

A TMS study of the ventral projections from V1 with implications for the finding of neural correlates of consciousness

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Abstract

The study of subliminal perception in normal and brain lesioned subjects has long been of interest to scholars studying the neural mechanisms behind conscious vision. Using brief durations and a developed methodology of introspective reporting, we present an experiment with visual stimuli that gives rise to little or no subliminal perception under normal viewing conditions. Coupled with transcranial magnetic stimulation, however, we find a dissociation between correctness and conscious awareness. Furthermore, we find support for the hypothesis that the ventral projection streams from V1 are necessary for visual consciousness.

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1. Introduction

How to search for the neural correlates of visual consciousness has been a long-standing controversy in cognitive neuroscience. Although the most recent publications on the subject (e.g., Crick & Koch, 2003; Lamme, 2000) are far from agreement on this matter, there has been a general tendency since the works of Ungeleider and Mishkin (1982) and Milner and Goodale (1995; Milner, 1995) to associate visual consciousness with ventral stream (mid-temporal) processing. According to Milner and Goodale, the ventral and dorsal projection streams from primary visual cortex represent a functional segregation of visuomotor skills on the one hand and object naming and recognition on the other. This bifurcation theory has been used to explain a number of phenomena, such as blindsight. Blindsight patients, suffering from a lesion of V1 (primary visual cortex), report not to perceive anything in a portion of their visual field, yet they are significantly better than chance level when guessing about several attributes of stimuli presented in the blind field (Weiskrantz, 1986). The preserved functions could be explained within the

framework offered by Milner and Goodale: after a V1 lesion, the cells along the ventral stream seem not to be activated by visual stimuli, whereas the dorsal stream is still activated by routes going around V1.

There are, however, also arguments against such an explanation. For instance, it has been discovered that the two projection streams are far from completely functionally segregated. On the contrary, the two projection streams are interconnected by a number of pathways (see Nealy & Maunsell, 1994 or Pisella & Rossetti, 2000) as later also recognised by Milner and Goodale (1998). This is an argument against the explanation originally proposed by Milner and Goodale in that the ventral stream must be activated by dorsal stream processing, also in blindsight patients. Furthermore, blindsighters are not only good at making guesses about what is thought to be processed in the dorsal stream, but also about colours that usually are attributed to ventral stream processing (Serenio & Maunsell, 1998).

2. Methodological considerations

Lesion studies, as in the case of blindsight patients, have certain methodological limitations. The damages often cover large areas, and it is difficult to find a

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sufficient amount of patients with identical damages, specific enough to give conclusive evidence about the neural substrate of consciousness. Furthermore, due to much recent research, it seems unlikely that the neural correlate of consciousness should be one specific region in the brain (Dennett & Kinsbourne, 1992). For instance, it seems reasonable to hypothesise that a neural correlate of consciousness is a specific set of neurons firing in a specific way (e.g., at a certain amplitude level (Libet, 1993), or synchronized in a special way (Crick & Koch, 1998)). Lesion studies have little to say about how a given brain area is activated at any specific time, since it is a permanent condition. That is, since a lesion is permanent, it cannot be used to gain knowledge about how the damaged area contributes to consciousness at a given point in time during a processing of information.

We decided to employ the technique of transcranial magnetic stimulation (TMS)—a method with which it is possible to interfere in the neural activation in the brain at a given location for milliseconds by a magnetic stimulation of neurons. The discharging of a bank of capacitors through a copper-stimulating coil creates a brief but intensive magnetic field and induces a time-varying, high-current electrical pulse. Tissues, skull, and scalp represent no impedance to a magnetic field of rapidly changing intensity, which induce a current in the nervous system. Primarily, TMS has been used for motor cortex stimulation during which low intensity stimuli preferentially activate the pyramidal cells indirectly (transsynaptically) through excitatory interneurons and evoked potentials. TMS has previously also been used to study different psychological phenomena. In visual perception, it has for instance been shown that TMS can “take out” a part of the experienced visual field. If, say, all of V1 is stimulated, there will be no experience of vision at all. If only parts of the visual areas are stimulated, parts of the experienced visual field will fall out (Kamitani & Shimojo, 1999). It has also been possible to show delays of reaction times, when TMS is applied over the motor cortex for the target muscle (Day et al., 1989), and delays in judging own reaction time (Haggard & Magno, 1999). Such effects have common features with a “backwards masking” technique, widely used in the psychology of perception, where one stimulus is presented, immediately followed by a second one, blocking the further perception of the first.

Using TMS, one can present visual images to a subject just long enough for him or her to be conscious of them, and at the same time deliver TMS-pulses at areas in visual cortex. With this method, it will be possible to find how long, exactly, the latency period must be from the presentation of the stimulus to the TMS-pulse for it to block the experience. This will then reveal when that particular brain area is contributing to consciousness. In other words, this information in itself could add a

temporal dimension to theories of neural correlates of consciousness that primarily look at the relevant brain areas as were they non-dynamic structures. However, in theory at least, it could be used in even more interesting ways to gain knowledge of the neural substrates of consciousness. When one knows exactly when consciousness is affected when stimulating over a specific brain area, one can study the brain activity here at that point in time with time-sensitive methods, e.g., EEG or MEG, to see if there are any neural changes that co-vary with the phenomenal difference (that is, the subject’s reporting hereof). Hereafter, the experiment could be done with a different modality than vision, in order to see if there are any EEG-/MEG-measurable “kind of activity” that occurs whenever a transition from unconsciousness to consciousness occurs (Overgaard, 2001). In this way, a successful attempt to affect visual consciousness with TMS could be seen as a promising indication that one could use a similar set-up to study other modalities as well.

3. Experiment 1

We carried out a calibration study to find out how long the stimulus should be presented for the subjects to report having a clear experience of that stimulus. Furthermore, we decided to train the subjects in a relatively sophisticated reporting of their experiences: evidence from blindsight and unconscious perception have indicated that we should not expect a common neural correlate to the ability to guess correctly about a stimulus and to be conscious of it. Accordingly, there is no reason to assume that one can deduce anything about a subject’s experience from measures of correctness (as the so-called objective approach to the study of consciousness does).

3.1. Methods

3.1.1. Subjects

Subjects were five healthy volunteers (age range 22–32, 3 males and 2 females) with normal or corrected to normal vision. Two extra subjects were studied, but were excluded from further analysis because they, according to their own reports in an interview carried out after the experiment, did not succeed in using their response categories consistently throughout the experiment. All subjects gave their informed consent to the experimental procedure.

3.2. Stimulus presentation

Subjects were to focus on a fixation point (a white cross on black background) that was presented for a randomly selected duration, after which a stimulus was

presented for a duration span ranging from 16 to 192 ms, with duration intervals about 16 ms (according to the monitor refresh rate). The duration of each stimulus was randomised within this interval. The stimuli were brief presentations of simple figures; triangles, circles, and squares, with one of three colours; red, blue, and green. There were three possible locations where the presentation could appear: 1 cm above the fixation cross, 1 cm to the left or 1 cm to the right. The stimuli were presented on a black background, on a 15-inch SVGA colour computer screen (cathode ray tube; resolution 800 × 600) with a 16 ms. refresh rate, controlled by a 466 MHz CPU. The programme was made on Presentation version 0.40 in Windows 98. The viewing distance was fixed to 60 cm. The programme checked for uncertainties in timing, and the data was analysed accordingly. The sequence of stimuli presentations was randomised, and no combination of shape, colour, position, and duration was delivered more than once. In all, each subject underwent 366 trials. A mask consisting of all stimulus features merged together followed the presentation of a stimulus at all three possible locations, so that no single stimulus could be recognised (in free-view conditions) even when the stimulus and mask overlapped on the screen.

First, the subjects were told to report what they thought was presented, even if they had no experience of the stimulus. All stimulus features were to be reported (shape, colour, and position). Second, for each property of the stimulus, they were asked to report the degree of clearness of experience. Here, we suggested that they could use a scaling going from “no experience at all” to “an absolutely clear image.” The subjects were told that they should create their own categories. All subjects ended up using a four-point scale (which, thus, was not suggested to them in advance) with the elements: “no experience,” “brief glimpse,” “almost clear image,” and “absolutely clear image.” Of course, the subjects differed in their labelling of the categories, but they agreed in their definitions of the categories (see Fig. 3). Two subjects started out using more than four categories, but in both cases, the extra categories were defined as being between two other categories (with no real definition on their own). In both cases the categories were named “between weak glimpse and an almost clear experience” and “between an almost clear and a clear experience.” Furthermore, the subjects made almost no use of those extra categories. Four of the subjects made use of the

terms in Table 1. One subject reported the two middle categories as “50% clear” and “90% clear.” In the interview after the experiment, he described these two categories as did the other subjects.

Typically, a subject would report “red square up there (points); the position was clear, the colour was a glimpse, I had no experience of the shape.” Reports of the different stimulus features were scored for “clearness” (an ascending scale from 1 to 4, where 1 = “No experience,” 2 = “Brief glimpse,” 3 = “Almost clear image/experience,” and 4 = “Clear image/experience”). After the trial, each response was scored (by the examiner) for correctness (correct–incorrect).

3.3. Results

The subjects all agreed that the categories they developed to describe their experiences were rather straightforward and intuitive. Table 1 is a generalisation of all subjects’ description of each experiential category.

By assessing the percentage of correct answers for each degree of clearness, we found that, in the cases where our subjects reported “no experience” for colour or shape, they showed no or very little subliminal perception (defined as being significantly above the mean correctness of 0.33) at guessing what was presented. The subjects were at the P -values of 0.188 for experience of shape and 0.1 for colour (χ^2). This is in accordance with Kolb and Braun (1995) who showed that subjects show no dissociation between correctness and conscious awareness when using simple visual displays and when subjects are not forced into dichotomous reports. For cases where subjects reported “brief glimpse” experiences, though, the level of correct guesses rose to a statistically significant level in most subjects ($P < 0.001$ for both shape and colour). Responses for position were different from responses for colour and shape: subjects are generally more correct about position, and are seemingly never at chance level. Furthermore, subjects can be correct about position without being correct about other aspects of the stimulus, but, seemingly, not the other way around. The proportion of correct guesses grew as a function of the degree of clearness as illustrated in Figs. 1–3.

It shows that in several cases, the subjects are more correct when reporting different categories of clarity. This is, so to say, an objective argument that the conscious–unconscious dichotomy is a gross simplification,

Table 1
The subjects’ definitions of the categories they developed during experiment 1

No experience	No impression of the stimulus. All answers are experienced as mere guessing
Short glimpse	A feeling that something has been shown. Not characterised by any content, and cannot be specified any further
Almost clear	Feeling of almost being certain about one’s answer. Some aspects are experienced more vividly than others
Clear experience	Non-ambiguous experience of what has been shown. No doubt in one’s answer

Only definitions and terms generally used by the subjects are included.

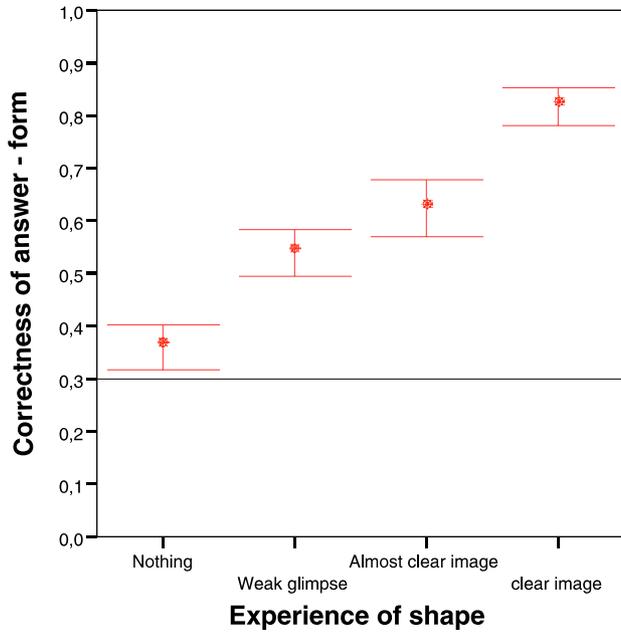


Fig. 1. The relation between subjects' correctness and categorising of their experiences. Error bars show the confidence intervals from the mean.

if the subjective argument that the different experiences relate to the categories is not already sufficient.

Since the duration of each stimulus was randomised, the subjects were not exposed to each duration the same number of times (yet always between 25 and 35 stimuli per duration). The subjects did not achieve a

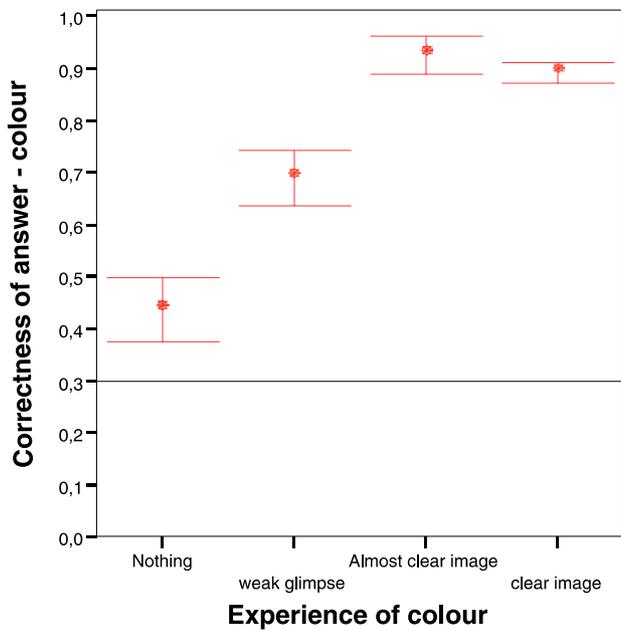


Fig. 2. The relation between subjects' correctness and categorising of their experiences. Error bars show the confidence intervals from the mean.

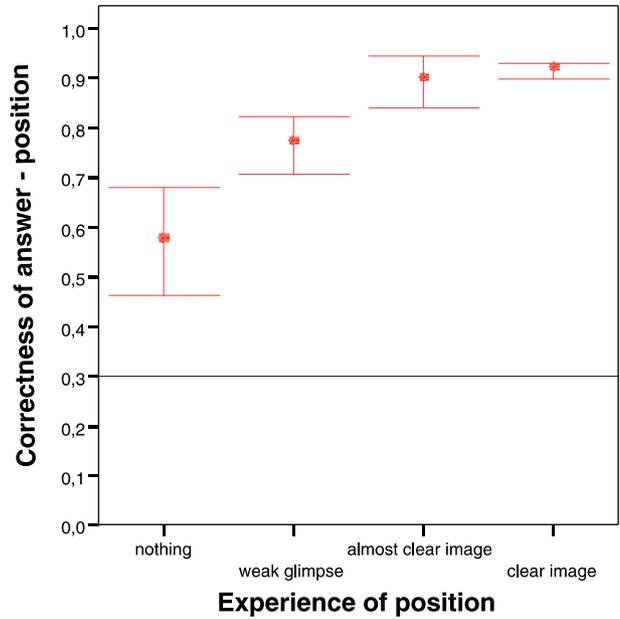


Fig. 3. The relation between subjects' correctness and categorising of their experiences. Error bars show the confidence intervals from the mean.

ceiling in their reports of clarity during the experiment (Fig. 4). Therefore, 192 ms. was chosen as duration time in experiment 2. Furthermore, for practical reasons, it was impossible to write down verbal reports given by the subjects in experiment 2. Therefore, the 4-point scale developed in experiment 1 became of great importance for experiment 2, where the subjects had to give their introspective reports by pushing buttons, each button representing one category in the scale. One could argue that the imposing of the categories developed by the subjects in experiment 1 on the subjects in experiments 2 is not ideal. On the other hand, given that some kinds of categories had to be imposed on the subjects, it seemed better to impose categories developed by comparable subjects in a comparable experimental situation than to impose categories that were invented by the researchers.

4. Experiment 2

The experiments based on which the ongoing debate about visual awareness is led, as described above, investigate the relation between the primal visual cortex and higher areas. A number of papers have been published using transcranial magnetic stimulation in the investigation of conscious experience. However, no experiment using TMS has targeted the ventral projection streams directly and, at the same time, collected reports explicitly about conscious experiences, even though those areas are presumed as a possible location for a

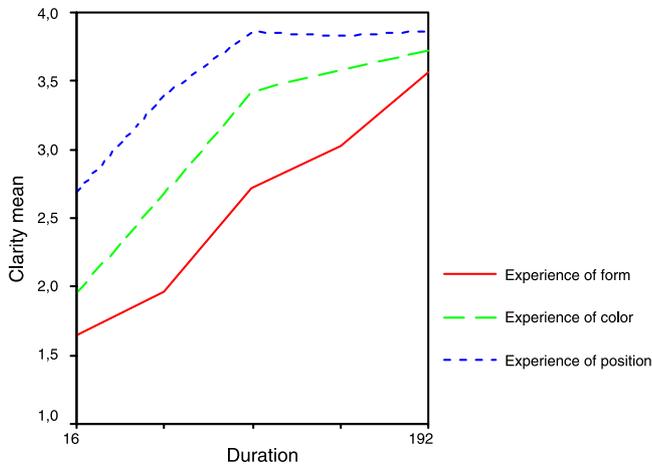


Fig. 4. The subjective evaluation of experience clarity compared to the duration of stimulus. Confidence intervals were between 1.55–3.44 (shape), 1.84–3.5 (colour), and 2.58–3.81 (position). Standard errors of mean were between 0.05–0.07 (shape), 0.04–0.06 (colour), and 0.02–0.05 (position).

neural correlate of visual consciousness (Anand & Hotson, 2002).

4.1. Methods

4.1.1. Subjects

Subjects were 10 healthy volunteers (age range 21–49 years, 7 female and 3 male). All subjects had normal or corrected-to-normal vision when tested. All subjects gave their informed consent to the experimental proce-

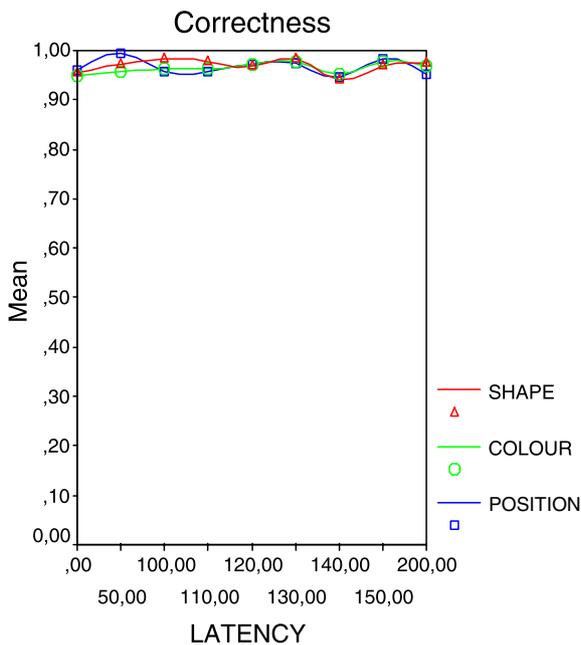


Fig. 5. Results showing the effect of TMS on subjects' correctness in the guessing task. "0" marks the sham condition. The lines were created using spline interpolation. The confidence intervals were between 0.9 and 1 for all variables. The standard errors of mean were between 0.009–0.02 (shape), 0.01–0.02 (colour), and 0.005–0.02 (position).

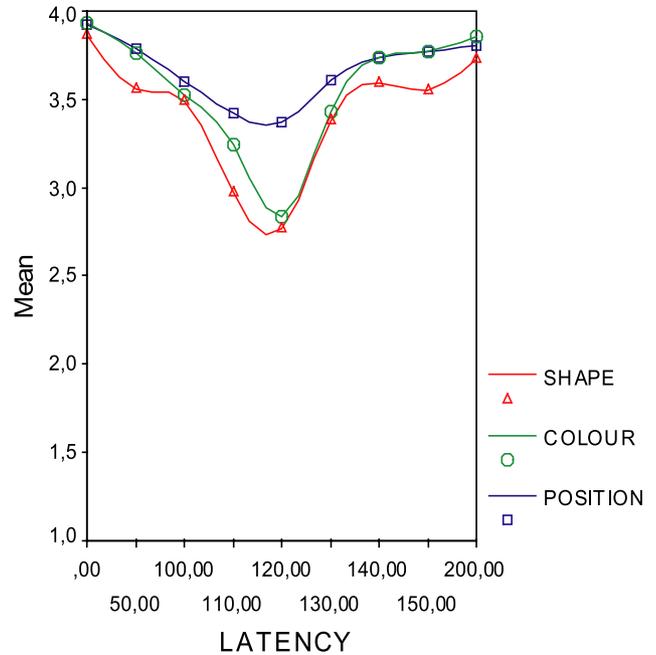


Fig. 6. Results showing the effect of TMS on subjects' rating of the clarity of their experiences. "0" marks the sham condition. The lines were created using spline interpolation. The confidence intervals were between 2.6–3.8 (shape), 2.7–3.9 (colour), and 3.2–3.7 (position). The standard errors of mean were between 0.03–0.08 (shape), 0.03–0.09 (colour), and 0.02–0.06 (position).

cedure that was approved by the local ethical committee. The subjects were seated on a chair and rested the back of their head against a supporter to keep their head still. The coil was fixed in a holder so the researcher could stand behind the subject, holding the coils steady at the right locations.

4.2. Stimulus presentation

The visual stimuli were identical to the ones used in experiment 1, yet they all had a duration time of 192 ms. After each figure, the subject was to report what was seen and how clearly it was seen. For this purpose, a screen picture appeared with the three possible shapes and the 4-point scaling to choose from. After having reported about the shape of the figure, a similar screen picture appeared where the subject was to report about its colour (and the clearness hereof), and, finally, about its position on the screen. The visual stimuli were presented on a 20-inch Philips Autoscans Professional colour computer screen (cathode ray tube; resolution 800 × 600) controlled by a 1.1 GHz CPU. The programme was made on Presentation version 0.50 in Windows XP. The programme checked for uncertainties in timing, and the data was analysed accordingly. The viewing distance was fixed to 60 cm. The sequence of stimuli presentations was randomised, and no combination of form, colour, position and duration was delivered more than once.

4.3. TMS protocol

TMS was carried out with two Magstim-200 magnetic stimulators (Magstim, Spring Gardens, Wales, UK). TMS was delivered simultaneously over the two hemispheres through two identical circular coils (9-cm external diameter) oriented so that the induced electric current flowed in clockwise/anti-clockwise direction. In order to standardise the stimulation intensity, cortical motor threshold was defined by moving the coil around on the fronto-parietal region (motor cortex) of the dominant hemisphere looking at visible contractions of the contralateral relaxed hand muscles. The coil was moved around until the “hot spot” was reached at which point muscle contractions were evoked by lowest stimulation intensity. Stimulation intensity usually started at an output of 30% of maximal stimulator output and increased in steps of 5%. The mid temporal regions (T3 and T4) were defined according to the 10–20 International System used in electro encephalography (EEG). The edges of the two coils were centred bilaterally at the mid temporal regions. Transcranial magnetic stimulation is a non-focal type of stimulation, and it is not possible to know exactly which area we stimulated. Transcranial electrical stimulation would have been more focal but is seldom used because it is painful. However, by placing the edge of the coil at T3/T4 we know from the EEG literature (e.g., Rugg & Coles, 1995) that we are stimulating the temporal region. Besides, there were no clinical indications that we stimulated other parts of the brain. At this location of the coil, we saw no muscle contraction (frontal cortical areas), no sensations were reported (parietal cortical areas), nor any visual sensations (occipital cortical areas).

Stimulation intensity was 150% of motor threshold intensity. This stimulation intensity was chosen in order to standardise the stimulation intensity between the subjects and for future replications. One might expect inter-individual variability in thickness of the skull, which would have an impact on the actual stimulation intensity of the neural tissue. Furthermore, a relatively high intensity makes it easier to reproduce the set-up with other magnetic stimulators because each magnetic stimulator has its own stimulation pulse characteristics. From studies of motor cortex we know a single stimulus of low intensity results in a descending volley recordable from the pyramidal tract, so-called I-waves or indirect waves indicating their origin. With higher stimulation intensities, neurons are also activated directly resulting in D-waves or direct waves, recordable 1.5–2 ms. prior to the I-waves. In the present experiment, using a stimulation of 150% of motor threshold, we might have activated neurons in the temporal regions indirectly as well as directly.

The TMS-pulses were delivered at latencies of 50, 100, 110, 120, 130, 140, 150, and 200 ms randomly,

counting from the onset of the stimulus presentation. Also, there were cases where no TMS-pulse was delivered (a “sham condition”). Each category consisted of 18 trials per subject, so that each subject underwent 162 trials with 18 trials per latency (and thus 144 bilateral TMS-pulses in all) during the experiment. For each 15 min, a 5-min break was held. Before the experiment, EEG signals were obtained at the locus targeted by the TMS, indicating that the visual signal arrived 100 ms on average after its presentation on the screen.

4.4. Results

The following results were obtained cumulated for all 10 subjects. See Figs. 5 and 6.

Data was analysed with a one-way ANOVA test, checking for significant differences in the material with a Tukey and a Scheffe post hoc analysis. For the cumulated results (average of 10 subjects), there is no significant effect of the TMS-pulse in terms of correctness. However, for their scaling of clarity, there is a significant effect after 110 and 120 ms: those two latencies are not significantly different from each other ($P = 0.249$), but from all other latencies (all at $P < 0.001$).

The results show a quite similar tendency for each subject. Correctness seems generally unaffected by the TMS-pulse. However, when it comes to the subjects' scaling of their experience, the effect is quite different. In most cases, the subjects experience a reduction in the clarity of the different aspects of the stimulus, shape, and colour especially, after 110 and, even more so, after 120 ms.

It is, however, difficult to say anything conclusive about this aspect of the experiment, since the graphs indicate a ceiling-effect—i.e., the task may simply have been “too easy” for any real effect to become visible.

5. Discussion

It has been suggested that the neural substrate of visual consciousness consists of the feed-back loops from higher to lower areas (Edelman, 1992). This hypothesis is supported by a relatively small number of findings. For instance, Pascual-Leone and Walsh (2001) have stimulated V1 and area MT successively: when V1 was stimulated first, subjects experienced moving dots (as they would if V1 was not stimulated at all), when MT was stimulated first, the subjects reported a decrease in the moving dots, or a total absence of them. This has been interpreted as a result of a feed-back connection from MT to V1 being necessary for visual consciousness. Our results could be considered as supportive of this hypothesis, considering that the neural signal arrives to the area app. 20 ms. before we find our maximum effect on the subjective scaling. That the signal is less

significantly affected at the arrival of the feed-forward sweep of information indicates that feed-forward systems do not exclusively depend on ventral stream processing. Seemingly, the feed-back signal is still efficient after 100 ms, so that the subjects to some degree can report clear experiences. This might indicate a strong interconnectedness between dorsal and ventral stream processes. The ventral streams seem much more crucial for processing of the feed-back signal. However, more variations of the experimental paradigm may be needed to give conclusive evidence for this.

We find it interesting that, in experiment 1, there is a general tendency for the subjects to be more correct about a stimulus when experiencing it more clearly. At the same time, however, experiment 2 does not seem to give any reductions in the subjects' capability to guess about the stimulus, while having significant effects on their experiences. The latter result seems to indicate that the brain processes behind object recognition differ from the ones behind consciousness, which in that case goes against a use of so-called objective measures when studying consciousness (e.g., asking a subject what is on the screen, and then second-guess whether the subject was conscious of the visual figure). It could be argued that this conclusion is challenged by the possible ceiling effect in experiment 2. Based on experiment 1, however, we can see that we have only "just arrived" at ceiling (at least with regards to the correctness of shape) with the stimulus duration of 192 ms. Therefore, one could at least assume that any larger effect (as the effect on experience) would also show up for correctness if this conclusion were not true.

Apart from those conclusions, we believe to have found an experimental framework appropriate in further research. One could record EEGs of the ventral streams to study what occurs in the "sensitive periods" in ventral stream processing (110–120 ms). Furthermore, by moving the coil along the ventral streams, one could literally "follow" the feed-forward and feed-back signal. This would clearly validate our results and help to gain more knowledge about the co-variation between this kind of processing and experienced visual differences.

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