Occlusion improves the interpolation of sampled motion

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Abstract

Several studies show that the perception of occlusion may affect various aspects of motion perception. Here we present data indicating that occlusion cues also influence the visual interpolation of sampled motion. Normally, sampled motion stimuli are perceived as less smooth and jerkier when the spatial gaps between successive presentations of the “moving” target stimulus increase. Adding surfaces occluding the spatial gaps, however, we found that the perceived smoothness of motion was not only better, but also independent of the gap width. We argue that this effect occurs because the visual system attributes the interruptions in the motion path to occlusion rather than to the moving object itself.

Keywords:
motion interpolation, occlusion, amodal completion

1. Introduction

Motion perception has traditionally often been studied and analyzed separately from other aspects of visual perception (e.g., Reichardt, 1957; van Santen & Sperling, 1984). In ecological viewing situations, however, motion is closely related to occlusion (Gibson, 1968; Gibson et al., 1969): An object...
traversing the visual field occludes and reveals parts of the background as it moves, and conversely, a moving object is often intermittently occluded by other objects in the foreground. This natural relation between motion and occlusion is not only a problem the visual system must cope with, but also a potential source of cues that can be utilized by the visual system to infer the movement and position of objects.

In line with these general considerations, it has been shown that several aspects of motion perception are strongly affected by cues to occlusion (Wallach, 1935; Sigman & Rock, 1974; Shimojo et al., 1989; Anderson, 1999; Duncan et al., 2000; van der Smagt & Stoner, 2008; Ekroll & Borzikowsky, 2010). Here we present data from an experiment suggesting that occlusion cues also enhance the perceptual interpolation of sampled motion stimuli.

1.1. Sampled motion

As is known from movies or flip-books, not only continuous motion stimuli can evoke compelling motion percepts, but also discrete sequences of sampled motion. This is trivial for sampling rates higher than the spatiotemporal resolution of the sensory system (Watson et al., 1986). However, even at lower sampling rates where sampling artifacts are clearly visible, interpolated, so-called “apparent motion” can be perceived (e.g., Wertheimer, 1912; Korte, 1915; Kolers, 1972; Ekroll et al., 2008). Fig. [1] illustrates continuous and sampled motion stimuli. The hatched areas in panel (b) indicate sections of the motion path at which the target stimulus, though “expected” when moving from left to right, never physically appears. Despite these inexplicable gaps between the successive positions of the target stimulus, interpolated apparent motion along its trajectory is perceived as long as the spatial sampling
rates are not too low (Burr et al., 1986b). This suggests that sampled motion stimuli activate motion processes in much the same way as continuous motion stimuli do.

1.2. Enhanced motion interpolation through amodal continuation?

Apparent motion of a target stimulus (the “target”) in sampled motion (Fig. 1b) can be smooth or jerky, depending on the amount of sampling artifacts. Typically, the motion interpolation is jerkier the larger the spatial and/or temporal gaps between successive target positions are (Burr, 1979).

In an earlier study (Scherzer & Ekroll, 2009) we presented sampled motion stimuli and asked the subjects to judge the motion smoothness. As expected, we found that motion was perceived as jerkier the larger the target displacement and the interstimulus interval (ISI) between two target presentations was. A possible explanation for this observation would be that spatial and temporal gaps provide evidence against the continuous existence of the object. Consequently, motion interpolation could be impaired, and this may result in a less smooth or jerky motion percept. Masking the entire scene with an opaque surface during the ISIs, however, we found that the perceived jerkiness was reduced (“smoothness effect”). Based on this idea we reasoned
that motion interpolation should be unimpaired if the evidence against the continuous existence of the object is removed, and that this can be accomplished by adding occluders accounting for the spatial and temporal gaps. The presence of occluders would allow for the continuous amodal existence of the moving target (Michotte et al., 1964/1991) despite its interrupted motion path and intermittent invisibility. Thus, the spatial and temporal gaps could be attributed to an extrinsic factor, namely occlusion (cf. Sigman & Rock, 1974; Shimojo et al., 1989), rather than to the moving object itself.

In the aforementioned study we concluded that the smoothness effect was triggered by occlusion cues exploited by the visual system. In that study transient dynamic occlusion cues might have completely accounted for the temporal gaps (ISIs) contained in the stimuli. Following this, here we hypothesize that the smoothness effect would also occur if static occlusion cues may account for the spatial gaps between successive target positions (“target gaps”). The space-time diagrams of those stimuli would be essentially just transposed versions of those used in the previous study, i.e., the space and time dimensions would be interchanged.

To test our hypothesis, we conducted two experiments with three types of sampled motion stimuli in which there were a) no occluders accounting for the spatial gaps between successive target positions, b) occluders accounting for half of each target gap, and c) broader occluders completely accounting for the target gaps (Fig. 2; see also supplementary demonstration S1): In the no-occlusion condition nothing but a square target stimulus in sampled motion was visible in front of a background; the gaps between successive target positions remained inexplicable (panel a). In the partial-occlusion condition
narrow surfaces half-occluded the horizontal target gaps, thus presumably reducing the amount of inexplicable interruptions in the motion path by half (panel b). In the full-occlusion condition broad surfaces occluded the spatial gaps completely and thus “explained” the interruptions in the motion path (panel c).

Figure 2: Sampled motion sequences (details of the canvas, not to scale) in which a square target stimulus (black) “moved” rightwards over the canvas, i.e., it was successively displaced by $\Delta x$ in discrete steps. Three types of stimuli were used: (a) no occluders; (b) partial occluders; (c) full occluders. In the experiment the square target stimulus was green and the background was slightly reddish.

2. Experiment 1

2.1. Methods

We presented the sampled motion sequences on a CRT monitor running at 85 Hz. In each sequence a green square stimulus (the “target”) with about
0.35° side length “moved” rightwards over a slightly reddish textured canvas, i.e., it was displaced successively in discrete steps as depicted in Fig. 2 (see also the supplementary demonstration S1). The viewing distance was about 80 cm and the canvas subtended approximately 13° × 13°.

The stimulus onset asynchrony (SOA) between two successive target presentations was varied in four steps: 47 ms, 96 ms, 141 ms, and 188 ms. There was no interstimulus interval (ISI), hence the display duration D of the target at each position always equaled the SOA. For each value of SOA, the horizontal gap width between successive target positions (“target gaps”) was varied in three steps: approximately 0.35°, 0.7°, and 1.05°, resulting in target displacements Δx of approximately 0.7°, 1.05°, and 1.4°, respectively. Whenever the target left the canvas on the right, it entered the canvas on the left again. After 10 cycles the sequence stopped.

As already mentioned, three types of stimuli were used (Fig. 2). In the no-occlusion condition, nothing but the moving target was shown. In the partial-occlusion condition and in the full-occlusion condition, additional gray surfaces of approximately 1.4° height were permanently displayed between successive target positions. The surfaces were half as broad as the gaps in the partial-occlusion condition and just as broad as the gaps in the full-occlusion condition, thus occluding the target gaps by half or completely, respectively.

In total there were 36 different conditions (4 SOA levels × 3 target gap width levels × 3 stimulus types), each repeated 10 times, resulting in 360 trials presented in random order over three sessions. The experiment started after a short introduction and a few test trials. The subjects’ task was to
judge the smoothness of perceived motion once the sequence had stopped, using the following response categories (here referred to as C1-C5) constituting an ordinal smoothness scale (1-5) where higher values represent a smoother motion percept (original German instructions in parentheses):

- **C5**: Very smooth forward motion, continuous. (“Sehr glatte Vorwärtsbewegung, kontinuierlich.”)
- **C4**: Fairly smooth forward motion, continuous. (“Recht glatte Vorwärtsbewegung, kontinuierlich.”)
- **C3**: Fairly smooth forward motion with short breaks/stops. (“Recht glatte Vorwärtsbewegung mit kurzen Stopps.”)
- **C2**: Jerky forward motion with short breaks/stops. (“Sprunghafte Vorwärtsbewegung mit kurzen Stopps.”)
- **C1**: Jerky jumps forth and back. (“Ruckartige Sprünge vor und zurück.”)

An additional response category—“No motion percept” (“Kein Bewegungseindruck”)—was never used by any subject. The subjects were asked to pursue the target with their eyes.

Nine naive undergraduate students from the University of Kiel participated in the experiment for course credits.

### 2.2. Results and Discussion

Fig. 3 shows that, as predicted by our hypothesis, when more parts of the target gaps were occluded, the perceived motion was smoother. The smoothest motion percepts were reported in the full-occlusion condition where
the gaps between successive target positions were fully occluded, and the jerkiest motion percepts were reported in the no-occlusion condition where the target gaps were not occluded. This difference was significant ($p < 0.05$) within all combinations of SOA and target gap width. In the partial-occlusion condition, the mean smoothness rating was generally lower than in the full-occlusion condition, but higher than in the no-occlusion condition.

Figure 3: Results of Experiment 1. The panels show the average rating of motion smoothness for different stimulus onset asynchronies (SOA), gap widths between successive target positions, and stimulus types (full/partial/no occlusion). The data show the smoothness effect: The more parts of the gaps between successive target positions were occluded, the better was the perceived motion smoothness. As can be expected, the perceived motion quality generally decreased with increasing SOAs. It also decreased with increasing gap widths unless opaque surfaces fully covered the gaps (black bars). Error bars represent ±1 SEM across observers.

It is well-known that the perceived motion smoothness tends to deteriorate with decreasing spatiotemporal sampling rates \cite{Burr1979}. This effect is also evident in our data. The motion smoothness typically decreased with increasing stimulus onset asynchronies (SOA), i.e., with decreasing sampling rates in time, and with increasing target displacement, i.e., with decreasing sampling rates in space. However, the sampling rate in space did not af-
fect the smoothness of motion in the full-occlusion condition, where broad occluders covered the horizontal gaps between successive target positions completely. In the partial-occlusion condition, where only half of the objective interruptions in the motion path was explicable by the presence of the occluders, the results were intermediate between those in the full-occlusion and the no-occlusion condition. Thus, the effect of occlusion is not all or none. Rather, it would seem that the motion smoothness is directly and quantitatively related to the amount of interruptions in the motion path not accounted for by occlusion. As can be appreciated in the supplementary demonstration S1, this effect is accompanied by a percept of a moving object amodally completed behind the occluders.

It does not seem possible to account for the entire pattern of results observed in our experiment based only on the amount of inexplicable interruptions in the motion path. This is not surprising, however, since an effect of the temporal variable SOA (stimulus onset asynchrony) is also to be expected. Therefore, we asked how well the entire pattern of results can be accounted for based on a combination of the two variables SOA and ‘amount of inexplicable motion path interruptions’.

2.2.1. Model fit

Fig. 4 shows the fit between the data and a model developed based on the assumptions that a) motion is perceived as jerky whenever SOA or the amount of inexplicable interruptions in the motion path (target gap width minus occluder width) is large, and b) the probability of classifying the motion stimulus as discontinuous is an increasing function $f_t$ of the temporal variable SOA and also an increasing function $f_s$ of the spatial variable ‘amount of inexp-
pplicable motion path interruptions’. Thus, since the probability $P$ of event $A$

or event $B$ is $P(A) + P(B) - P(A) \cdot P(B)$, the probability $P(D)$ of classifying
the motion stimulus as discontinuous ($D$) should be $P(D) = f_t + f_s - f_t \cdot f_s$.
The smoothness ratings $S$ should be positively related to the probability $P(C)$ of interpreting the motion sequence as continuous ($C$) which is equal to $1 - P(D)$. In the model, we assume that the scale of smoothness ratings effectively used by the subjects reflects the probabilities $P(C)$. That is, letting $a$ and $b$ be the lower and upper bounds of the smoothness scale effectively used by the subjects, the smoothness rating $S$ is related to $P(C)$ by the equation $S = a + (b - a) \cdot P(C)$. To model the data, we used cumulative Gaussians for $f_t$ and $f_s$. Thus, the model has the free parameters $a, b$ in addition to the means $\mu_t, \mu_s$ and the standard deviations $\sigma_t, \sigma_s$ of the Gaussians. The predictions shown in Fig. 4 represent a least-squares fit of this model to the mean data. The corresponding estimated dependence of SOA and the amount of inexplicable interruptions in the motion path is shown in Fig. 5.

Figure 4: The same data as in Fig. 3 (bars) and a fit using our model that is based on a combination of the two variables SOA and ‘amount of inexplicable motion path interruptions’ (lines). Error bars were omitted for better readability.
3. Experiment 2

The results of Experiment 1 show that the perceived smoothness of apparent motion was enhanced when the spatial gaps were filled with static stimulus elements that could be interpreted as occluders. This suggests that when discontinuities in the motion path that would normally result in a jerky motion percept can be attributed to occlusion, motion is perceived as smoother. If cues to occlusion are indeed the cause of the observed smoothening effect, one would expect that adding binocular disparity cues consistent or inconsistent with the occlusion interpretation should have a corresponding influence on the perceived smoothness. To test this prediction, we used similar stimuli as in Experiment 1, but added binocular disparities indicating that the target was in front of, behind, or in the same depth level as the occluders.

3.1. Methods

The same three types of stimuli as in Experiment 1 were used (full-occlusion, partial-occlusion, and no-occlusion condition). However, now the
stimuli were displayed stereoscopically (see the supplementary demonstration S2), and relative binocular disparity was added either to the occluders (occluders-in-front condition), to the target (target-in-front condition), or to none of the elements (same-depth condition). Because the occluders-in-front condition could not be combined with the no-occlusion condition, there were 3 \times 3 - 1 = 8 conditions in total. In order to add horizontal disparity to our stimuli, it was necessary to rotate the stimulus display such that the target “moved” in the vertical instead of the horizontal direction, i.e., from the top to the bottom of the canvas. The (vertical) target gap width was varied in the same manner as the (horizontal) target gap width in Experiment 1 (0.35°, 0.7°, and 1.05°), whereas the SOA was held constant at 94 ms in this experiment. Hence, in total, there were 24 different conditions (3 target gap width levels \times 8 different combinations of occlusion types and disparity types), each repeated 10 times, resulting in 240 trials presented in random order over two sessions. The subjects’ task was the same as in Experiment 1, and nine students who had not participated in the first experiment served as subjects.

3.2. Results and Discussion

3.2.1. Comparison with Experiment 1

The stimuli in the same-depth condition were identical to those used in Experiment 1 at SOA level 94 ms except for the direction of target movement that was horizontal in Experiment 1 but vertical in Experiment 2. As can be seen in Fig. 6, the results of the two experiments are grossly similar: In both experiments the smoothest motion percepts were reported in the full-occlusion condition and the jerkiest motion percepts in the no-occlusion
condition. Also, the perceived motion smoothness decreased with increasing levels of target gap width except in the full-occlusion condition. However, the mean response difference between the partial-occlusion condition (gray bars) and the no-occlusion condition (white bars) at gap width levels $\geq 0.7^\circ$ was somewhat smaller in Experiment 2 than in Experiment 1.

3.2.2. General results

The full-occlusion condition contains static T-junctions, which are known to be strong cues to occlusion (Anderson et al., 2002) indicating that the target moves behind the occluders. Adding binocular disparity cues consistent with this interpretation should therefore not influence the perceived smoothness, whereas binocular disparity cues inconsistent with the occlusion interpretation should impair the perceived smoothness. This is indeed the case. As can be seen in Fig. 7 (left panel), there is essentially no difference between the occluders-in-front condition and the same-depth condition, while the smoothness ratings are lower in the target-in-front condition.
Figure 7: Results of Experiment 2. Binocular disparity was absent (gray bars), added to the occluders (black bars) or to the target (white bars). The panels show the average smoothness ratings of the full-occlusion, partial-occlusion, and no-occlusion condition, respectively. The pattern of results is similar to the corresponding pattern of results of Experiment 1 (SOA = 94 ms). Error bars represent ±1 SEM across observers.

The occlusion-inconsistent disparity does not abolish the smoothness effect completely, which can be appreciated by considering that the smoothness ratings in the target-in-front condition in the presence of full occluders (white bars in the left panel) do not reach the base-line level represented by the corresponding white bars in the right panel. This is not surprising, since there is a conflict here between the T-junctions signaling occlusion and the inconsistent disparity (Shimojo & Nakayama, 1990). Equal results in the full-occlusion condition with inconsistent disparity and the no-occlusion condition would only be expected if the visual system relies exclusively on the disparity signal and disregards the T-junctions completely. It is unclear, though, why the smoothness ratings do not decrease with target gap width, as one would expect based on the occlusion account, due to the decreasing size of the inexplicable spatial gaps.

In the partial-occlusion condition one would expect the smoothness rat-
ings to be generally lower than in the full-occlusion condition, because only half of the spatial gaps were occluded. This is indeed the case. Also, as in the full-occlusion condition, one would expect the ratings to be lower in the occlusion-inconsistent disparity condition than in the zero-disparity condition. This is also the case. A difference between the full-occlusion and the partial-occlusion condition is that the latter does not contain T-junctions signaling occlusion. Thus, there are no strong monocular cues to occlusion in this condition making the situation more ambiguous than in the full-occlusion condition. Therefore, we would expect disparity signals indicating occlusion to have a disambiguating effect leading to a smoother motion percept than in the same-depth condition, which is also the case. A second difference between the full-occlusion and the partial-occlusion condition is that while the spatial gaps are completely accounted for by occlusion in the former case, half of the gaps are left inexplicable in the latter condition and the size of these gaps increases in proportion to the target displacement. Accordingly, we would predict that the smoothness ratings decrease with the target gap width in the latter condition, but not in the former. This is also the case.

It may appear surprising that the ratings for partial-occlusion conditions with occlusion-inconsistent disparity are better than the ratings for the corresponding no-occlusion conditions. One might argue, though, that on the monocular level—despite the occlusion-inconsistent disparity—the stimuli in the partial-occlusion condition are still better compatible with an occlusion interpretation than the stimuli in the no-occlusion condition.

It is unclear why the ratings in the no-occlusion condition are worse in the
target-in-front than in the same-depth condition\textsuperscript{1} This effect, which is obviously not related to occlusion, may be due to a yet unknown factor related to the disparity of the target relative to the background. Thus, we cannot definitely rule out the possibility that the differences between corresponding disparity conditions in the two occlusion conditions are due to this unknown factor rather than to occlusion. It should be noted, however, that this unknown factor cannot account for the (admittedly small) differences between the two partial-occlusion conditions in which the target-to-background disparity is zero (namely, the occluders-in-front and the same-depth condition). Furthermore, it is difficult to see how this unknown factor could account for the clear effects of the monocular occlusion cues observed both in this experiment and in Experiment 1.

4. Manipulation check

To see whether the different disparities used in Experiment 2 actually resulted in the intended occlusion interpretations, we performed a supplementary experiment—prior to Experiment 2—in which we asked the subjects to judge whether the target was perceived behind or in front of the occluders, which were neutrally referred to as “bars” in the instructions. We presented a subset of stimuli used in Experiment 2, namely stimuli with full and partial occlusion, constant SOA (94 ms), and constant target gap width (0.7°), to the same nine subjects.

As can be seen in Fig. 8 the judgements in the partial-occlusion condition

\textsuperscript{1} It may be of interest to note that a similar observation was recently reported by Kim et al. (2011, see their Fig. 7a).
Figure 8: Results of the manipulation check. The subjects were asked to judge whether the occluders or the target were perceived as in front. In conditions with occlusion-consistent disparity (black bars) the occluders were always perceived as in front both in the full-occlusion condition (left) and in the partial-occlusion condition (right). In conditions with no relative disparity (gray bars) the occluders were almost always perceived as in front in the full-occlusion condition, but only about half of the time in the partial-occlusion condition. In conditions with occlusion-inconsistent disparity (white bars) the occluders were perceived as in front still about one third of the time in the full-occlusion condition, but very rarely in the partial-occlusion condition. Error bars represent ±1 SEM across observers.

are simply related to the disparity between target and occluders. When the disparity indicated that the occluders were in front, the occluders were always perceived as in front. When the disparity indicated the converse, the target was almost always perceived as in front. At zero disparity the target was perceived as in front about half of the time and as behind in the other half. This intermediate result is not surprising given the lack of clear cues to the relative depth of the target and the occluders in this condition.

The results in the full-occlusion condition are similar, but indicate a stronger tendency to perceive the occluders as in front (except in the trials with occlusion-consistent disparity, where the occluders were always perceived as in front already in the partial-occlusion condition). This can be
attributed to the presence of monocular T-junctions.

5. Discussion

5.1. The effect of occlusion on perceived motion smoothness

In two experiments we presented sequences of a target stimulus in sampled motion and asked subjects to judge the perceived smoothness of apparent motion. Three types of stimuli were used, a) with occluders covering the spatial gaps between successive target positions, b) with smaller occluders covering half of the gaps, and c) without occluders.

In Experiment 1 we found that the perceived smoothness of motion could not only be enhanced by reducing the spatial gaps between target positions, but also by adding occluders covering them. The quantitative modeling indicates that occluding a given portion of a spatial gap has the same positive effect on perceived motion smoothness as removing it by reducing the distance between successive target positions correspondingly. Therefore, the results of Experiment 1 are compatible with the hypothesis that interruptions in the motion path have no detrimental effect on perceived motion smoothness provided that the visual system can attribute them to occluders covering portions of the motion path.

In Experiment 2 we used binocular disparity cues consistent or inconsistent with occlusion of the target’s motion path to test this hypothesis further. The results suggest that perceived occlusion is indeed the critical variable: Occlusion-inconsistent disparity reduced the smoothness effect, and occlusion-consistent disparity enhanced the smoothness effect when the monocular occlusion cues were ambiguous (i.e. in the partial-occlusion con-
dition). The results of a manipulation check in which subjects reported whether the occluders or the targets were perceived as in front also support this hypothesis. A feature of Experiment 2 that is not accounted for by this hypothesis, though, is that the perceived smoothness did not decrease with target gap width in the full-occlusion condition with occlusion-inconsistent disparity (Fig. 7 left panel, white bars).

5.2. Possible explanations of the smoothness effect

The well-known fact that discrete sampled motion sequences can evoke impressions of smooth continuous motion is indicative of visual processes of spatiotemporal interpolation (Burr, 1979; Burr et al., 1986b,a; Burr & Ross, 1986; Burr & Morgan, 1997; Nishida, 2011). It therefore appears natural to assume that the perceived smoothness reflects the output of these visual interpolation mechanisms. Fig. 9 illustrates an idea we believe is useful for understanding the present results. Panel (a) shows the space-time diagram of a sampled motion stimulus with four stations (frames). Panel (b) shows the same sampled motion stimulus with a corresponding object in smooth linear motion superimposed. The difference between the ideal linear motion stimulus and the actual stimulus may be thought of as sampling artifacts that should impair the perceived smoothness (Adelson & Bergen, 1985). Panel (c) shows that occluders may account for portions of this difference. Therefore, if the visual system attributes these sampling artifacts to the presence of the occluders rather than to the motion stimulus itself, one would expect that sampled motion should appear smoother with occluders covering the spatial gaps between successive target positions. Note that the interpolation assumed in panel (c) involves a moving object broader than the actual target.
Figure 9: (a) A space-time diagram of a target in sampled motion. The insets in the right column show the percepts at times $t_1$ and $t_2$. (b) The same sampled motion stimulus as in panel (a). The diagonal gray band/arrow represents a corresponding object (with the same width as the stimulus elements) in smooth linear motion (ideal interpolation). (c) The same sampled motion stimulus as in panels (a) and (b), but with occluders covering, and thus also accounting for, the spatial gaps between successive target positions. Since the actual width of the stimulus is unspecified due to the occluders, it is reasonable to assume that it is computed based on the speed of the linearly interpolated motion and the objective duration of the target presentations. Therefore, the estimated width of the moving object is greater than in the condition without occluders.
stimuli presented in each single frame which would slide behind the occluders. In the stimulus with occluders, the width of the target is not uniquely specified by the stimulus, because the corresponding object may extend behind the occluders. If one assumes that the width of the inferred moving object is computed based on the speed of the linearly interpolated motion and the objective duration of the target presentations, one obtains the situation shown in panel (c), where the width of the inferred object exceeds the actual width of the target elements.

A slightly different explanation for the smoothness effect appeals to visual persistence and purely spatial amodal completion (as opposed to the spatiotemporal amodal completion implied in the above explanation) is illustrated in Fig. 10. It is well-known that visual stimuli may be perceived as lasting up to several hundreds of milliseconds longer than they are physically present, a phenomenon called visual persistence (Coltheart, 1980). Assuming, for instance, that the duration of visual persistence equals half of the SOA, the number of simultaneously perceived target elements would oscillate between one for half of the time (at times $t_1$ and $t_3$ in Fig. 10a) and two for the other half of the time (at time $t_2$). If the number of simultaneously perceived target elements oscillates in this manner, it would of course be incompatible with a fixed number of smoothly moving single targets. If the visual system’s assumption about the number of objects is continually updated correspondingly, different interpolation attempts corresponding to these different assumptions may be continually and cyclically initiated and aborted (Moore & Enns, 2004; Moore et al., 2007). That is, rather than a single interpolation process, an unstable succession of contradictory interpre-
Figure 10: (a) A space-time diagram of a target in sampled motion as in Fig. 9a. The portion of each stimulus element above (before) the white dotted lines represents the physical stimulus, while the portion below (after) represents possible visual persistence. The insets in the right column show the percepts at times $t_1$, $t_2$, and $t_3$. Note that the number of simultaneously experienced stimulus elements oscillates between one and two.

(b) The same sampled motion stimulus as in panel (a), but with occluders covering the spatial gaps between successive target positions. The diagonal gray band/arrow represents a corresponding object in smooth linear motion (ideal interpolation). Note that although the interpolated motion path represents a single moving object, one would expect two portions of it to be simultaneously perceived at time $t_2$.

Oscillations would ensue, which would presumably lead to an unstable and jerky motion percept. In the presence of occluders (Fig. 10b), however, such an oscillation in the number of phenomenally visible target elements is compatible with a single unitary object moving behind them: The two target elements
simultaneously phenomenally present at time $t_2$ may be joined into a single unitary object by spatial amodal completion. Thus, in contradistinction to the case without occluders, a consistent visual interpolation based on the assumption of a single moving object is now possible, which would explain why motion appears smoother.

Based on the literature (Coltheart, 1980), one may expect that visual persistence primarily occurs at brief target presentation durations (which correspond directly to SOA in our experiments), and indeed our informal observations suggest that multiple target elements were perceived to be simultaneously present only at the briefer SOA levels. Thus, while visual persistence and purely spatial amodal completion may have contributed to the overall smoothness effect, it cannot account for the effect at higher SOA levels.

It may be of some interest to ask whether eye movements may have contributed to the smoothness effect observed in our experiments. Since our subjects were instructed to follow the moving target with their eyes, and the smoothness of pursued eye movements in rhesus monkeys has previously been found to be affected by the presence of occlusion cues (Churchland et al., 2003), this does not appear unlikely. From this point of view, Churchland’s and our study agree in demonstrating that occlusion cues can approve the quality of interpolated motion.

The present study is in many ways complementary to a previous study, in which we presented evidence suggesting that intermittent occlusion cues displayed during the interstimulus interval (ISI) might enhance the smoothness of apparent motion (Scherzer & Ekroll, 2009). The space-time diagrams

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of the stimuli used in the present study are essentially just transposed versions of those used in the previous study, i.e., the space and time dimensions have been interchanged. Accordingly, the argument against an explanation in terms of Reichardt detectors (Reichardt, 1957; van Santen & Sperling, 1984; Adelson & Bergen, 1985) provided in Scherzer & Ekroll (2009) can be directly applied to the present study also. Both of our studies agree in indicating that occlusion cues can enhance the interpolation of sampled motion. It may be of some interest to note, however, that the effect observed in the present study appears to be more compelling than the one observed in our previous study.

The finding that motion interpolation is smoother in the presence of occlusion cues suggests that the visual system completes the fragmented physical motion path into an amodal representation that is continuous and unbroken. The results of Kim et al. (2011) agree with the present study in demonstrating the importance of such amodal representations in motion perception. They found that the straight apparent motion that can be perceived between two stimulus elements is replaced by curved apparent motion in the presence of a curved occluder.

The present findings add to a growing body of evidence indicating that the intimate ecological link between motion and occlusion is exploited by the visual system in many different ways: Wallach (1935) has demonstrated that occlusion cues are utilized by the visual system in the computation of motion direction (i.e., to solve the “aperture problem”; see also Shimojo et al., 1989; Anderson, 1999; Duncan et al., 2000). Sigman & Rock (1974) have shown that occlusion cues can completely inhibit apparent motion when the
sudden disappearance (appearance) of a stimulus element can be attributed to the sudden appearance (disappearance) of an occluder rather than to object motion (see also Shimojo & Nakayama, 1990; Ekroll & Borzikowsky, 2010). In a similar vein, Ramachandran et al. (1986) reported that entrained motion of a suddenly disappearing static target element can be perceived if an occluder behind which the target can move is available. It has also been proposed that the enigmatic phenomenon of pure “phi motion” (Wertheimer, 1912; Steinman et al., 2000; Petersik & McDill, 1981; Tyler, 1973) is related to temporal occlusion cues (Ekroll et al., 2008). Furthermore, Yantis (1995) found that occlusion cues can influence the tendency to perceive group motion in Ternus motion displays.

6. Conclusion

Our findings indicate that sampled motion stimuli are perceived as smoother if the spatial gaps between successive target positions that interrupt the motion path can be attributed to occlusion rather than to inexplicable characteristics of the moving target itself. This suggests that the intimate ecological link between motion and occlusion is utilized by the motion interpolation mechanisms of the visual system.

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