Long-lasting modulation of feature integration by transcranial magnetic stimulation

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The human brain analyzes a visual object first by basic feature detectors. On the objects way to a conscious percept, these features are integrated in subsequent stages of the visual hierarchy. The time course of this feature integration is largely unknown. To shed light on the temporal dynamics of feature integration, we applied transcranial magnetic stimulation (TMS) to a feature fusion paradigm. In feature fusion, two stimuli which differ in one feature are presented in rapid succession such that they are not perceived individually but as one single stimulus only. The fused percept is an integration of the features of both stimuli. Here, we show that TMS can modulate this integration for a surprisingly long period of time, even though the individual stimuli themselves are not consciously perceived. Hence, our results reveal a long-lasting integration process of unconscious feature traces.

Introduction

A visual object is analyzed in parallel by various feature detectors (Hubel & Wiesel, 1959, 1968). How the outputs of these feature detectors are integrated to form a global, meaningful percept is known as the binding problem. Research on the binding problem has focused on how two clearly distinguishable features such as color and shape are attributed to one object (Engel, Konig, Kreiter, Schillen, & Singer, 1992; Milner, 1974; Singer & Gray, 1995; Treisman & Gelade, 1980; von der Malsburg, 1981).

Here, we address a different type of feature integration in which features of two stimuli are collapsed over time into one percept, i.e. feature fusion. For example, when a red and a green disc are presented in rapid succession, the *two* discs fuse and are perceived as only *one* yellow disc (Efron, 1967, 1973; Yund, Morgan, & Efron, 1983). Likewise, if verniers with opposite offset directions are presented in rapid succession at the same retinotopic location, the *two*
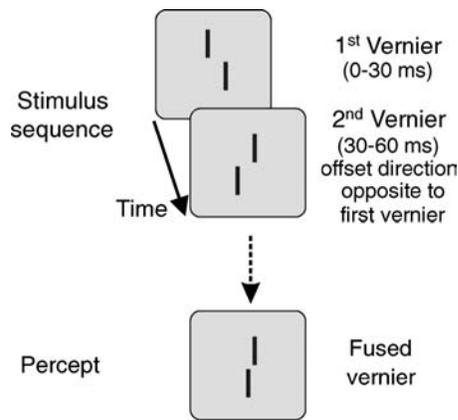
Figure 1. Feature fusion Paradigm. We presented a vernier, i.e. a pair of vertical bars that are spatially offset in the horizontal direction, followed by a second vernier with an offset of the opposite direction than the first vernier. On each trial, the first vernier was randomly offset either to the left or right, and the second vernier to the right or left, respectively (see Methods). Because of their short durations, the verniers are perceived as *one* fused vernier only. The fused vernier appears almost straight because the opposite vernier offsets are integrated and, thus, almost cancel each other out. Still, on each individual trial, a small offset of the fused vernier is perceived. *On average*, the second vernier dominates the fused percept (Kammer et al., 2003; Scharnowski et al., 2007), i.e. observers report more often the fused vernier to be offset in the direction of that of the second vernier.

verniers are not perceived individually but as *one* fused vernier which appears to be almost aligned (Figure 1). This fused vernier offset is a combination of that of both verniers. Given that the fused vernier is composed of offsets which are presented at different times, the interactions between them can be assessed, thus allowing to investigate the *dynamics* of the feature integration process.

Here, we show that even though the verniers are themselves not individually perceived (Experiment 2), their respective short-term memory traces can be manipulated by transcranial magnetic stimulation (TMS) for a substantial period of time (Experiment 1). Taken together, our results suggest a window of integration of several hundred milliseconds during which individual features can be manipulated.

Methods

Participants

Five observers (three females; aged 19–31 years) gave informed written consent for participation in the study, which was approved by the local ethics committee. Participants had normal or corrected-to-normal visual acuity as measured by the Freiburg visual acuity test (Bach, 1996). All but two observers were naïve to the purpose of the study. Naïve observers were paid 25 CHF/hour for their participation.

Visual stimulation

The stimuli of 80 cd/m^2 were presented on a Tektronix 608 X–Y display equipped with a P11 phosphor, controlled by a PC via a fast 16 bit DA converter, with a 1 MHz dot rate and a 200 Hz refresh rate. Viewing distance was 2 m. The room was dimly illuminated by a background light ($\sim$0.5 lx). A fixation point lasting for 1 s was presented 400 ms before the presentation of the stimuli. Verniers were composed of two vertical bars that were slightly displaced in the horizontal direction. The bars were 10′ (arcminutes) long each, 30″ (arcseconds) wide, and separated by a vertical gap of 1′.

In Experiment 1 (Modulation of feature fusion by TMS), a sequence of two verniers lasting 30 ms each with opposite offset directions was presented foveally in rapid succession. The offset direction of the first vernier (left or right) was chosen randomly for each trial. The second vernier had an offset direction opposite to that of the first vernier. Hence, if for example, the first vernier was offset to the left, the second vernier was offset to the right, and vice versa. Observers perceived only one fused vernier and were asked to report the offset of the lower bar with respect to that of the upper one by pressing one of two push buttons. Observers were instructed to respond as rapidly as possible consistent with accuracy. In this experiment, naïve observers did not know that a sequence of two verniers was presented.

For each observer, we computed the proportion of trials on which the response matched the offset direction of the first vernier. Thus, values above 50% indicate dominance of the first vernier; values below 50% indicate dominance of the second vernier. For each observer, offset sizes were adjusted such that performance without TMS was on average balanced at approximately 50% dominance, i.e. none of the verniers dominated. Across participants, offset sizes ranged from 45″ to 60″ for the first vernier and from 30″ to 50″ for the second vernier. Using such offset sizes, all participants saw only one fused vernier and none of the participants reported apparent motion percepts, which agrees with previous reports (Scharnowski, Hermens, Kammer, Oğmen, & Herzog, 2007). To make sure that performance without TMS remained at 50%, the no-TMS condition was repeatedly measured throughout the experiment. TMS onset asynchrony conditions were blocked within 60 trial runs and the order of conditions was randomized across participants. For each participant, conditions were repeated in reversed order to counteract practice and fatigue effects in the averaged data, resulting in a total of 120 trials for every condition. Within each block of 60 trials, a different pseudo-random sequence of left and right vernier offset directions was presented.

Experiment 2 (No conscious access to individual vernier offsets) is identical to the no-TMS condition of Experiment 1, except that we informed observers that a sequence of two verniers with opposite offset directions was presented. In this experiment, we asked observers to

report whether the first or the second vernier was offset to the right by pressing one of two push buttons. Observers were forced to make a choice even though they only perceived one fused vernier. For each observer, we computed the proportion of correct trials.

In Experiment 3 (No TMS effects on a single vernier), offset thresholds for a single vernier lasting 30 ms were determined by applying the adaptive PEST procedure (Taylor & Creelman, 1967). Participants had to indicate the offset direction of the vernier (left or right), which was chosen randomly for each trial. TMS onset asynchrony conditions were blocked within 60 trial runs and the order of conditions was randomized across participants. The threshold and slope of the psychometric function (cumulative Gaussian) were estimated by means of a maximum likelihood analysis (Wichmann & Hill, 2001a, 2001b). The guessing rate was set to 50% and the rate of motor errors was set to 3%.

Transcranial magnetic stimulation

Magnetic stimulation was applied to the occipital pole with a Medtronic MagPro X100 stimulator (Medtronic, Skovlunde, Denmark) in biphasic mode. A circular, passively cooled coil (13 cm diameter) was placed with its lower rim 1.5–2 cm above the inion. For each observer, stimulator output was set to maximize effects while preventing eye blinks and muscle contractions. Across participants, outputs ranged from 70%–90% of maximum stimulator output. Four of the five participants reported seeing phosphenes at the center of their visual field, where the stimuli were presented.

Statistical analysis of the modulating effects of TMS

To assess the reliability of the effects in Experiment 1, we performed a bootstrap analysis of the data (Efron & Tibshirani, 1993). For each participant, we drew 120 data points (1 experimental block) with replacement from the original data and computed the percentage of vernier decisions for each set of 120 re-sampled data points. We repeated this procedure 10,000 times to obtain an estimate of the distribution from which our experimental data was sampled. Based on this distribution, we could determine the outmost 2.5% means on both sides of the distribution, thereby providing an estimate of the 95% confidence interval. Note that the error bars derived from this analysis no longer need to be symmetric (the distribution can be skewed).

Results

Experiment 1: Modulation of feature fusion by TMS

We presented a sequence of two verniers with opposite offset directions and asked participants to indicate the perceived offset of the fused vernier as accurate and as fast as possible. To balance performance at approximately 50% we increased the offset of the first vernier, i.e. *on average* both verniers contributed equally to performance (Figure 2; 'no TMS'). Still, on each individual trial a small vernier offset was perceived. We then applied TMS over the occipital
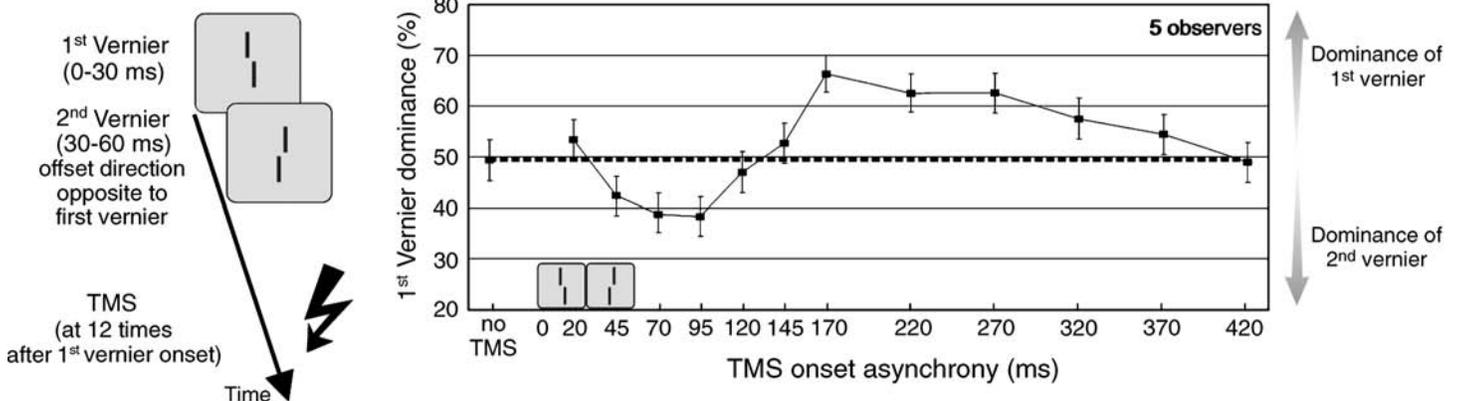

Figure 2. Effects of TMS on Feature Fusion. First, we adjusted the offset size of the first vernier such that performance was at 50%, i.e. *on average* both verniers contributed equally to performance ('no TMS'; indicated by the dashed line). Next, we applied TMS at different times after the onset of the first vernier (TMS onset asynchrony; see Methods). For onset asynchronies ranging from 45 to 95 ms, the second vernier dominated performance. For TMS onset asynchronies of more than 145 ms, the first vernier dominated. The surprising result is that TMS has differential effects for up to 370 ms after the onset of the first vernier, even though only one fused vernier is consciously perceived. Similar results were obtained with a more focal figure-of-8 coil instead of the circular coil used here (Figure A2). Error bars indicate 95% confidence interval based on a bootstrap analysis (see Methods); vernier presentations are indicated by the small depictions in the graph; performance was quantified as the percentage of responses in which the perceived offset direction of the fused vernier corresponded to that of the first vernier.
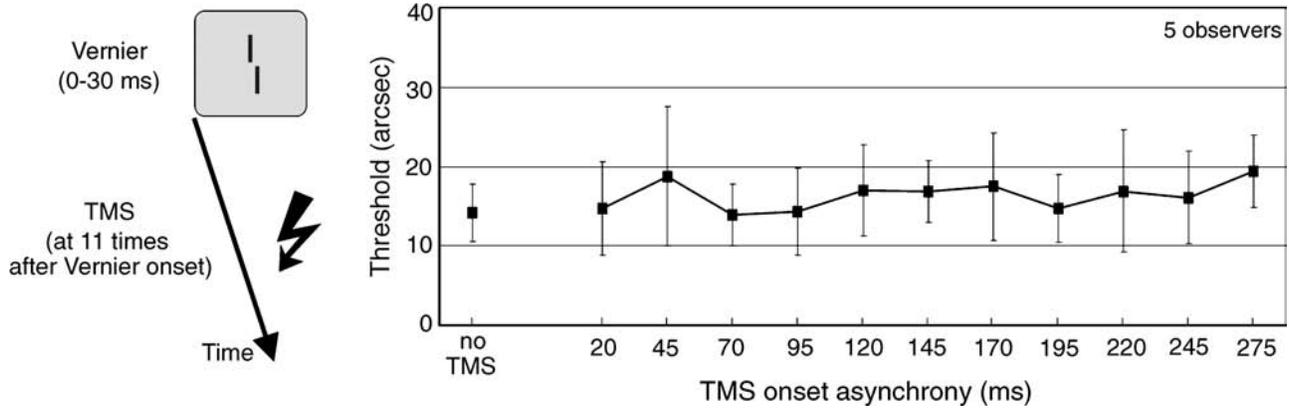
Figure 3. Effects of TMS on a Single Vernier. Vernier offset discrimination thresholds for a 30 ms vernier (same duration as the 1st as well as the 2nd vernier of Experiment 1) were determined as a function of TMS onset asynchrony (see Methods). A one-way repeated measures ANOVA in which we tested whether the mean thresholds for each of the 12 measurements differed revealed no significant difference. Error bars indicate *SEM*.

cortex at different times after the onset of the first vernier in order to interfere with visual processing (Amassian et al., 1989; Corthout, Uttl, Walsh, Hallett, & Cowey, 1999; Kosslyn et al., 1999; Walsh & Cowey, 1998). When TMS was applied from 45 ms to 95 ms after the onset of the first vernier, the second vernier dominated. For later onset asynchronies of up to 370 ms, the first vernier dominated (Figure 2).

Hence, TMS can have a marked effect on the perceived offset of the fused vernier even when applied more than 300 ms after the disappearance of the second vernier, i.e. the two verniers are presented until 60 ms, then there is a blank screen for more then 300 ms, and after that the TMS pulse still influences performance. This effect is specific to stimulation of the occipital cortex, i.e. TMS over the frontal lobe does not modulate feature fusion (Figure A1).

Experiment 2: No conscious access to individual vernier offsets

To show that observers indeed cannot access the individual verniers consciously, we asked the observers to perform an additional task after completion of the TMS experiments. We informed participants that in our paradigm two verniers with opposite offsets were actually presented, and asked them to indicate whether the first or the second vernier was offset to the right. Performance on this task was at chance levels (51%, *SEM*: 2.67; $d' = 0.024$), showing that the verniers cannot be individually resolved.

Experiment 3: No TMS effects on a single vernier

Whereas TMS modulates the relative contribution of the first and the second vernier to the fused vernier depending on the onset asynchrony, we now show that TMS does not interfere with an individual vernier in isolation. For this, we presented only the first vernier alone, which is equivalent to

presenting the second vernier alone, and applied TMS at various onset asynchronies. To avoid ceiling effects, we determined offset discrimination thresholds rather than vernier dominance. Offset discrimination of the single vernier was not obviously affected by TMS at any onset asynchrony (Figure 3). Moreover, thresholds were considerably lower ($<20''$) than the offsets used in Experiment 1 ($30''–60''$). Hence, TMS does not interfere with an individual vernier in isolation.

Discussion

Visual objects such as vernier stimuli are analyzed in parallel by various feature detectors whose outputs are integrated in subsequent stages of the visual hierarchy (Hubel & Wiesel, 1959, 1968). Often, such integration is assumed to be accomplished by pooling the outputs of the feature detectors (e.g. Baldassi & Burr, 2000; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Riesenhuber & Poggio, 1999). However, these models are often not specific with respect to the time course and assume that basic features are inaccessible after their integration, just as coffee and milk inseparably mix in a cappuccino. The feature fusion paradigm allows one to study the dynamics of such integration processes because the two vernier offsets, which are presented at different times, are perceptually fully integrated.

In feature fusion, only one vernier is perceived (Figure 1). Hence, the neural representations of the two vernier offsets must be *unconsciously* integrated into the one perceived offset.

This feature integration is not completed before 370 ms in the sense that the vernier offsets are not completely collapsed into one and thereby irretrievably lost. Had the vernier offsets been fully integrated beforehand and the individual offsets lost, TMS could not render one or the other vernier

dominant anymore (Experiment 1). Due to the experimental design, performance would then have been at the baseline level of 50%, which is also chance level performance. In short, as long as TMS can modify performance to be above or below 50%, feature integration cannot be completed.

What are the mechanisms underlying this unconscious feature integration? Our results show that there must be persisting neural activity related to at least one vernier offset (otherwise TMS could not interfere selectively with the vernier offsets). This is in accordance with physiological findings showing that neural activity can outlast the presentation of a stimulus by several hundred milliseconds (e.g. Macknik & Martinez-Conde, 2004). It is important to note that such a persisting neural activity is a necessary but not sufficient condition for feature integration. Neural persistence neither explains why feature integration lasts that long nor how the integration itself is accomplished.

Completely independent vernier representations

There are several possible scenarios how the integration might take place. It might be that both verniers are *completely independently* stored for longer periods of time and that their integration into one offset occurs only just before awareness is reached (Figure 4A). Different dominance values might be reached because TMS selectively affects the first or the second vernier representation differently depending on the TMS onset asynchrony, thereby biasing perception towards the other, less-affected vernier. In this case, processing of the first vernier would be impaired with earlier TMS and processing of the second vernier would be impaired with later TMS, which would bias vernier offset perception towards the second or first vernier, respectively. However, such a scenario is unlikely because if we assume that the modulating effects of TMS are due to interference with completely independently stored verniers, we would expect that TMS also interferes with a single presented vernier, which is equivalent to a completely independently stored vernier. In Experiment 3, we show that this is not the case even though the verniers were of considerably smaller offset sizes which are more prone to TMS interference (Figure 3). The fact that TMS does not have an effect on an individual vernier is not surprising because the vernier was of high luminance (Weber contrast ~1) and therefore too strong for TMS to interfere. Other studies that have found TMS masking effects have typically used much weaker stimuli (Amassian et al., 1989; Corthout et al., 1999; Jolij & Lamme, 2005; Kammer, Scharnowski, & Herzog, 2003; Kastner, Demmer, & Ziemann, 1998; Ro, Breitmeyer, Burton, Singhal, & Lane, 2003). The representation of the single vernier in Experiment 3 is of course not directly comparable to the representations of the vernier stimuli in Experiment 1 because in the latter case the two vernier representations interact. However, when assuming completely independent vernier representations in Experiment 1, they are comparable to the individual verniers of Experiment 3. Hence, Experiments 1 and 3 show that TMS can interfere with the vernier representations only when they are interacting with each other (Figure 4B).

Interacting vernier representations

We can only speculate about the exact nature of the neural interaction between the two vernier representations in Experiment 1, which eventually leads to an integrated conscious percept. One possibility is that the interaction weakens the representations of each single vernier, e.g. by lateral inhibition, thus making each vernier more susceptible to TMS interference. Depending on the TMS onset asynchrony, TMS is then more strongly interfering with one or the other vernier representation, thereby indirectly affecting the outcomes of the feature fusion. An analogy would be to compare the vernier representations with two kids on a teeter-totter. When there is only one kid on one side of the teeter-totter, TMS cannot tip it over (Experiment 3). Only when the kids on both sides are balanced can TMS
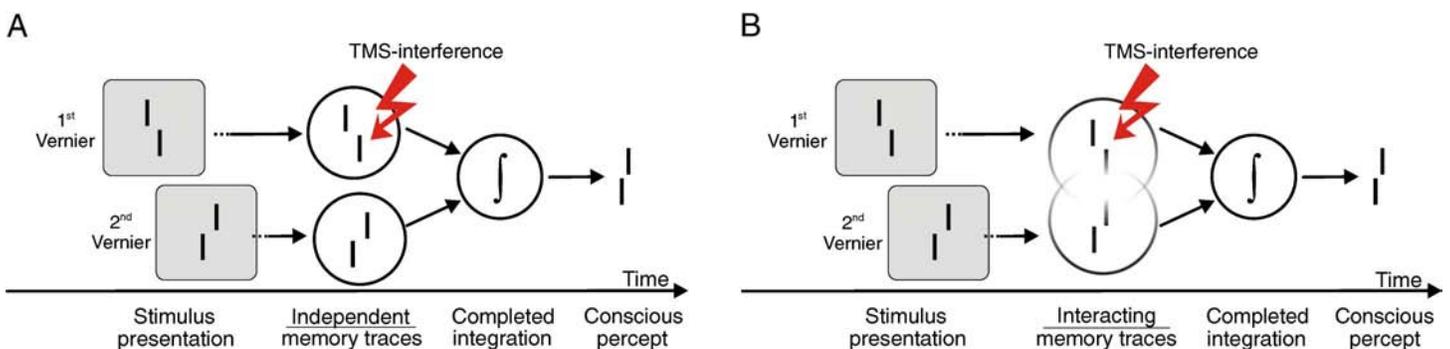

Figure 4. Possible Stages of TMS Interference. (A) The consecutively presented verniers are completely independently stored before they are integrated to a conscious percept. TMS interferes with the processing of the completely independent vernier memory traces. (B) The vernier offset representations interact before feature integration is completed and a conscious percept is elicited. Given that TMS does not interfere with single verniers, we suggest that TMS exerts its effects during this interaction stage.

affect one side depending on the timing, thereby causing the other one to dominate (Experiment 1).

Window of integration

It might be that the competition between the vernier representations actually is part of their integration process. In this regard, it is important to note that the interaction between the vernier representations does not render one or the other vernier and its offset invisible like in classical forward or backward masking. Instead, the verniers and their offsets are integrated into one aligned vernier just as the red and green discs are integrated and perceived as a yellow disc. TMS might bias this integration process towards one or the other vernier depending on the TMS timing. In feature fusion, the sequentially presented verniers do not mask each other unspecifically but rather their offsets are integrated. We speculate that similar integration processes may occur as well in typical pattern masking paradigms (among other deteriorating processes). In this sense, our results show that masking, which is related to feature fusion, is a rather long lasting process.

A window of integration of more than 300 ms appears surprisingly long. Other studies have found that object detection can be accomplished much faster, apparently without any temporal buffering (Thorpe, Fize, & Marlot, 1996; van Rullen, Guyonneau, & Thorpe, 2005). On the other hand, such a broad time window of integration might be necessary to accomplish other tasks such as, for example, to track moving objects, to accumulate information in low contrast scenes, or to compute figure-ground segregation (Heinen, Jolij, & Lamme, 2005). These and many other tasks require the integration of visual information over long periods, which can only be accomplished by a visual short-term memory (Pasternak & Greenlee, 2005). Whereas other investigations focused mainly on the capacity and spatial organization of a visual short-term memory (Coltheart, 1980; Haber, 1983; Neisser, 1967; Sperling, 1960), our results shed light on the dynamics of the *integration* processes ongoing in this short-term memory (for other investigations of the dynamics of visual short-term memory see also DiLollo, 1977, 1980; Eriksen & Collins, 1967).

A conscious decision is reached only after integration is completed. Other experimental and theoretical findings also support the existence of a window of integration before awareness (Allport, 1968; Dennett, 1991; Eagleman & Sejnowski, 2000; Haber & Hershenson, 1973; Haggard & Eimer, 1999; James, 1890; Libet, 1985; Libet, Gleason, Wright, & Pearl, 1983; Pascual-Leone & Walsh, 2001; Stroud, 1956; Tononi & Edelman, 1998; van de Grind, 2002).

Preservation of temporal order

Interestingly, the differential effects of TMS not only imply that individual feature information is accessible for a long time, but also that the temporal order of the vernier memory traces is preserved. Despite the short onset asynchrony of only 30 ms between the presented verniers, the first vernier is rendered less dominant by early TMS, and the second by late TMS. Hence, the visual short-term memory retains the temporal order of the sequential visual stimulation, even though the percept is of a unique event rather than a sequence. This is a direct consequence of persisting neural activation and might be explained by sequential sampling models (Smith & Ratcliff, 2004; Townsend & Ashby, 1983) or by the buffering of feature information in a stack-like (Bauer & Samelson, 1957) object file (Kahneman, Treisman, & Gibbs, 1992; Wolfe & Bennett, 1997). Computationally, a stack arranges information in a pile one after the other, i.e. starting with the first presented vernier followed by the second one. The second vernier might be affected by TMS for a considerably longer time than the earlier presented verniers because it is without any subsequent entry.

On a physiological level, this could be due to the second vernier benefiting from prolonged persisting neuronal activity because there is no subsequent stimulus as there is for the first vernier. Therefore, TMS can affect the second vernier for longer.

Cortical substrate

We can only speculate what would be the area of the cortex where such long-lasting integration processes take place. The fact that frontal TMS did not affect feature fusion (Figure A1) suggests that the modulating effects of TMS are specific to TMS interference with processing in the occipital cortex. With the more focal figure-of-8 coil we found very similar effects as with the large circular coil (Figure A2). It has been proposed that the target sites of TMS are parts of V1 as well as V2 and V3, including optic radiation and back-projecting fibers (Cowey & Walsh, 2000; Kammer, Puls, Strasburger, Hill, & Wichmann, 2005; Kastner et al., 1998). Nevertheless, any focal stimulation is not restricted to the region directly underneath the coil, but spreads along a network of functionally connected areas (Bestmann, Baudewig, Siebner, Rothwell, & Frahm, 2004; Paus et al., 1997; Ruff et al., 2006).

Appendix A

Experiment A1: TMS over the frontal lobe

To control that the effects are specific to interference of TMS with processing in early visual areas, we repeated Experiment 1 with 4 new naïve observers (three males; aged 20–27 years) while stimulating frontal instead of occipital areas. For this, the circular coil was placed
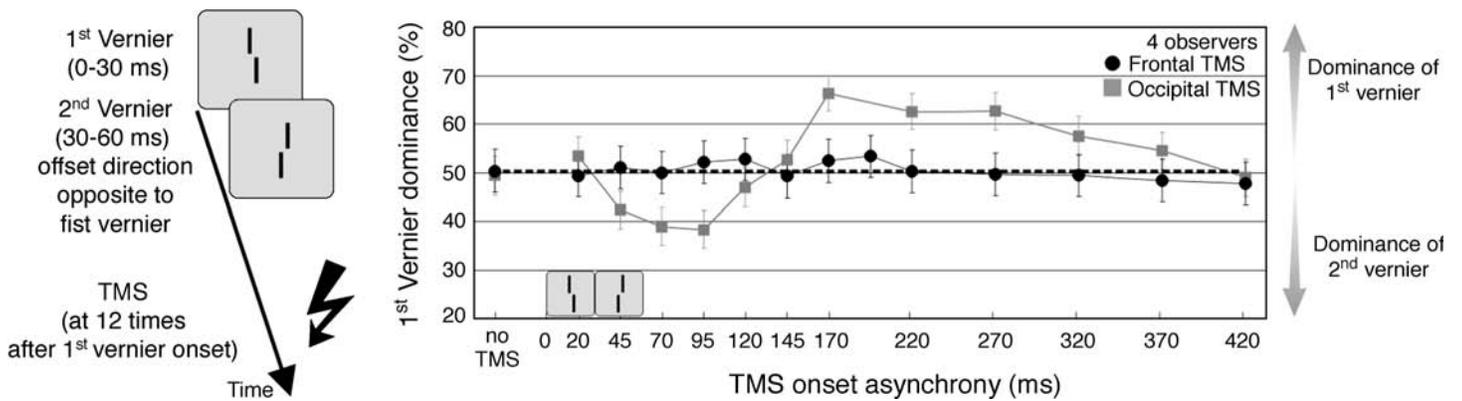
Figure A1. Effects of Frontal TMS on Feature Fusion. Whereas TMS over the occipital lobe modulates feature fusion (the data from Experiment 1 is shown in gray), there is no effect of TMS on feature fusion when applied over the frontal lobe. Error bars indicate 95% confidence interval, based on the bootstrap analysis; the presentation of the two verniers is indicated by the small depictions in the graph.

tangentially to the head along the midline with its lower rim ~9.75 cm above the nasion. The effects of frontal TMS on feature fusion are shown in Figure A1. In contrast to occipital TMS, TMS over the frontal lobe did not modulate feature fusion.

Experiment A2: TMS with a focal figure-of-8 coil

TMS with a focal figure-of-8 coil also modulates feature fusion. The experimental design was essentially the same as in Experiment 1 with the circular coil except that:

1. Five observers were tested (two females; aged 23–40 years). They were instructed to keep fixation on a dot presented at the center of the screen for the duration of the trial.
2. Observers were not required to respond fast.

3. Conditions were not repeated, resulting in a total of 60 trials for every condition.
4. The first vernier was presented for 40 ms, the second vernier for 30 ms. Adjusted offset sizes ranged from 50″ to 80″. Verniers were presented in the periphery, i.e. 900″ below and to the right of the fixation dot, to ensure unilateral cortical activity that can be influenced by a focal figure-of-8 coil.
5. Magnetic stimulation was applied at 9 onset asynchronies to the left occipital pole using a figure-of-8 coil (MC-B70).

Because a figure-of-8 coil stimulates a much more circumscribed region than a circular coil, it is important to target the cortical area which covers the part of the visual field in which the stimuli are presented. We accomplished this by selecting the position of the coil so that evoked phosphenes overlap spatially with the presented stimuli (Kammer et al., 2005). The optimal position of the coil in relation to the head was monitored
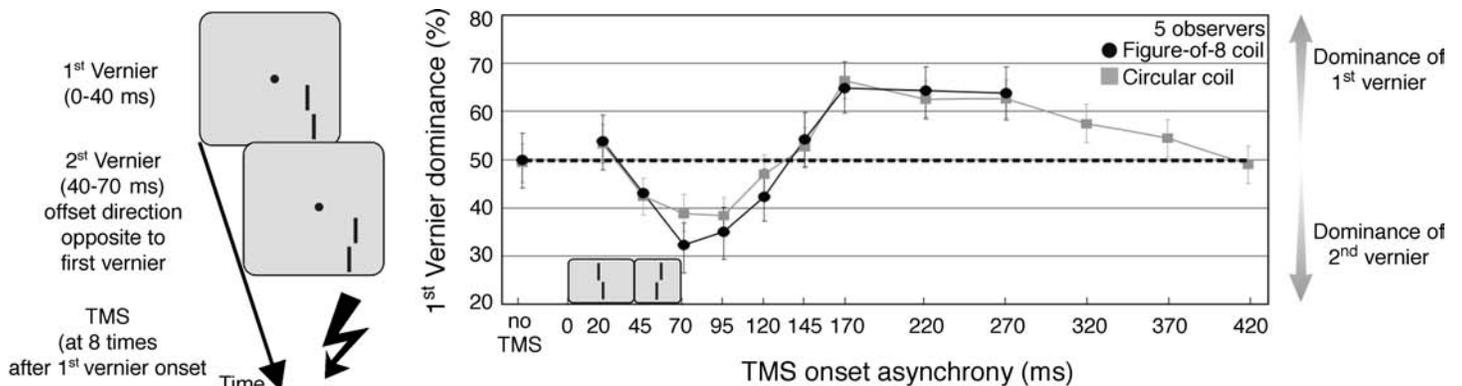

Figure A2. Effects of Focal TMS on Feature Fusion. To allow effective stimulation with the focal figure-of-8 coil, the verniers were presented extrafoveally. For the onset asynchronies measured, the same modulating effects were found as for the circular coil (the data from Experiment 1 is shown in gray). Error bars indicate 95% confidence interval, based on the bootstrap analysis; the presentation of the two verniers is indicated by the small depictions in the graph.

continuously with a custom-made positioning system (Kammer, Beck, Thielscher, Laubis-Herrmann, & Topka, 2001). The results are shown in Figure A2.

The striking similarity of the effects demonstrates that coil geometry is not a critical parameter for feature modulation. It suggests that the same cortical or subcortical structures are depolarized with the coils placed over the occipital cortex.

Also the instruction to focus only on accuracy without the need to respond fast did not affect performance except for a change in reaction times: when observers were asked to respond fast (Experiment 1) mean reaction times were ∼1000 ms; when they were not asked to respond fast (Figure A1) mean reaction times were ∼1200 ms.

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