are plotted at the relative time of cue onsets. In all tests, performance already increased when the cue was shown before target onset (data points on the left-hand side) and began to diminish shortly before the mask when cues were still presented in the line pattern (data points on the right-hand side). While HCN was sensitive enough to identify some targets in 10 ms presentations (76% correct at line pattern onset), the other subjects needed target durations of 50-100 ms to reach similar performance levels (Fig.2c,d). But all subjects could make use of early cues presented before the target, and already revealed diminished ratings before the target was masked. The early decay was particularly pronounced with long presentation times (100 ms; Fig.2d).

Discussion

The data illustrate three main components of the temporal cuing process. (i) The identification of a cued target required a certain amount of *integration time* to accumulate the neuronal signals before a reliable decision could be made. That time differed between observers. HCN could identify targets from shorter presentations (almost 100% performance rates with 40 ms target duration) than the other observers (still not yet 100% with 100 ms). (ii) There was a systematic *delay* between cues and rating modulations. All participants could identify targets that were not yet visible at the moment of cuing and already showed reduced ratings with targets that were cued shortly before the mask and had still been visible when the cue occurred. Part of this delay might be caused by the required integration time; if the target disappeared during that interval, identification rates should be reduced. The advanced decay was however less pronounced with shorter target durations (Fig.2b,c). (iii) The third component is a *waiting mode* during which subjects maintained selection until the target occurred. This is seen in the high identification rates of early cued targets long before target onset (left-hand graphs of Fig.2). When subjects were ready to detect and identify (cued) targets,

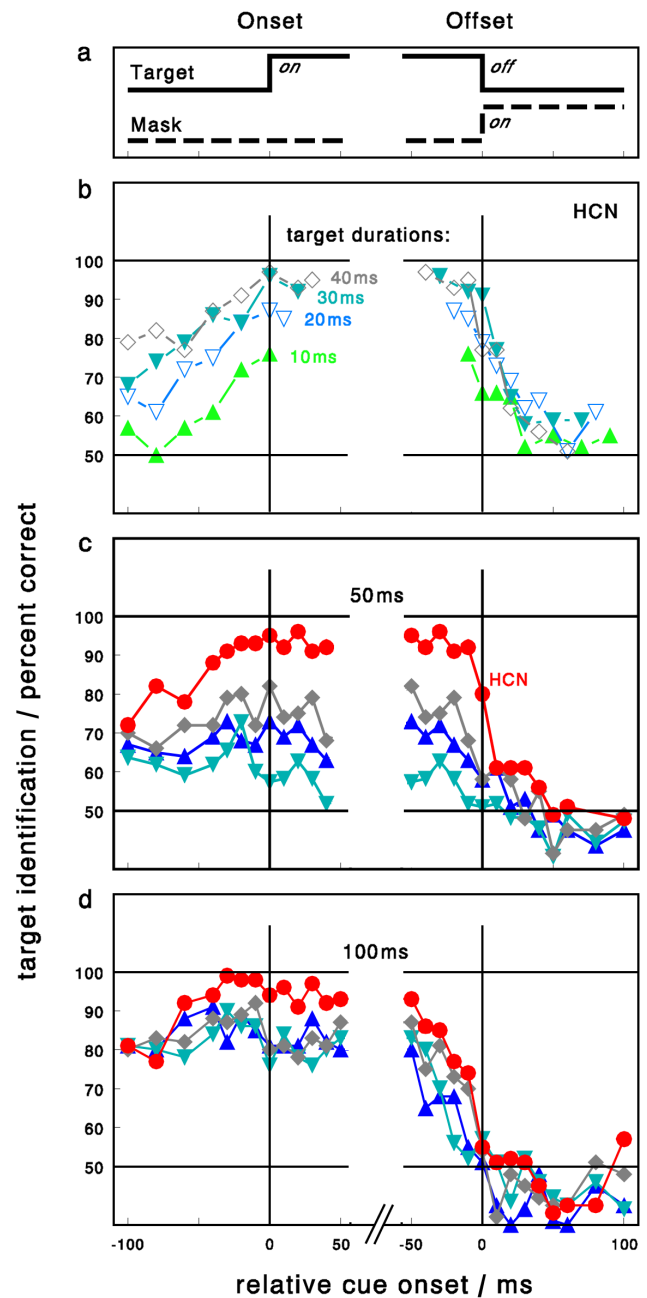


Figure 2. Cued target identification at pattern onset and offset (Experiment 1). **a.** Sketched timing of stimulus and mask. **b.-d.** ratings of four observers tested with various target durations (**b.** observer HCN tested with short target presentations, **c.-d.** all observers tested with target durations 50 ms and 100 ms). In all data curves, target onsets and offsets are aligned (vertical lines) and rating performances are plotted at the according cue delays. Rating performance generally increased before the target was presented and diminished before it was replaced by the mask.

they obviously could ignore periods of absent or irrelevant information and wait for the first relevant target to be seen even if that was delayed. This was the typical experimental setting in classical cuing experiments, in which valid cues pointed to the (later) occurrence of targets. Cuing then had put observers into a mode in which they awaited the target (likely) at the cued location. This waiting mode may open the cuing window for a remarkably long period of time. Before the current Experiment 1, all subjects (except HCN in his early tests) had participated in another test in which they deliberately had to identify targets delayed for up to 2 s after the cue. Although long delays had generally reduced the number of correct ratings, most subjects could still select and identify quite a few targets after 2 s (Nothdurft, 2017a, Exp.1). Only if there was target information to be reported, in particular about dynamic variations at the onset of the mask, the evaluation of cued target information was temporally restricted and better timed. Interestingly, while the cuing window thus seems to remain open for coming events, provided nothing else has caught attention before, the attentional window can apparently not be expanded into the past. Subjects could generally not report target properties when the targets were cued *after* they had been masked (Nothdurft, 2017a; cf. the demo on www.vpl-goettingen.de/cvs/).

Prolonged visibility of targets after application of a salience marker, but never before, was also seen in an earlier study with a similar paradigm (Nothdurft, 2002; Experiment 2). There, the line pattern was temporally embedded in the mask pattern; it appeared from the mask at target onset, and it disappeared into the mask at target offset. Also in that situation, targets presented after the salience marker (then a ring cue) were still often identified (Nothdurft, 2002, Fig.14; ratings on the right-hand side of the hatched area), but never targets that were presented before the salience marker (ratings on the left-hand side).

Altogether, Experiment 1 has confirmed the, in principle, high temporal accuracy of CVS. If targets were shown long enough, they could be identified, but no observer saw lines after they had been replaced by the mask. There were basically three factors that have reduced the temporal accuracy; the necessary integration time to evaluate target properties, the individual cuing delay at which observers recognized the cued target, and the target awaiting mode during which observers made use of the pointing character of the cue to report targets that appeared much later at the cued location.

Experiment 2:

Cuing of dynamic target variations

A reasonable way to avoid the waiting mode before target onset is to present targets that continuously change their properties so that there is always cued information to be reported. This was tested in two stimulus dimensions, *orientation* and *color*, with lines that switched their orientations and patches that changed their colors. Aim of the experiments was to identify the moment when a cued target was identified.

Methods

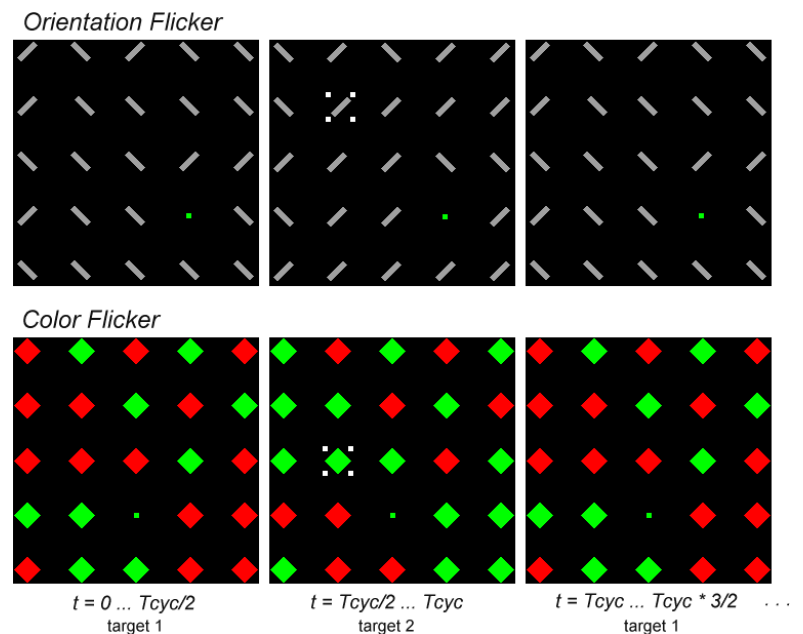
In all series of Experiment 2, two complementary patterns were alternated in time. Items were randomly oriented oblique lines in one pattern, and the orthogonal lines in the second pattern, or randomly painted green and red patches (rhomboids) in one, and red and green patches in the other pattern (Fig.3). Cycle durations, T_{cyc} , and hence the target presentation times (half-cycle durations, cyc), were systematically varied. Tests were blocked for features (orientation, color) and cycle durations. Within each run, cue delays were systematically varied over an entire cycle, from the onset of the first pattern until the offset of the second pattern. Subjects were asked to report the orientation or color of the cued target. To avoid flicker onset effects, stimulus presentations began with extra cycles at least 500 ms before the cued rating measurements. Reports of the first target in a cycle were counted as correct, independent of its orientation or color. For analysis, performance ratings with a given flicker rate were fitted with sinusoidal functions to measure amplitudes and phase shifts; these procedures will be described below.

Four observers (one female) performed the experiment. With one of them (OC), the tests were performed with a reduced monitor frame rate of 60 Hz; cues were then presented for 33 ms (two frames). All other observers were tested with 100 Hz frame rate and cue durations of 20 ms.

Results

Typical ratings with orientation and color flicker are shown in Figure 4. When the flicker was slow (1.25 Hz),

Figure 3. *Test patterns in Experiment 2.* In different test series, items alternated in orientation (orientation flicker) or color (color flicker). At one moment in the cycle one item was cued and observers indicated which target they had seen. The figure shows arbitrary patches of stimulus patterns (which originally covered 9 by 9 items as depicted in Fig.1) and three stages of a much longer stimulus sequence. Full-cycle time is T_{cyc} . After half a cycle showing one stimulus (e.g., left-hand patterns) all items were replaced by complementary items (middle) and after another half cycle the first stimulus was shown again (right-hand patterns). Initial item attributes and target locations were randomized and refreshed in every new trial. Cues (here shown in the middle patterns) were presented, one per trial, at various delays all over the cycle.



the observer could reliably identify the cued targets and achieved ratings of 100% and 0%, respectively, for the correct identification of the first and second target in a cycle. Note however, that target ratings were not in exact synchrony to the stimulus but appeared to be shifted ("phase shift") such as if the subject had seen targets as cued that appeared later in the cycle.

Amplitudes. When flicker rates increased (2-4 Hz), performance deteriorated and the observer could not identify all targets, even not when the cue-target delay was optimal. Performance ratings were still modulated with different cue delays over the flicker cycle, but 100% and 0% values were not reached anymore. With further increasing flicker rates (4-5 Hz), rating amplitudes finally disappeared. At flicker rates of 5 Hz rating curves were flat, i.e. the observer could not reliably identify the cued target at any cue delay (although cue duration, 20 ms, covered only one tenth of the full cycle duration at this flicker rate). The variations in amplitude suggest that the subject needed time to evaluate the target properties. Only when the target was shown long enough and the information could be accumulated during that time, target properties could be correctly identified (1.25 Hz - 2.5 Hz). When targets changed too frequently, none of the two targets was reliably seen. For subject VSE, the fastest rating modulations were obtained with flicker frequencies of 4.2 Hz, for orientation, and 3.6 Hz, for color,

corresponding to *full-cycle* durations of 240 ms (orientation) and 280 ms (color), respectively. The next flicker rates tested did not produce modulated ratings. Independent of when the target was selected in this cycle, either the target flicker was not resolved or the integration window had accumulated responses from both stimuli. A different measure of the cuing window is given by the integration time needed to just obtain full rating modulations. In that case, the cuing window would accumulate target information from an entire half-cycle. Longer presentations (slower alternations) should not improve rating modulation; shorter presentations (faster alternations) would diminish it. In Figure 4, these limits are reached with *half-cycle* durations of about 200 ms, for orientation, and 200-280 ms, for color. Thus, both estimates of the size of integration windows (the largest full-cycle duration with zero amplitude; the shortest half-cycle duration at maximum amplitude) lead to similar results with this subject.

Rating performances with orientation and color differed with this observer; orientation ratings followed the stimulus up to slightly faster flicker rates (4.2 Hz) than color ratings (3.6 Hz) indicating that the required integration time to evaluate target features was shorter for orientation than for color.

Phase shifts. The second important parameter in the graphs of Figure 4 is the location of rating peaks and, in

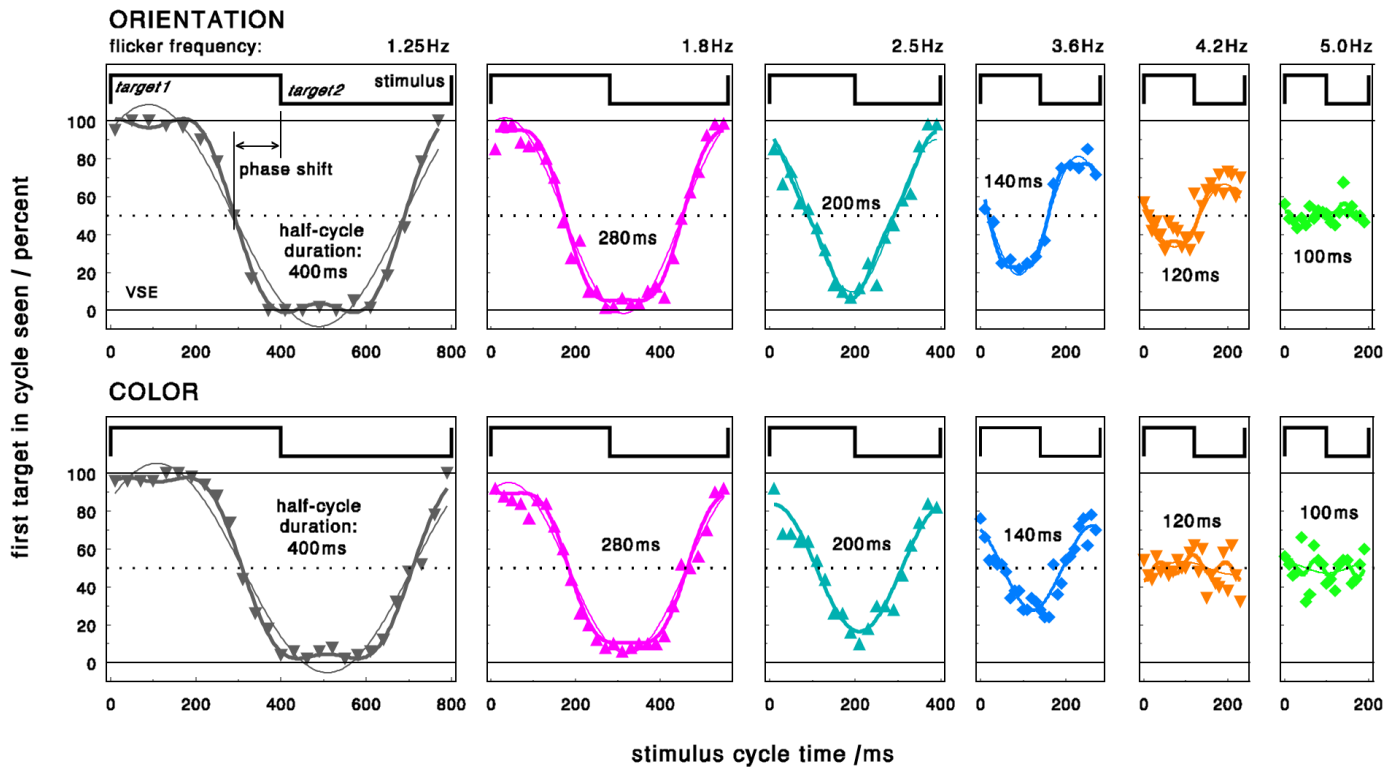


Figure 4. Cued target identification in orientation and color flicker (Experiment 2); data from one observer. Rating performance (measured as percentage of the first target seen; "target 1") is plotted along the stimulus cycle (indicated on top of each graph) at the relative time when the cue occurred. The graphs illustrate the major observations with different flicker rates. Rating modulation diminished when flicker frequency was increased and stimulus duration shortened (from left-hand to right-hand graphs). Zero amplitudes were reached at slightly slower flicker with color than with orientation. Rating modulations were systematically shifted ("phase shift") against stimulus variations, indicating that the observer reported later presented targets as being cued. Various parameters of these rating modulations are systematically analyzed in the following figures. Thin and thick lines in each graph show the fits of first (thin) and first + third Fourier components (thick), respectively, to the data.

particular, of "zero" transitions between the two stimulus patterns. Apparently, the cue-target synchrony of the stimulus was shifted in the percept of cued targets ("phase shift"). For example, when the cue was delivered at the end of the first half-cycle, not the momentary first target but already the second target in the cycle was seen. Also the transition from target 2 to target 1 at the end of the cycle was seen much earlier than it was cued, in fact already with cues presented more than 100 ms before the switch (for orientation). This indicates that cue efficiency was delayed, so that earlier presented cues helped to identify later presented targets. An equivalent description would be that the target perception was advanced compared to the cue. In the 1.25 Hz flicker with orientation, the delay has caused a phase shift of -111 ms between stimulus flips and the 50% transitions (chance

level) in the rating curves. In a linear system, phase shifts should be constant in time, not in cycle phase, for different flicker rates (cf. Appendix A). In particular with quickly alternating patterns (high flicker rates), there is a principle uncertainty since we do not know to which cycle of the target flicker the observer is responding. Even with the 1.25 Hz example, she might have responded to targets presented 689 ms before the cue, not 111 ms after it. But this delay would not be constant across different flicker rates, and would also contradict the general observation that target properties in these patterns are not notably memorized (Nothdurft, 2017a). The delay uncertainty between identical conditions is given by multiples of the flicker cycle duration. While this uncertainty, in principle, cannot be solved, the comparison with potential delays in other flicker rates may provide a plausible solution.

The measured phase shifts of rating curves were 20 ms larger for orientation (−111 ms) than for color (−91 ms) in this observer.

Fourier components. Amplitudes and phase shifts can be easily obtained by fitting Fourier components to the data. These fits are superimposed on the data in Figure 4. There is a (minor) problem with these fits. Stimulus variations followed a rectangular form (targets *switched* their properties), whereas Fourier components to the response patterns are sinusoidal. To represent the stimulus in a Fourier transform would require all higher odd frequency components. The fit of only the first Fourier component to the ratings (thin continuous curves in Fig.4) may reduce the accuracy of estimated phase shifts under slow flicker and may, in particular, overestimate the rating amplitudes (cf. the over- and undershoots of thin curves in the 1.25 Hz fits). This was corrected for by fitting a combination of the 1st and 3rd Fourier components to the data, which followed the responses to slow flicker much better (thick continuous curves). To correct the rating amplitudes (which are theoretically given by the series $a_1 - a_3 + a_5 - a_7 + a_9 \dots$, with a_i specifying the amplitude of the i -th Fourier component) I have made the following simplification. For 3rd Fourier components that were notably larger than zero, I computed the corrected amplitude as the average of a_1 and $(a_1 - a_3)$; $\langle a_1, a_1 - a_3 \rangle$. This was much closer to the true amplitudes than either a_1 or $a_1 - a_3$ (cf. left-hand graphs in Fig.4) and simultaneously avoided to fit too many parameters to the data. Phase measures should be unaffected by amplitude variations, as long as the measured rating modulations are large enough to allow for reliable fits and phase shift calculations.

Analysis. Figure 5 plots the parameters of Fourier functions fitted to these data; orientation discrimination is

plotted in black, color discrimination in green. As was already seen in Figure 4, *amplitudes* of the first Fourier components (f_1 ; filled circles in the upper graph) exceeded the experimentally achievable maximum of 50% at slow flicker rates (right-hand side of the graph) but continuously diminish to almost 0% when the flicker rate was increased (left-hand side). Amplitudes of the third Fourier component (f_3 , crosses) start at much smaller values and vanish when the amplitudes of the first Fourier

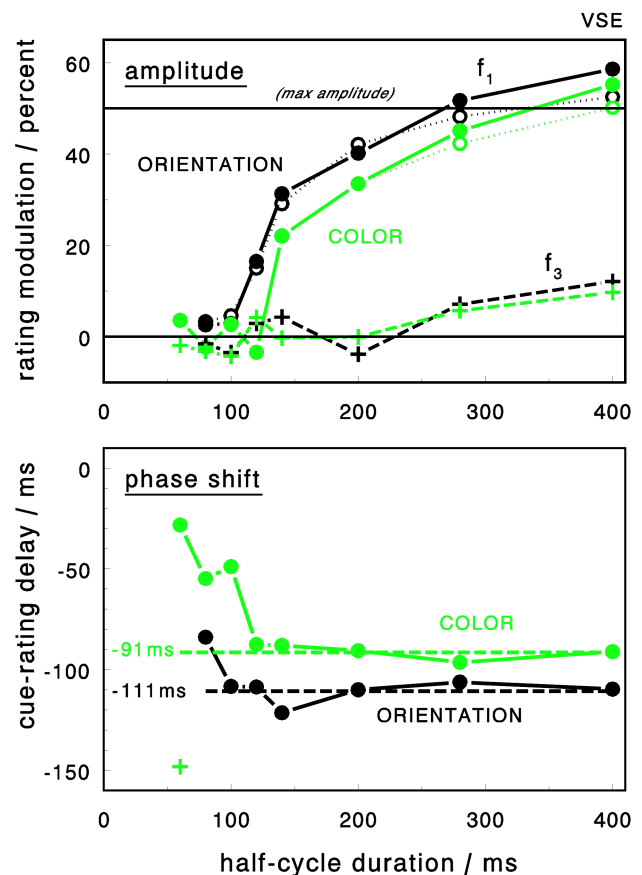


Figure 5. Amplitudes and phase shifts in the data of Figure 4; orientation (black) and color tests (green). The upper graph shows the amplitudes of various sinusoidal fits to the original data. Curves " f_1 " plot the amplitudes when only the basic frequency was fitted to the data (filled circles), curves " f_3 " plot the amplitudes of the third harmonics (crosses) when a combination of the basic frequency and the third harmonic was fitted. The two fits are also depicted in Fig.4. Amplitudes of the basic-frequency fit often exceed the data and the experimentally available range ("max amplitude") at long cycle durations; this is compensated by computing the averages of amplitudes of the first and the first minus third harmonics, $\langle a_1, a_1 - a_3 \rangle$ (open circles). The lower graph shows the obtained phase shifts between the stimulus and rating curves. Negative values indicate that the modulation of cued rating curves was advanced against the stimulus. For this observer, phase shifts were constant across cycle durations as long as the stimulus flicker could still be resolved (rating modulation > 0). Since pattern cycles were repetitive, phase-shift estimates are not unambiguous but may vary with multiples of the full cycle length. If other phase-shift estimates happen to fall inside the graph, they are indicated by crosses. The in principle ambiguous estimates are usually less ambiguous from the data continuity between neighboring measures. Note that data in this figure are reversed against Fig.4; data points on the left-hand side correspond to graphs on the right-hand side in Fig.4, and *vice versa*.

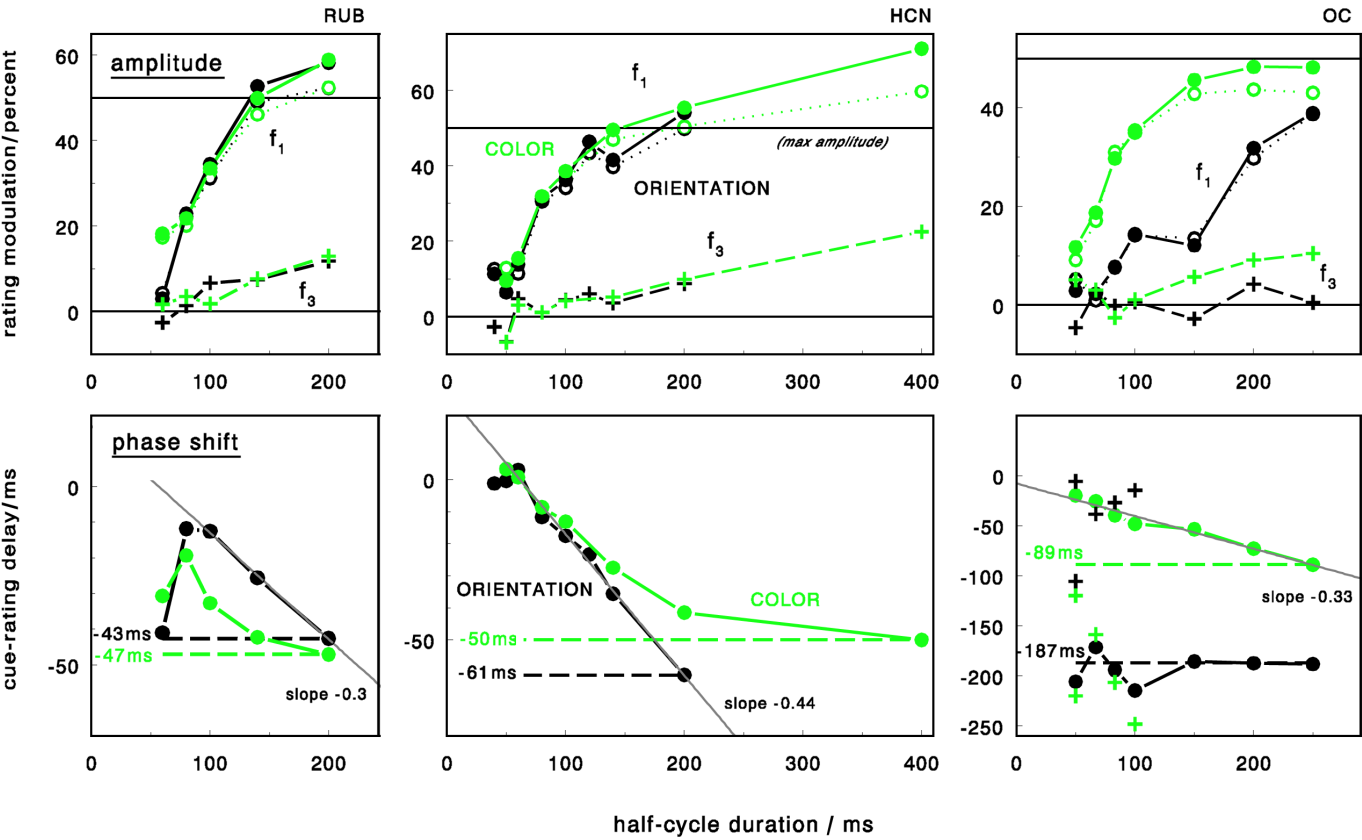


Figure 6. Amplitude and phase shifts of other subjects. Presentation as in Fig.5. Note however that most observers showed less constant phase shifts across cycle durations; instead, phase shifts varied systematically in an almost linear way; the according slopes are indicated (gray lines). If phase shifts varied across cycle durations, the values from the longest cycle durations were taken (horizontal dashed lines).

components begin to diminish, in good agreement with the considerations above. Corrected amplitudes taking the averages of the first and the first minus third Fourier components, $\langle a_1, a_1 - a_3 \rangle$, avoid the overshoot (open

circles). Best *phase shifts* of the fits (Fig.5, lower graph) show nearly constant values with slow flicker rates, and become uncertain or arbitrary when the rating modulations are too small. The above mentioned uncertainties of phase

	Orientation				Color			
	size			delay	size			delay
	lower	upper	sigma		lower	upper	sigma	
VSE	190	297	58	-111	245	392	63	-91
RUB	113	162	36	-43	120	167	36	-47
HCN	98	167	35	-61	83	159	33	-50
OC	121	>400	77	-187	76	330	36	-89
means	130.3	>256	51.3	-100.3	131.1	262.1	42.0	-69.4

all values in milliseconds

Table 1. Cuing windows in Experiment 2. Lower and upper size estimates were made from fitted zero (full-cycle) and 50% ratings (half-cycle durations) in Figures 5 and 6. Sigma (σ) refers to reconstructed Gaussian sensitivity profiles (Appendix B). Delays as indicated in Figs.5 and 6. See text for details. Note that σ spans only a small part of the presumed integration window; the full duration at half maximum is given by $2 \cdot \sqrt{2 \cdot \ln(2)} \cdot \sigma$ which is about $2.355 \cdot \sigma$. The entire Gaussian profile is practically covered by 5-6 σ or more.

shift estimates from cycle repetitions (crosses in the lower graph) fall mostly outside the plotted scale (values should be shifted by ± 200 ms at half-cycle duration 100 ms, and by ± 160 ms at half-cycle duration 80 ms); only one alternative value is plotted, which however falls far off the neighboring phase shift values.

The analysis of rating amplitudes in Figure 5 reveals that orientation flicker was better resolved, down to shorter half-cycle durations, than color, which was already seen in the original rating data (Fig.4). The largest *full-cycle* durations at which targets could not anymore be identified (zero modulation) and the smallest *half-cycle* durations with full rating modulations (50% modulation) were 190 ms and 297 ms, for orientation, and 245 ms and 392 ms, for color (Table 1); the values were taken from exponential fits to the rating data in Figure 5. The measured phase shifts between cues and perceived targets were negative; thus both target orientation and target color were perceived before the cue, orientation a little earlier than color, and the integration time this subject needed for reliable color discriminations was slightly longer than that for orientation discriminations.

Additional observers. Figure 6 shows the analogue data of the other observers. Phase shifts (i.e., delays of the effective cuing windows) and rating modulations were different to those of subject VSE (Fig.5). While subjects RUB and HCN revealed high sensitivities (short delays and particularly small cuing windows; cf. Table 1), observer OC was partly even slower than subject VSE (with a cuing delay of nearly -190 ms, for orientation). With two observers (RUB, HCN), the differences between color and orientation were small; both feature dimensions generated similar cuing delays and integration times. Subject OC showed an earlier and more extended decrease of rating amplitudes for orientation than for color; his cuing delay for orientation was about double as long as that for color.

An obvious difference between observers are the systematic phase-shift variations seen with some observers in certain tests (Fig.6), compared to the constant phase

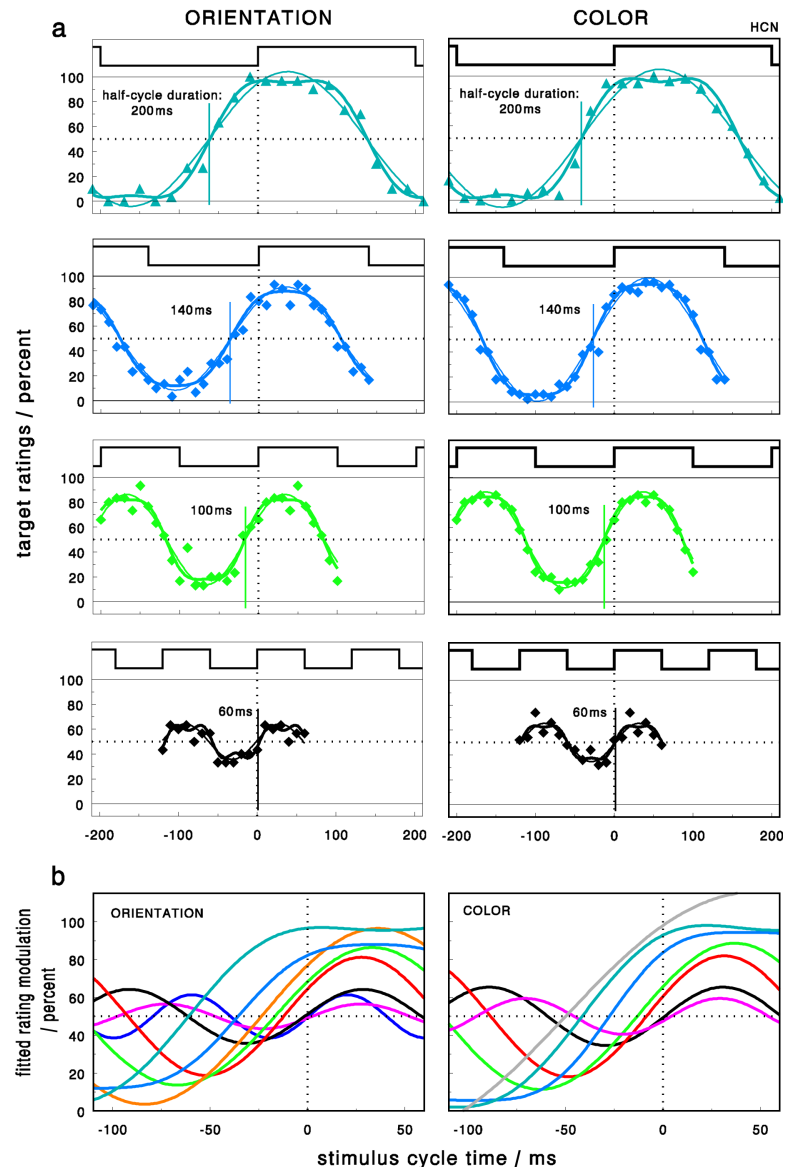


Figure 7. Phase-shift variations of subject HCN in the original rating data. **a.** Selected orientation and color ratings; for better visibility of the varying phase shifts, cycles are displaced (and eventually repeated) compared to Fig.4 (cf. $t = 0$ ms). **b.** amplitude fits of all tested flicker rates superimposed. Different to observer VSE in Fig.4, this observer showed systematic phase shift variations with decreasing cycle durations (cf. Fig.5). The zero transitions in the fits (**b**) are notably displaced (contrary to the prediction in Fig. A4), although the original data (**a**) do not indicate strongly asymmetric responses.

shifts found with VSE (Fig.5). To document these variations, original rating data with selected flicker rates

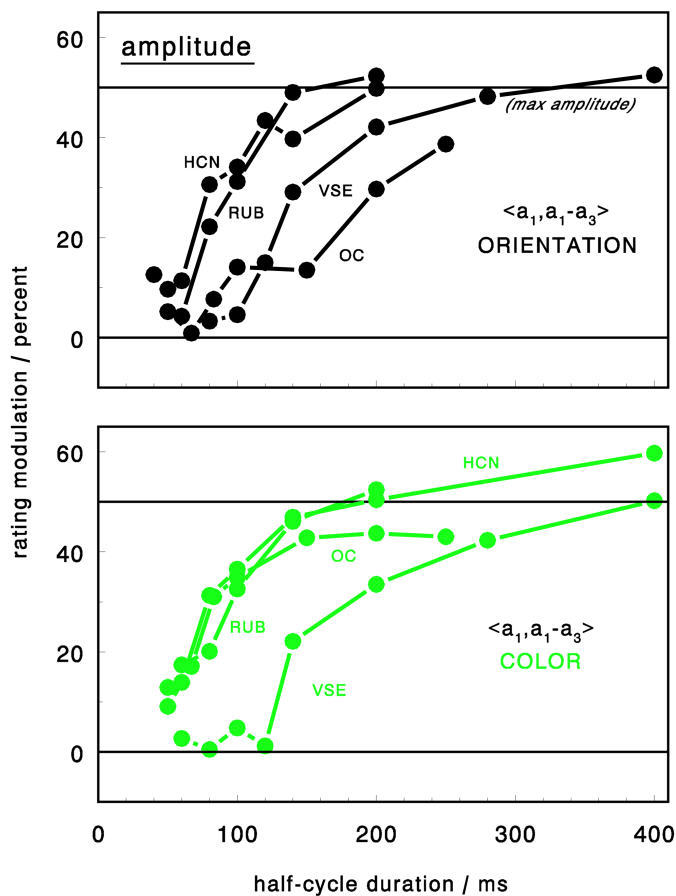


Figure 8. Amplitude variations of all subjects in Experiment 2. Re-plots of corrected amplitude data (open circles) from the upper graphs in Figs.5 and 6. There is considerable variation between subjects, which cycle lengths can and which cannot be resolved.

and the systematic shift of zero transitions for all tested cycle durations are documented in Figure 7, for observer HCN. To illustrate the variations, curves are aligned for target 1 onset ($t=0$ ms), and previous and test conditions with other cycles are eventually repeated in the presentation. The systematic shift of zero transitions (vertical lines) with increasing flicker rates is obvious, although rating modulations do not seem to be disturbed or deteriorated (see discussion).

A direct comparison of amplitude variations of all subjects is made in Figure 8. With orientation, there was notable variability between observers. With color, however, the data of three observers fell close together. Note that the corrected rating amplitudes of one observer did not reach the 50% level at slow flicker rates.

Computation of underlying Gaussian sensitivity profiles. While the upper and lower estimates of integration windows can be easily deduced from the 0% and 50% rating amplitudes in Figures 5 and 6, the amplitude variations *between* these extremes should provide more information about the temporal sensitivity profiles. Obviously, integration windows can't be boxcar functions, since amplitude ratings should then vary linearly with cycle length between these extremes. Instead it was assumed that integration windows were given by Gaussian sensitivity profiles, and their spatial parameters were reconstructed from the rating amplitudes measured (cf. Appendix B). Depending on target duration and the size of the Gaussian profile, responses and hence ratings

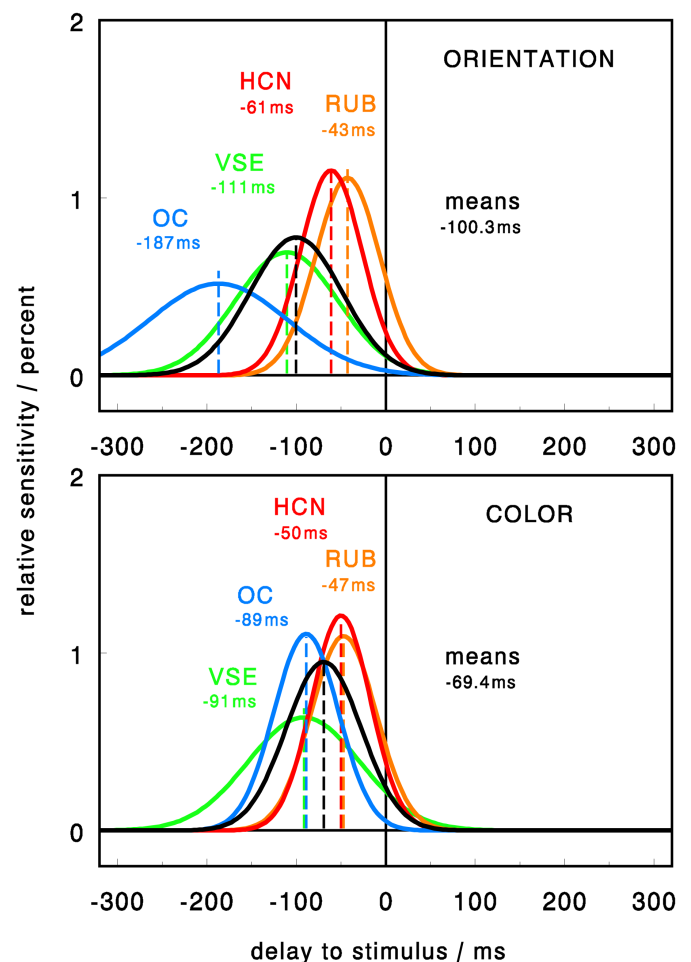


Figure 9. Gaussian sensitivity profiles reconstructed from the data in Figures 5 and 6, and their means. For details, see text and Appendix B.

can be predicted; this may, in turn, be used to compute the Gaussian sensitivity profile underlying a given rating performance in the experiment. The Gaussian sensitivity profiles that should have generated the rating amplitudes in Figure 8 are shown in Figure 9. Values of the according parameter sigma, σ , which define the size of underlying Gaussian profiles, are also listed in Table 1. These values are much smaller than the lower and upper estimates of cuing windows made above. But one has to keep in mind that σ covers only a small part of the profile. The full duration at half maximum is given by $2 \cdot \sqrt{2 \cdot \ln(2)} \cdot \sigma$ which is about $2.355 \cdot \sigma$. While the full width of a Gaussian profile should theoretically expand to infinite, a factor of 5-6 σ might be sufficient to reach maximum rating amplitudes of 50%.

Discussion

Several aspects in these data deserve discussion. First, there were remarkable variations in the size and the delays of cuing windows both between observers and between the two tested feature dimensions. Some observers needed integration times of about 160-170 ms to reach full rating modulations, others required much longer target presentations of about 300-400 ms or more, eventually for one feature dimension only. The differences between orientation and color flicker were small in observers RUB and HCN but larger and eventually reversed in the other observers. Particularly long integrations windows were found with VSE in color and with OC in orientation. Second, all ratings showed negative delays between cues and perceived targets; the identified targets were not the targets shown with the cue but the targets that appeared several milliseconds later at the cued location. This indicates that the target properties orientation and color were faster identified than selected—a perhaps somewhat surprising observation. Also the delays varied between observers (−43 ms to −187 ms); but the differences between dimensions, if present, did not show a systematic ranking.

It is not clear why some observers needed longer integration times than others. This was also observed in accompanying studies (e.g., Nothdurft, 2017a, b). The fact that observers could be slow with one feature and fast with another one (cf. color and orientation with VSE and OC) suggests that the variations are likely not caused by cuing and selection but by individual differences in the

sensitivity for certain target properties. Both processes might be improved by training and exercise. But all observers in Experiment 2 had performed other CVS experiments before and should be considered being well trained in these tasks. In earlier CVS studies, similar variations across observers were attributed to crowding effects and could be partly compensated by a reduction of target eccentricity (Nothdurft, 2017a,b).

Experiment 2 has confirmed the general expectations from the Introduction; when cues are applied to a dynamic stimulus they may help to extract the cued information in space *and* time. This observation is quite remarkable. It illustrates that cues cannot only be used to guide an observer's attention to a certain location in the visual field, which has often been demonstrated in the past, but also to that location at a certain moment. As Experiment 2 has shown, cues may be used to select the momentary percept of a dynamic, variable, and changing stimulus. This might help to study the dynamics of perceptual processes that otherwise can not be easily resolved in time. But Experiment 2 has also shown that there might be, and indeed was, a delay between the physical application of the cue and the selected percept; all observers saw cued target properties that, in fact, appeared later at the cued location.

The cued selection of dynamic target properties should be strongly influenced by the presentation time needed to identify a target. When the flicker is perceptually not resolved, even a brief cue cannot extract the momentary target properties. It should therefore be interesting to compare the cut-off frequencies in cued target identification in Experiment 2 with the flicker fusion frequency of alternating targets. Unfortunately, the flicker resolution of (non-cued) target visibility was not measured in the current study. For the author, a later and quick estimate indicated that the percept of non-cued alternating features decayed at about the same flicker frequencies as did cued target identification. In that case, cut-off frequencies might be less an estimate of the shortest integration time needed to identify a cued target than perhaps a general limitation of the system to resolve fast stimulus variations in time. A solution of this question may be the analysis of performance variations between the upper and lower estimates of the integration window, as it was done by reconstructing the Gaussian sensitivity profiles underlying the data (Fig.9). Over a considerable range of flicker rates, the measured rating amplitudes were linearly related to predictions made from the Gaussian profiles (Appendix B), and, as we will see in Experiment 3, these profiles

were similar to those obtained in flicker-free target presentations. This indicates that limited flicker-resolution was likely not an important parameter in the measurements of cuing windows in Experiment 2.

Methodological considerations. The evaluation of integration windows and cuing delays from the amplitudes and phase shifts of modulated performance ratings appears to be valid, plausible, and reliable. Almost all observers showed clearly modulated rating curves, in which amplitudes and phase shifts varied smoothly and continuously with the tested flicker rates.

The coarse *estimate of integration time* from rating amplitudes is straight-forward. Zero amplitudes show that the target was not identified; the accumulated signals did then not reach the necessary signal-to-noise level for a reliable decision. This might have been because the integration window had covered a full flicker cycle of the stimulus or more; that duration might then be taken as an estimate of the minimal integration time required for target identification. It could however also mean that the resolution limit of feature flicker was reached, with no particular information about the required integration interval. The upper limit of the integration interval is reached when rating modulations just reach the maximum (50%). At this duration, the integration of target information from *one* pattern (i.e., half a cycle) should be sufficient to let all targets be correctly identified, at an optimally adjusted cuing delay. Shorter presentation times would reduce this duration and diminish performance. Longer presentations, however, cannot improve ratings beyond the maximum but should likely expand perfect ratings to neighboring, non-optimal delays (as is, for example, seen in Fig.4 at 1.25 Hz and 1.8 Hz). In most test series, there was a difference between the lower and upper estimates (Table 1) indicating that the minimal integration window (with zero modulation) is not necessarily identical with the full integration window (with 50% modulation). Most interesting however should be the region between these extremes, which was used to reconstruct the underlying Gaussian sensitivity profiles.

The *computation of cuing delays* from the phase shifts of fitted Fourier components is easy to visualize from Figure 4. Phase shifts, and hence cuing delays, are centered in the integration interval (Appendix A). For example, if amplitude variations would indicate an integration window of 200 ms, and phase shift estimates a cuing delay of -100 ms, the analysis of target feature

information should be accumulated from $t = -100 - 200/2 \text{ ms} = -200 \text{ ms}$ until $t = -100 + 200/2 \text{ ms} = 0 \text{ ms}$. This illustrates that phase shifts combined with large integration intervals do not necessarily imply that the physically cued target information (at $t=0 \text{ ms}$) is completely ignored; it may still be added to the accumulated signal when the integration interval is large enough.

Theoretically, *phase shifts should be constant* with a given integration time, since the cuing delay should not depend on the flicker rate. This was tested in a simple model and confirmed with various profiles of possible integration windows (Appendix A). Phase shifts only occurred when the integration window exceeded the full-cycle time, but then rating amplitudes should be rather flat anyhow. The constant phase shift prediction was indeed seen with subject VSE (Fig.5) and with subject OC for orientation (Fig.6). An interesting observation however is that in some graphs of Figure 6 phase shifts continuously diminished in size when the half-cycle duration was shortened and amplitudes decreased below 50% (RUB, HCN, OC color). Apparently, these phase shift variations were systematic and almost linearly aligned; their slopes vary from -0.3 to -0.44 (delay variations with increasing cycle time). The reason of these variations is not yet clear, but we can exclude a number of possibilities. Since the first patterns (red or green targets; right- or left-tilted lines) were randomly chosen and the ratings were averaged, the phase shift variations cannot be explained by possible response asymmetries between the two colors or orientations. They also cannot be due to an incorrect link of computed phase shifts to stimulus cycles. This principal uncertainty is given by multiples of full-cycle durations; incorrect links should thus vary with much steeper slopes (at least -2) than those found in Figure 6. One reason I could think of was the possible occurrence of *transient* rating components, with stronger responses to target changes than to continuous target presentations. Such transient components should have produced systematic phase shift variations with the flicker rate (cf. Appendix A) with slopes of -0.5 (increasing negative phase shifts with increasing cycle time) which would be in the same order as the observed slopes. But transient response components were not predominant in the according rating data (Fig.7). Another possibility is that integration windows were dynamically adjusted to the stimulus. While I have assumed in the computations for Appendix A that their widths were fixed for a certain observer and target feature,

their upper and lower estimates often differed considerably (cf. Table 1). In particular in the range between full rating modulations (when the integration window is supposed to match the duration of one half-cycle of the flicker) and flat ratings (when the integration window is assumed to exceed the duration of a full stimulus cycle), the effective target integration time is variable and might have been adapted to the target duration. If integration windows were exactly matched to half-cycle durations, that again should have created phase-shift variations with slopes of -0.5 in the plots of Figure 6, since phase shifts are centered in the integration window (Appendix A). Whether phase-shift variations as in Figure 7 thus reveal a kind of artifact from the stimulus or perhaps a true systematic fastening of attentional delays such as if observers were particularly curious not to miss any cued target in the faster flickers, must left be open.

Experiment 3: Cuing of single events

In the last series of experiments, I tried to separate integration times and cuing delays which both were intermingled in the previous experiments. Subjects were asked to identify an exactly timed, very short single event, the one-step movement of a vertical bar. Cues were given before, during, and after that event to estimate the cuing delay. Bars could jump in one of two directions, and subjects were asked to report the movement direction they have seen. Beyond measuring the cuing window for this single event, the experiment also expanded the analysis of cuing windows into the new feature dimension *motion*. To compare the data with the analyses of Experiment 2 a similar single change was also tested in *orientation*, *color*, and *luminance polarity*. Different to step movements, however, changes in these dimensions will always be associated with the (visible) presence of different features before and after the change. The data confirm the findings of Experiments 1 and 2, and expand the analysis into the luminance domain.

Methods

Experiment 3 covered four different test series (Fig.10). In *series A*, patterns displayed an array of vertical line bars

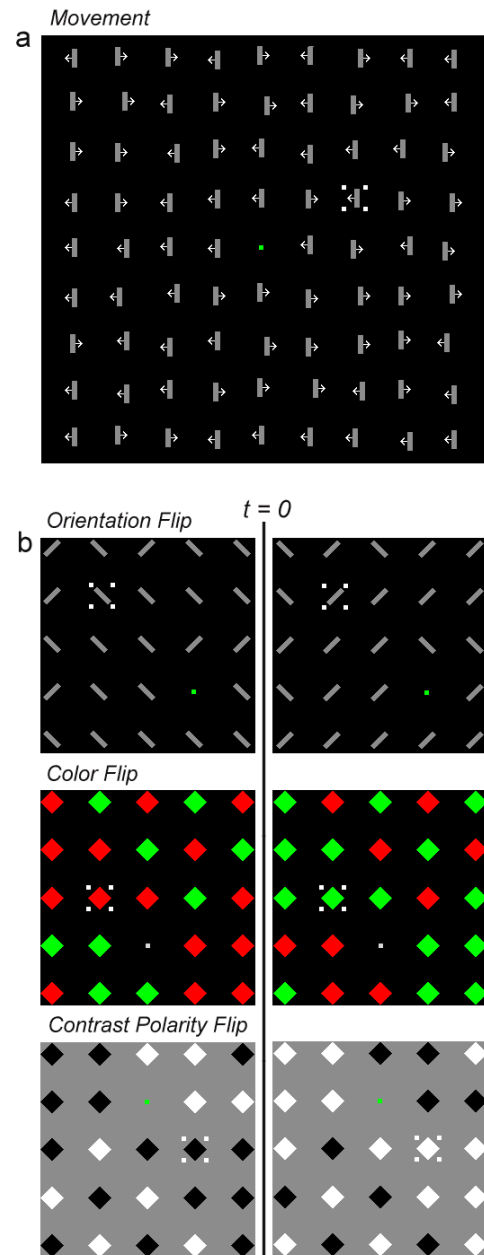
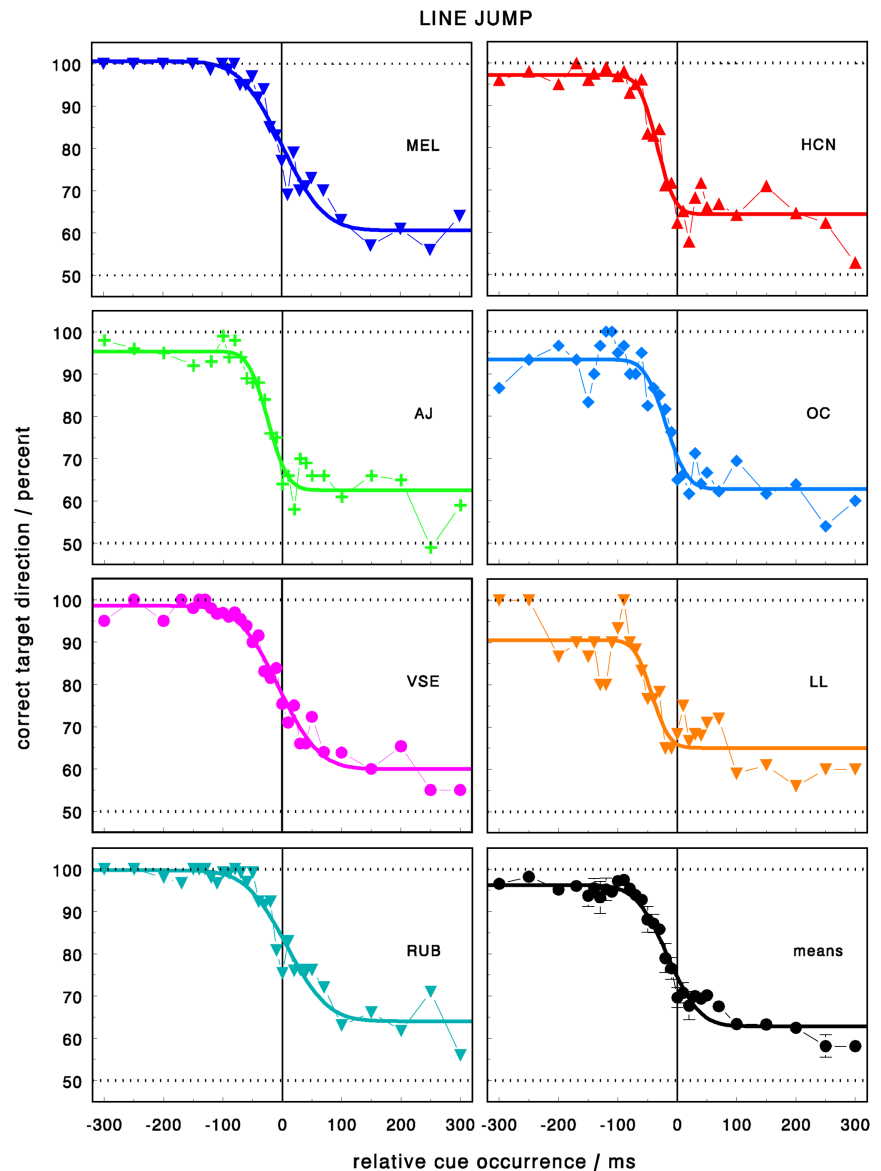


Figure 10. Test patterns in Experiment 3. Test series were designed to measure the cued perception of single events. **a.** Small line jumps; **b.** single replacements of items by complementary items. All items jumped or changed at the same moment ($t = 0$); four-dot cues (here plotted in all patterns) were briefly presented around one item before, during, or after that moment. Subjects had to identify movement direction (*a*) or tested properties (*b*) of the cued items. Patterns showed arrays of 9 by 9 items (as in the previous experiments) with a central fixation spot like in *a*; only arbitrary sections of these stimulus patterns are plotted in *b*.

Figure 11. Identification of jump (movement) directions in Experiment 3. Rating data of all seven observers (colored) and means (black). Jumps occurred at $t=0\text{ms}$; the ratings obtained with various cuing delays are plotted at the time when the cue occurred. Continuous curves show fitted (inversed) cumulative distributions functions (cdf's). All observers revealed high performances when cues were shown long before the jump, but performances already began to diminish for cues presented shortly before the jump. After the jump, ratings did not diminish to chance (50%) but remained increased at 60-70% performance for rather long delays. The likely explanation is that neural responses evoked by the jump lasted for quite a while and could still be recalled when an item was cued. In this and all subsequent figures, error bars with mean data indicate s.e.m.



which all jumped, randomly to the left or right, at $t=0\text{ms}$. Movement amplitudes were small (0.07 deg). In different trials, a single line was cued before, at, or after that jump, and observers were asked to report the movement direction seen. In *series B-D* (Fig. 10b), arrays of randomly oriented lines flipped their orientations, and arrays of color patches abruptly changed their colors or contrast polarities. In principle, this flip is similar to the stimulus changes tested in Experiment 2, with an enlarged cycle time ($T_{\text{cyc}} = 1000\text{ ms}$) and cuing being restricted to delays around one particular flip. To avoid that observers simply responded to the first or last pattern in a trial, the cued

feature changes were embedded in other flips at the same frequency before and after the cue. Fixation points were green (*series A, B, and D*) or white (*color series C*).

The general timing of trials was similar in all test series. After about 500 ms with a blank screen and the fixation point, the (first) pattern was shown. In *series A* (motion), this pattern was replaced after 500-800 ms by a second pattern in which all lines were slightly displaced. Cues were presented at various delays before and after this replacement. Half to one second later the screen was blanked, except for the fixation point. In *series B-D*, items were replaced every 500 ms. Measurements began shortly

before the 2nd cycle, and flicker continued until subjects responded, maximally for one more cycle; then the screen was blanked except for the fixation point. In each trial one item was cued at various delays, and subjects had to report which target properties they had seen with the cue. Reported movement directions and target properties were taken as "correct" if they agreed with the true line displacements or the properties of the new target.

Seven subjects (three female) performed the tests in series A (line movement) and three of them (all male) also the additional tests in series B-D, for comparison.

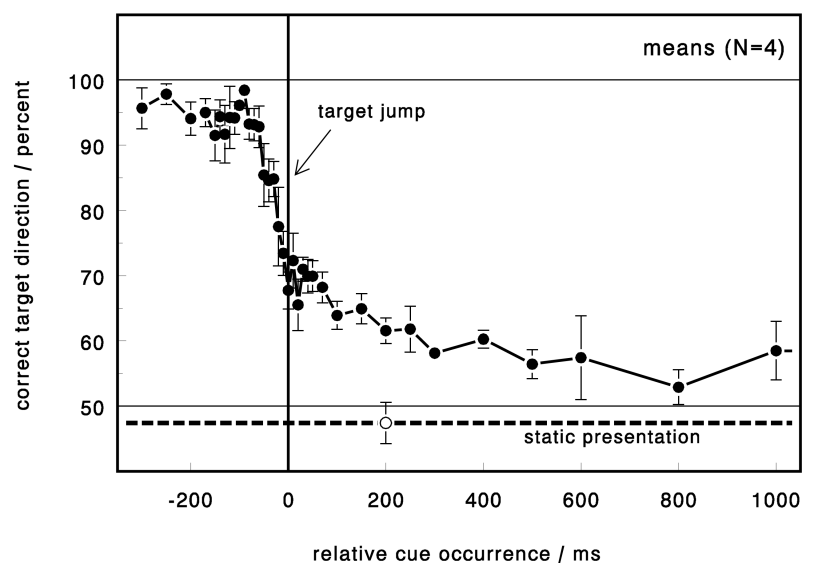
Results

Cuing windows of motion direction. Figure 11 shows the performance ratings and means of all tested subjects. Interestingly but not unexpected after Experiment 1, they all could reliably identify the movement direction of the target when the cue was given long before the jump ($t=-300$ ms). But when the cue was presented shortly before ($t=-100$ ms) or simultaneously with the line jump ($t=0$ ms), they made an increasing number of errors. In fact, four observers identified less than half of the target movements when the lines were simultaneously cued; the performances of the other three observers (MEL, VSE, RUB) were also notably diminished. This indicates that there is a small delay between the full efficiency of the cue and the encoding of movement directions. Cues must be shown a little before the jump to let observers correctly

identify *all* targets. What might be, on the first view, astonishing, is that subjects could still identify the correct line movements in a number of trials when the cue was presented several hundred milliseconds *after* the jump (e.g., $t=200$ ms). Performance ratings did not fall down to chance (50%) but remained increased at about 60-70%, for all subjects. That is, subjects could still see the movement direction of 20-40% of all targets at these delays.

The first suspicion was that the slightly displaced line positions before and after the jump might have provided hints from which the observers could make partly successful guesses on the previous movement direction. Even though line positions were randomly jittered, each line had jumped from a small offset from the cue center to one side, to a similar small offset on the other side (cf. Fig.10a). This had caused a tiny (static) asymmetry of lines positions in the cue before and after the jump. The relative offset of lines and cue centers was small (2 minarc = 0.03 deg), much smaller than the distance of the four-dot cues from the cue center (0.6 deg) and the jitter of line positions (± 0.15 deg). To control for such an effect, four subjects were asked to perform the task with the static patterns shown after the jumps. They were asked to indicate in which (horizontal) direction the cued target had presumably moved, but the first pattern was not shown and thus there was no line movement at all. The results are shown in Figure 12 (dashed line), together with the mean data of these observers in the standard test. Ratings were close to chance and do not indicate that the increased ratings at cue delays $t > 0$ ms were due to artifacts from line

Figure 12. Further tests with cued line jumps: evaluation of possible artifacts and of performance with late cues. Mean results and s.e.m. of four observers who ran additional tests with larger cue delays after the line jump and with static line patterns (dashed line). Increased rating performance with delayed cues (after the line jump) decayed slowly, but even 1s delays were not enough to reduce performance down to chance (50%). Static line patterns, on the other hand, with the line configurations after the (not visible) jump did not create similarly increased ratings (open circle, dashed line).



configurations. In an additional test series on these four observers, cue delays were expanded up to 1000 ms (Fig.12). The averaged performance level diminished at the longer delays, but even 800-1000 ms were not enough to bring it completely down to chance. Together with the rejection of visible spatial artifacts, this suggests that the movement information must still have been available at cued locations, even when the cues were delivered several hundred milliseconds after the jump. This observation is remarkable, as we shall discuss below.

Reconstruction of cuing windows. For accurate estimates of cuing windows, the data of each subject were fitted by inverse cumulative Gaussian distribution functions (cdf's; superimposed in Fig.11), from which the underlying Gaussian probability density functions can be reconstructed (pdf's; Fig.13). Beside certain deviations

discussed below, they show the individual cuing windows for cued target movement which are the basis for the accumulated rating modulations in Figure 11. Most but not all cuing windows are centered at slightly negative delays, as also are the means of all seven observers (black). This may however be due to the fact that ratings did not diminish down to chance (50%) with positive delays. The cdf's and pdf's should then appear displaced (see Discussion). If the 75% ratings of the fits in Figure 11 were taken instead (vertical dashed lines in Fig.13), the variations are better centered and the mean falls closer to $t=0$ ms. Also the widths of cuing windows varied between observers. Three observers revealed particularly wide windows, indicating that their cued motion sensitivity was less restricted in time than that of the other observers. The Gaussian sensitivity profiles (pdf's) of all observers are superimposed in Figure 14.

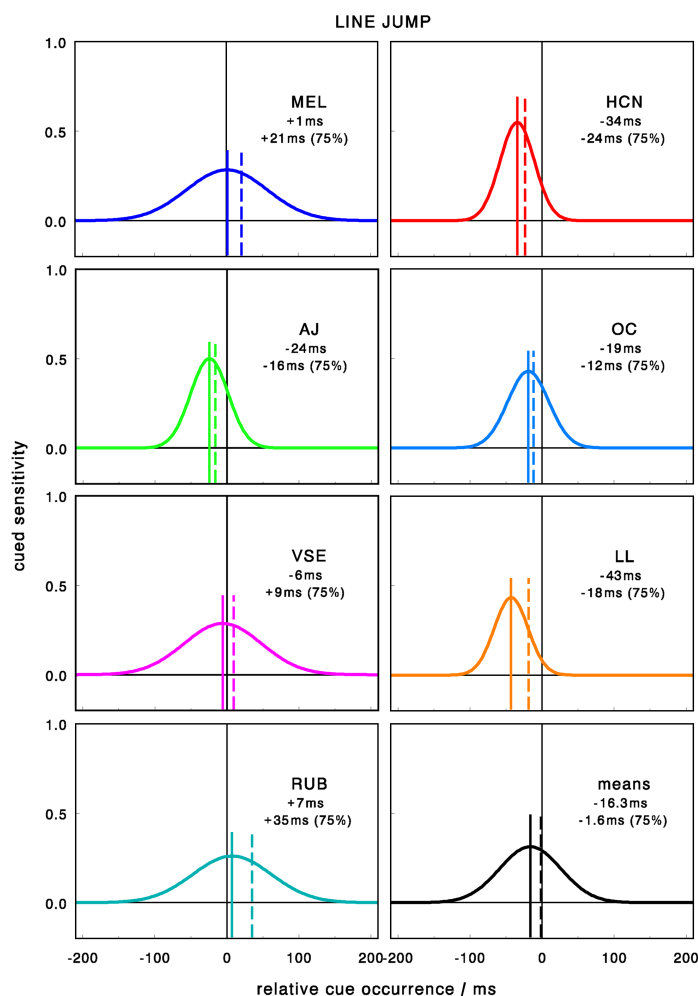


Figure 13. Probability density functions (pdf's) of data in Figure 11. The reconstructed curves represent the Gaussian cuing windows of movement direction; their integration would produce the (inversed) cumulative distribution functions (cdf's) fitted in Fig.11. Because of the increased ratings with positive delays (cf. Fig.11), centers of cuing windows (continuous vertical lines) are shifted towards negative values (for details, see text). If the 75% ratings of Fig.11 were plotted instead (dashed lines), all curves would be shifted to the right and means would peak at -1.6 ms, indicating that cues and cued motion direction are about simultaneously perceived.

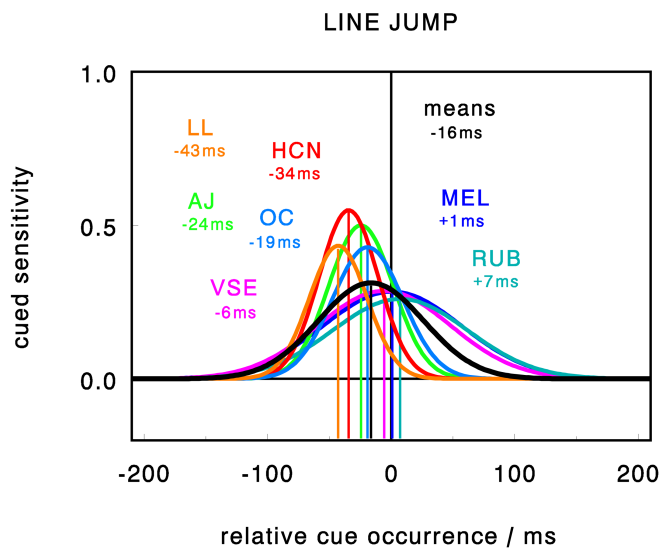


Figure 14. Cuing windows to motion direction. Data from Fig.13 superimposed show the variability of size and timing (delay) of Gaussian pdf's across observers. The shift to negative values is likely an artifact from the computation of cdf centers (see text).

Cuing windows in other feature dimensions. It should be interesting to compare these cuing windows for motion with the data obtained for other features. Without destroying the general experimental design (and changing the variety of tested features), it was not possible to measure true single events in these dimensions; instead participants were asked to report cued target properties near feature *changes*. Stimulus examples are illustrated in Figure 10b.

Figures 15-17 show the rating data from single orientation, color, and luminance changes, averaged over the two feature changes in the same domain (e.g., red-green and green-red changes). With *orientation* (Fig.15), the identification of new targets already began when cues were presented 300 ms (OC), 200 ms (LL), or 150 ms (HCN) before the target change. After steep increases in performance, all three observers already reported the new targets being cued even when cues were still presented with the old targets before the switch. Thus, the cued target percepts were notably advanced, exactly as found in Experiment 2. Similar curves and cuing delays were observed with *color* changes (Fig.16) and changes of *luminance contrast* (Fig.17). From the cdf's fitted to the individual ratings and to the means (a-d), the underlying pdf's were reconstructed (f, g, and e, f, respectively),

which directly represent the temporal sensitivity of cuing windows in these experiments. Cuing windows differed between dimensions and varied among observers. The cuing window for orientation changes was relatively sharp for HCN, who also revealed the shortest delay among the three observers (Fig.15f). The delays in color and contrast polarity were more similar across observers; only LL revealed a slightly shifted and much wider cuing window in the latter dimension.

An overview of all cuing windows measured in Experiment 3 is given in Table 2. While the parameter σ measuring the width of the Gaussian sensitivity profiles does not show systematic differences between the identified features—with all features, some observers needed longer integration times than others—there were consistent and systematic differences in the delays between identified features. These differences were strongest between motion, on one side, and all other stimulus categories orientation, color and luminance polarity ($p < 0.05$; two-sided unpaired t-tests), and were consistently seen with each tested observer. Delay differences between the latter categories, however, are seen in the means but not systematically found with each observer.

Discussion

The cued selection of line jumps provided a solid basis to analyze cuing windows in motion. Subjects detected the jump and correctly identified its direction, when cues were presented shortly before until shortly after the jump. Since the line displacement itself was a singular event, with virtually no duration, one might expect that integration intervals should not have affected the results. This was however not true. Integration does not happen along the stimulus but along the neural responses to the stimulus. Since many line displacements could still be identified when the cues were notably delayed (Fig.12), we must assume that the neural representation of the line jumps had lasted much longer than the displacement itself. For the analysis of motion direction, responses could then have been accumulated over much longer integration intervals than would be implied by the single-step line movement in the stimulus. This observation may thus support, now for motion, the same close link of cued visual selection to the dynamics of neural population responses that was earlier concluded from CVS with oriented bars (Nothdurft,

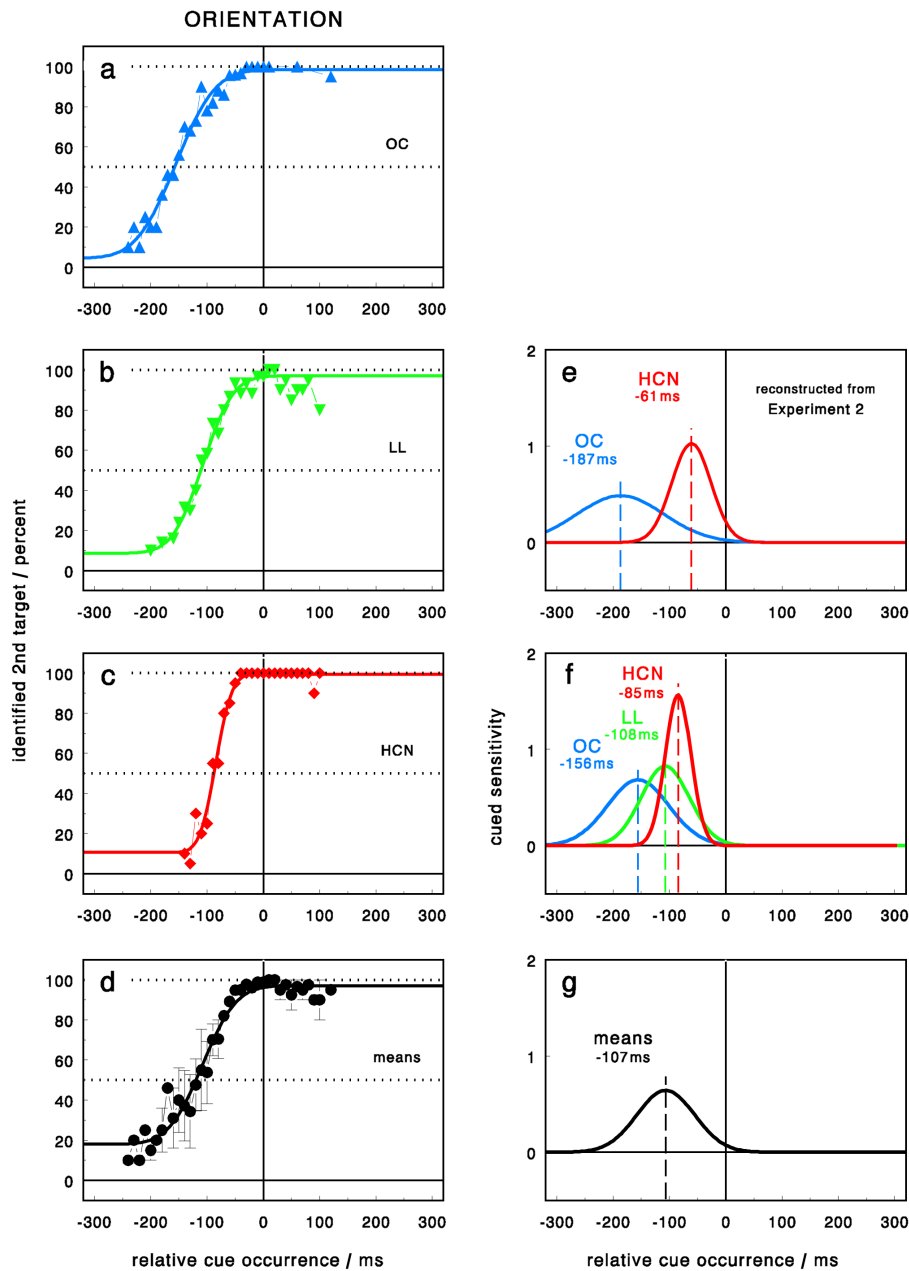
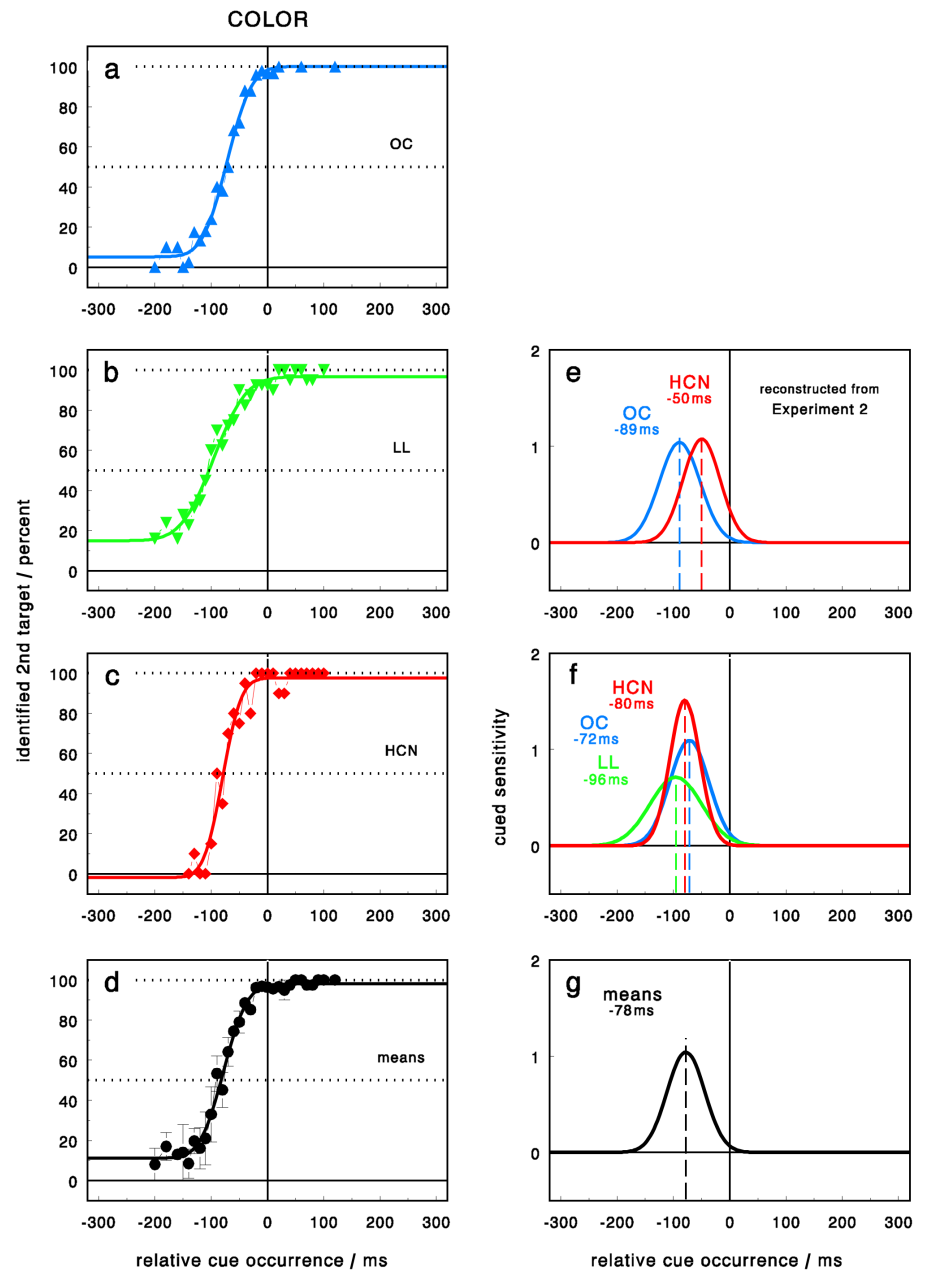


Figure 15. Ratings of a cued orientation change in Experiment 3. **a.-c.** Original ratings and **d.** means of three observers are fitted with cumulative distribution functions (cdf's, continuous lines), from which **f., g.** Gaussian sensitivity profiles (pdf's) are reconstructed. Cued sensitivity was advanced, i.e. all observers saw the cued target change earlier than it was cued. **e.** Reconstructed Gaussian sensitivity profiles from Experiment 2 (Fig.8) of the two observers also tested in Experiment 3. The general properties and differences between observers are similar.

2017a,b). It is not yet clear, however, *where* this movement is encoded in long-lasting neuronal responses. MT cells prefer, on average, faster movements and larger motion amplitudes (cf. Maunsell & Van Essen, 1982), although the line jumps in the present experiment (4 minarc displacement within the 10 ms frame cycle correspond to 6.7 deg/s) should have been within their responsive range. I also did not find any reports of long-lasting encoding of direction selectivity that could explain

the performance in Figure 12. The perceptual sensitivity to such small displacements was studied already 50 years ago (cf. Braddick, 1974; Ramachandran & Anstis, 1983) and had been explained by (monocular) local direction selectivity. But whether these low-level mechanisms might also account for the long-lasting, direction-selective responses with cue delays of up to one second after the jump, would be merely speculative at this moment (but see Baker & Cynader, 1994).

Figure 16. Ratings of a cued color replacement in Experiment 3. Presentation as in Fig.15. **a.-c.** Original ratings and **d.** means with fitted cdf's; **f., g.** reconstructed sensitivity profiles. Cued sensitivity was advanced, as with orientation in Fig.15, and generally less variable across observers. **e.** Gaussian sensitivity profiles of the two observers already tested in Experiment 2, for comparison.



A second interesting observation in Experiment 3 is the variability of cuing windows across observers. Since two observers (HCN and OC) had also been tested in Experiment 2, it is interesting to compare their results in both experiments. For that, Gaussian sensitivity functions were reconstructed from the rating data in Experiment 2 (cf. Appendix B) and plotted in Figures 15e and 16e. With orientation (Fig.15), the widths and delays of cuing windows are similar (though not identical) in both

experiments; the major differences seen in Experiment 2 are also replicated in Experiment 3. With color (Fig.16), the measured cuing windows had similar sizes but revealed a small difference in the cuing delays in Experiment 2 which was not replicated in Experiment 3. However, since it is mainly HCN whose cuing delay was reduced in Experiment 2, the difference might also be due to the systematic phase shift variations with this observer in Experiment 2 that were discussed above.

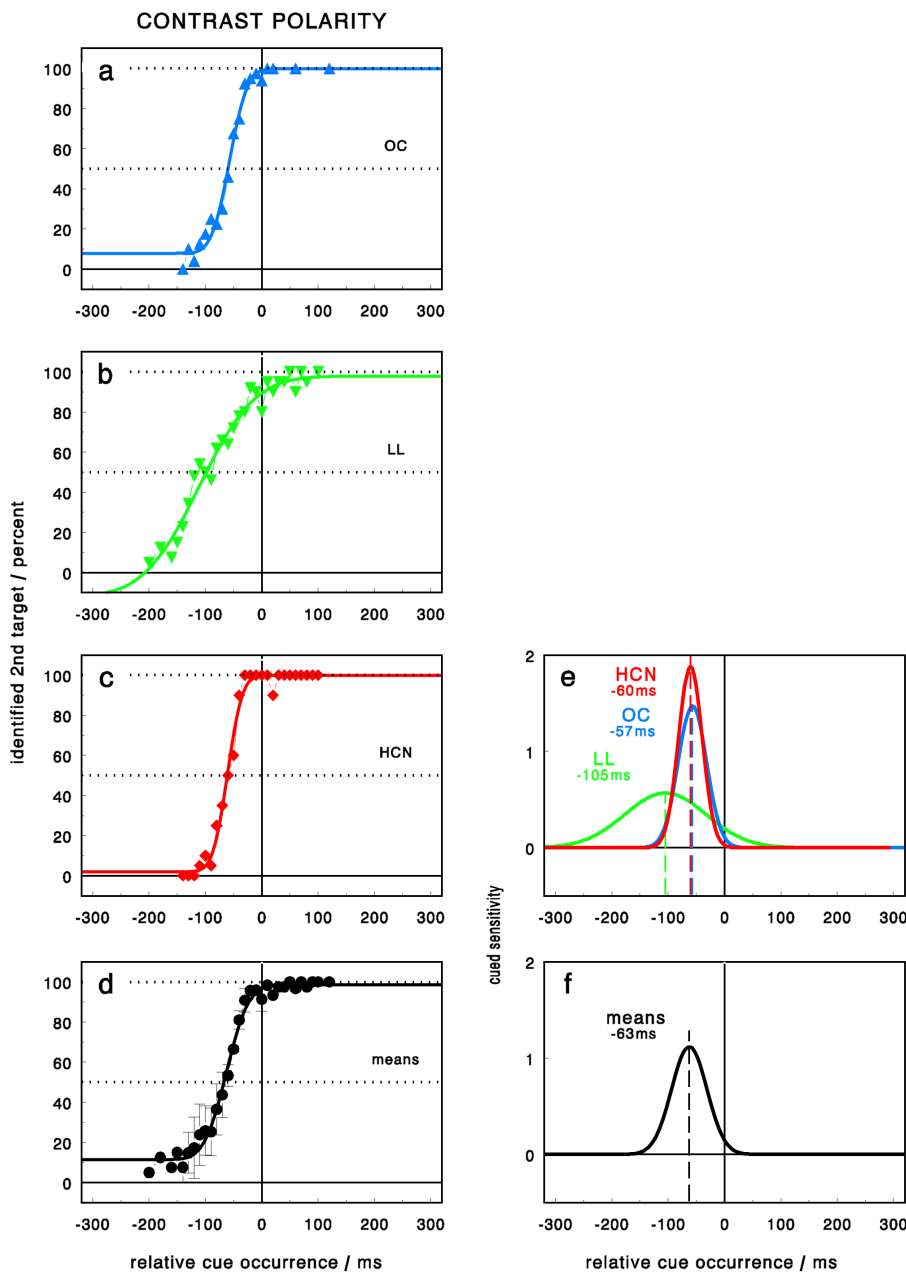


Figure 17. Ratings of cued changes of contrast polarity in Experiment 3. Same presentation as in previous figures. **a.-d.** Original ratings and means with fitted cdfs; **f., g.** reconstructed sensitivity profiles. Cued sensitivity was advanced and similar in two subjects.

Last not least, Experiment 3 has revealed notable differences between the cued identification of motion direction, on the one side, and the cued identification of orientation, color, and luminance polarities, on the other side. These differences were not measured directly but in relation to the presentation of the cue. With respect to the cue, color is earlier identified than motion (cf. Figs. 14 and 16), an observation that is shared with several studies (Moutoussis & Zeki, 1997a,b; Viviani & Aymoz, 2001;

Holcombe & Cavanagh, 2008; McIntyre & Arnold, 2018). Some of these studies have reported that color is earlier *perceived* than motion direction; therefore, direction changes must precede color changes when both should appear to change in synchrony. The present study has confirmed these findings for CVS. Beyond of that, the data did also find a similar difference between orientation and motion and, to a smaller extent, between color and orientation (Moutoussis & Zeki, 1997b; but see Viviani &

Table 2. *Cuing windows in Experiment 3.* Widths (σ) and delays are directly taken from the fitted inverse cumulative distribution functions in Figs.11 and 15-17.

	<i>Motion</i>			<i>Orientation</i>		<i>Color</i>		<i>Luminance polarity</i>	
	<i>width</i>	<i>delay¹⁾</i>	<i>delay²⁾</i>	<i>width</i>	<i>delay^{1,2)}</i>	<i>width</i>	<i>delay^{1,2)}</i>	<i>width</i>	<i>delay^{1,2)}</i>
MEL	56	1	21						
AJ	26	-24	-16						
VSE	53	-6	9						
RUB	55	7	35						
HCN	24	-34	-24	23	-84	26	-80	21	-61
OC	28	-19	-12	55	-156	35	-72	25	-57
LL	23	-43	-18	43	-108	46	-96	78	-111
means	42.6	-16.3	-1.6	51.2	-106.6	33.3	-77.8	31.1	-62.6

all values in milliseconds

¹⁾ center of cdf's

²⁾ values at 75%

Aymoz, 2001). It would be interesting to see if a similar perceptual asynchrony is also seen for luminance and motion, but not for color and luminance, as would be predicted from the present data.

Methodological aspects. It would be adequate to mention some methodological particularities with the analysis applied in Experiment 3. In principle, the underlying assumptions are plausible and the computations straight forward. With a shifting cue delay in CVS, more and more targets are correctly identified. Performance ratings can be fitted by cumulative Gaussian functions, from which the underlying Gaussian sensitivity profiles can be reconstructed. This was successfully done in all tested dimensions. Compared to motion, however, there were two differences. One laid in the different paradigms. The target jump was a singular event which could only be detected, and motion direction be identified, when that event was seen. With all other feature dimensions, the target switch was reconstructed from identifying the targets before and the targets after the switch (depending on the occurrence of the cue), which is, in principle, a different task. It may suffer more strongly from the need of integration time and, eventually, the speed of target identification than would the discrimination of one-step movements. Fortunately, the data do not indicate that subjects were particularly slow in identifying target orientation, color, or luminance polarity.

The other difference was computational. Since the ratings of movement directions were still increased for several hundred milliseconds after the jump (which is likely due to persistent responses; see the discussion above), ratings did not fall to chance but remained increased at 60-70%. The fitted inverse cdf's and reconstructed pdf's, therefore, had smaller amplitudes (about 35% instead of 50%) and their midpoints representing ratings of 82.5% instead of 75% in the inverse cdf's were shifted towards negative values. If the 75% ratings are taken instead (indicated in Fig.13), the pdf centers shift to more positive values and the mean delay closer to 0 ms (-1.6 ms).

GENERAL DISCUSSION

In three series of experiments, the temporal cuing windows in CVS were analyzed for different target properties. When targets were presented long after the cue and nothing was to be detected before, observers could remain in a *waiting mode* until the next target occurred (Exp.1). In this mode, the *spatial* selection was maintained (although with a slow decay over time; cf. Nothdurft, 2017a) but the dynamics of attentional cuing were not reflected in the responses. Beyond this special situation, however, observers could generally quickly identify cued targets from short time windows. There often was a delay

between the physical occurrence of the cue and the extracted target properties; this delay varied between features and, to a smaller amount, between observers. Target jumps (motion) were, on average, identified in close synchrony to the cue, other target properties (orientation, color, luminance polarity) were identified faster so that the seen properties of *cued* targets corresponded to target properties presented later. Cue efficiency then appeared to be delayed. This delay reached to almost –190 ms in certain tasks (cf. Tables 1 and 2) and varied among subjects. In the means, the delay was largest for orientation changes (–100 ms to –107 ms), smaller for color changes (–70 ms to –78 ms) and changes of contrast polarity (–63 ms), and smallest for the line movements (–1.6 ms). Such large differences might be surprising as they do not relate to latency differences of neuronal responses in the early visual system (Bair, Cavanaugh, Smith, & Movshon, 2002). They do however replicate similar differences and rankings found in other studies (e.g., Moutoussis & Zeki, 1997b). Perhaps even more astonishing might be the large variability between observers. But here the different delays were also affected by the widths of cuing windows, as delays are centered in these windows (Appendix A). If an observer required target integration over a particularly long interval, also the cue-target delay should be increased. The positive ends of the negative cuing windows, where target integration began were far less variable between observers (Figs. 15f, 16f, 17f). This is, of course, not true for the identification of line jumps for which the cuing windows were centered around cue-target synchrony (Fig. 14).

It is interesting to note that Experiments 1 to 3 though using different experimental approaches to measure the timing properties of CVS, have by and large generated similar results. Experiment 1 had revealed the important role of temporal integration (which was confirmed in Experiments 2 and 3). The (negative) delays of cuing windows in Experiments 2 and 3 were also seen in Experiment 1 when target ratings already increased before the target was cued. Cuing delays and target integration time had direct consequences for the timing of cued target offsets; target identification was then already diminished before the target was masked (Fig. 2). After all, however, it is quite remarkable that it was possible to extract cued information from dynamic patterns. The parameters that control these extracts are the integration time and the relative delays of the cuing windows.

CONCLUSIONS

In general, the study has confirmed that cued visual selection (CVS) is based on high temporal accuracy, which once more proves it a useful tool for analyzing neural mechanisms and representations. The fact that cues do not only spatially but also temporally select the information to be looked at, may help to study dynamical perceptual processes that can otherwise not be temporally resolved. But with certain properties cues may only become efficient after a delay. Particularly in the order of cuing delays (up to a few hundred milliseconds) it may thus be important to base the interpretations and conclusions on the detailed analyses of cuing windows, integration times and cuing delays, especially when different target properties are to be compared.

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APPENDIX

The Appendix is added to provide the background for analyses made in the paper and to illustrate certain relationships between parameters.

A. Constant phase shifts and systematic phase-shift variations in feature flicker (Experiment 2)

The interplay of integration intervals and phase shifts in feature flicker was studied in a simple model.

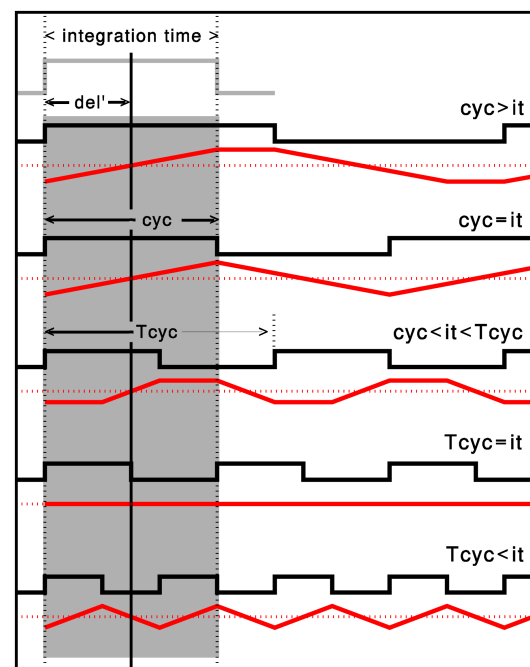


Figure A1. Schematic illustration of phase shifts obtained with a constant integration window. The figure sketches five cases of stimulus flicker (black lines) and presumed rating performance (red curves), if performance is based on the cumulated sensitivity over a constant (boxcar-like) integration window (gray area). While maximal and minimal responses vary with cycle duration, the zero transitions between them occur at a constant delay, del' , (vertical black line) relative to stimulus onset; $del' = it/2$. This constant relationship is valid as long as the full pattern cycle, T_{cyc} , is larger than the integration window. If pattern cycles are too short ($T_{cyc} < it$), phase shifts may vary. However, rating amplitudes should then be strongly decreased, as ratings would be based on the cumulated input from different (complementary) patterns.

Delays and integration windows. As Figure A1 illustrates, the response accumulation with a boxcar-function sensitivity profile ("integration time") leads to an apparent delay even if there is no delay between stimulus modulations and neural sensitivity. This apparent delay, del' , depends exclusively on the integration time, it , during which the neural information is accumulated, and is constant for different flicker rates, as long as the integration time, it , is shorter than a full flicker cycle, T_{cyc} ($T_{cyc} = 2 \cdot cyc$). Only when the flicker rate is increased so that the integration time *exceeds* the full flicker cycle ($T_{cyc} < it$), phase shifts begin to vary; however, rating amplitudes should then be very small because information is accumulated from both alternating stimuli. If there is a true negative delay, as was observed in Experiment 2, so that target properties are seen earlier than the cue, the measured delays must be accordingly modified (Fig.A2). They still remain constant for a constant it ($it > T_{cyc}$). With the assumed true ("biological") delay, del , the apparent delay, del' , should be measured as

$$(1) \quad del' = del + it/2,$$

from which the true delay, del , can be obtained,

$$(2) \quad del = del' - it/2.$$

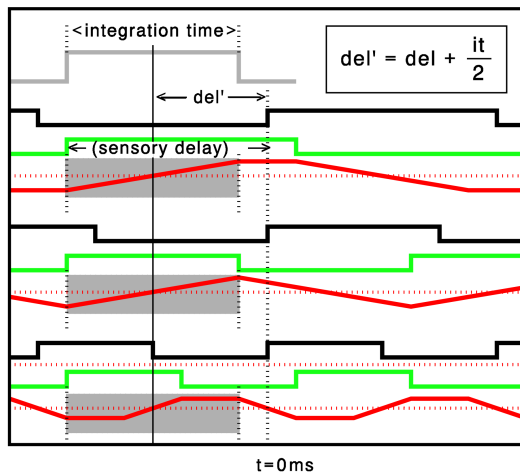


Figure A2. Schematic illustration of phase shifts in the presence of an internal perceptual delay. The figure sketches the situation as in Fig.A1 when sensitivity is truly ("biologically") delayed. The stimulus cycle (black lines) is onset at $t=0ms$; the sensory delay, del , is here assumed to be negative and to precede the stimulus cycle (green lines). Integration (gray) must then be performed on this percept to obtain the presumed rating performance (red curves). With the apparent delay from the size of the integration window, the measured delay del' is given by $del' = del + it/2$. This measure should be constant for constant delays and cycle durations longer than the constant integration time.

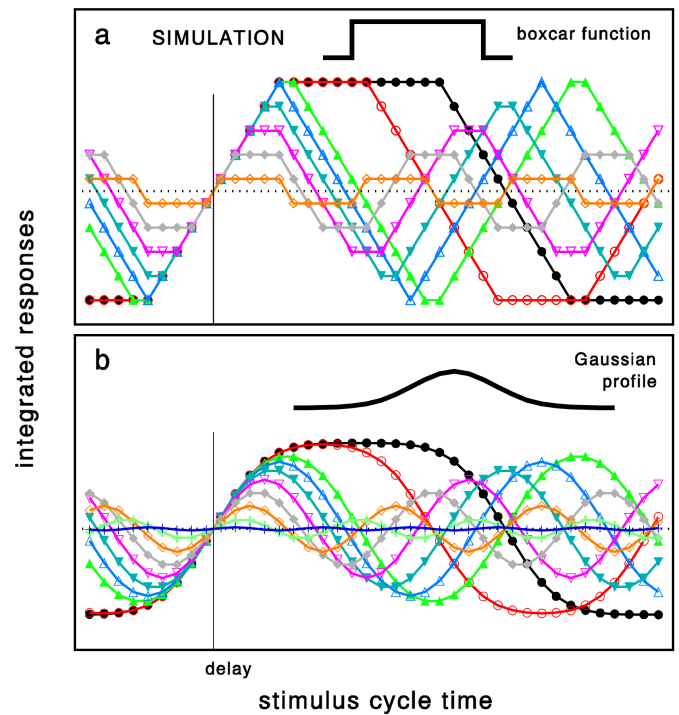


Figure A3. Response simulations with **a.** boxcar and **b.** Gaussian-like integration windows. Assumed rating performance was accumulated, for various cycle durations, over the two sensitivity profiles (a, b) centered at del . Zero transitions indicating the apparent phase shifts are strictly superimposed.

The reason why delays are constant despite target durations (cyc) change is that the phase shifts are calculated from sinus functions fitted to the data. Ratings with alternating target features (left- vs. right-tilted lines, green vs. red patches) are symmetrical around chance (50%). Curves are fitted so that the transitions from one rating to the next are aligned with the transitions from one stimulus to the next. This creates the apparent phase shift, del' . The equations show that del' (and del) depend on it and thus should vary when the integration time is changed.

Constant phase shifts are not a special result of the boxcar function but are also obtained for Gaussian-like integration windows (Fig.A3).

Phase-shift variations. While phase shifts should thus be constant unless integration windows cannot resolve the flicker (i.e. for $T_{cyc} \leq it$), systematic phase shifts were observed for $cyc \geq it \geq T_{cyc}$, with some observers (Fig.6). The following considerations are made to search for an explanation.

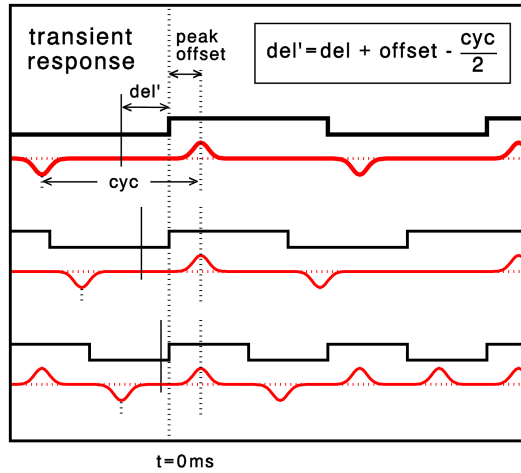


Figure A4. Schematic illustration of phase-shift variations with an "asymmetric" response profile (due to, e.g., transient response components or adaptation). If rating responses (red lines) were not centered in the individual target presentations (black lines) but for example shifted towards target (and complementary target) onset, the apparent delay, del' (vertical black lines), would not be constant over different cycle durations. The relationship should be linear (as long as the response asymmetries are not disturbed) with a slope of 0.5; $\Delta del' = 0.5 \cdot \Delta cyc$.

With a constant integration window, it , the only valid possibility for phase-shift variations in the observed magnitude seems to be the occurrence of transient responses in the rating performance, such as if observers had better identified targets that just have changed their properties than targets that had remained unchanged for a while, when the cue occurred. Such transient rating responses were, however, not predominant in the data (cf. Fig.7).

A schematic example is given in Figure A4. If ratings were not homogeneous during the time of target presentation but showed notable transient modulations, the apparent delay, del' , will be shifted in proportion to the tested target duration, cyc . When the same transient response components occur in the ratings to both complementary stimuli, zero transitions should be shifted according to its *offset*.

$$(3) \quad del' = del + offset - cyc/2$$

Different to the constant integration interval in equation (1), this measured delay, del' , should now vary with the cycle duration. This implies that even for a constant biological delay, del , the measured delay, del' , should now

increase with decreasing cycle duration, cyc , with a slope of -0.5,

$$(4) \quad \Delta del' = -\Delta cyc/2.$$

B. Reconstruction of Gaussian sensitivity profiles from rating data in Experiment 2

For a given *boxcar*-like integration window, upper and lower limits in target identification rates are given by cycle durations in which the integration window either covers one target cycle, cyc (maximal ratings; rating amplitude 50%) or the full cycle, T_{cyc} (minimum ratings, amplitude 0%). In-between ratings should vary linearly with the cycle length.

This was obviously not found; ratings varied nonlinearly with the cycle length (Figs.5 and 6).

For an assumed *Gaussian* temporal sensitivity profile, ratings can be predicted from the cumulated responses to both targets. Depending on the cycle length, T_{cyc} , and the durations of both targets cycles, $cyc = T_{cyc}/2$, the maximal cumulated response of a given Gaussian can be calculated and should lead to a predicted rating amplitude. In Figure A5, this relationship is illustrated for three cycle lengths defined as multiples of the standard deviation σ , a parameter that defines the width of the Gaussian normal distribution. In Figure A5a, for example, the presence of target 1 would accumulate to a rating performance of 68.27% percent, which should be diminished by 31.46% from the presence of the complementary target 2 in the same temporal window. But earlier and later repetitions of target 1 within that window might also add to the accumulated signal. The total rating should thus accumulate to $68.27\% - 31.46\% + 0.27\% = 37.08\%$ for target 1, and accordingly to -37.08% for target 2. Since ratings were measured from 0% (=100% target 2) to 100% (=100% target 1), the resulting ratings should be $50 + 37.08/2 = 68.54\%$ and $50 - 37.08/2 = 31.46\%$, with a rating amplitude of 18.54%. Various multiples of σ and predicted rating amplitudes were used to link σ to cycle length via the rating measures of a particular observer (Figs.5 and 6).

For that, rating data were fitted by exponential curves, from which the half-cycle durations at various rating amplitudes were taken. Figure A6 shows this relationship for two observers. Variations of multiples of σ with half-cycle length, cyc , are particularly linear for target durations (half-cycle durations) between two and four σ

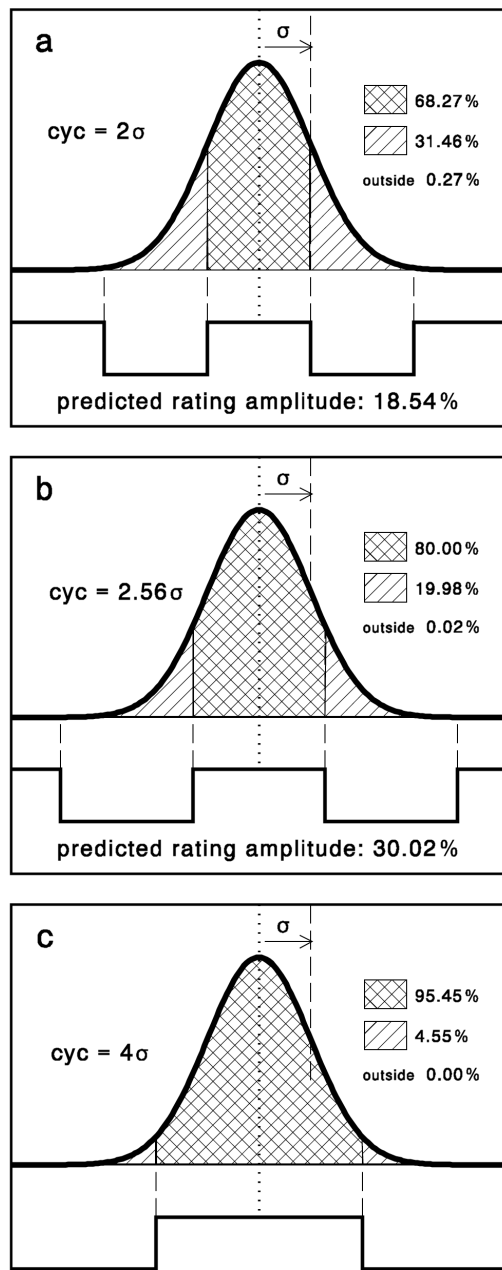


Figure A5. Schematic illustration of target duration and target integration with a Gaussian sensitivity profile. **a.-c.** For certain cycle lengths, the expected rating amplitudes can be predicted from the cumulated sensitivity of the Gaussian profile, as indicated. This correlation was used to reconstruct the underlying Gaussians, and in particular their parameter σ , from rating amplitudes with different cycle lengths in Figs.5 and 6. Best ratings are obtained when the according target duration, *cyc*, is centered in the sensitivity profile. Via predicted rating amplitudes, σ can thus be linked to cycle length for a given performance.

(the range illustrated in Fig.A5); ratings above and below this range deviated from linearity, probably due to the poorer resolution of data on either axis. The range between two and four σ was then used to estimate σ in milliseconds and to reconstruct the underlying Gaussian sensitivity profiles (cf. Table 2 and Fig. 9).

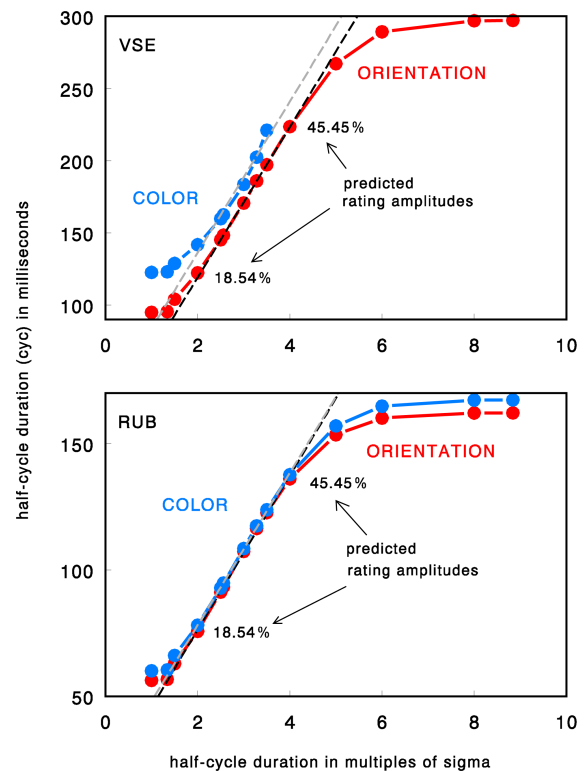


Figure A6. Correlation of target duration and the width (σ) of a hypothetical Gaussian sensitivity window in Experiment 2. For Gaussian profiles, rating amplitudes obtained with certain half-cycle durations should be directly related to the standard deviation sigma (σ) of the Gaussian normal distribution (cf. Fig.A5). Graphs show this relation exemplary for two observers. Cycle durations were obtained from exponential fits to the ratings in Figs.5 and 6. While linearity deviates at low and high values, the correlation is highly linear between 2σ and 4σ . Data from this range were averaged to estimate σ (via cycle time) in ms.

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