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Review

Variability of perceptual multistability: from brain state to individual trait

Andreas Kleinschmidt[1,2,3,*], **Philipp Sterzer**[4] **and Geraint Rees**[5,6]

[1]*Institut National de la Santé et de la Recherche Médicale, Unité 992, Cognitive Neuroimaging,*
91191 Gif-sur-Yvette, France
[2]*Commissariat à l'Energie Atomique, Direction des Sciences du Vivant, Institut d'Imagerie Biomédicale,*
NeuroSpin, 91191 Gif-sur-Yvette Cedex, France
[3]*Cognitive Neuroimaging Unit, Université Paris-Sud, 91405 Orsay, France*
[4]*Department of Psychiatry, Charité Campus Mitte, Charitéplatz 1, 10117 Berlin, Germany*
[5]*Institute of Cognitive Neuroscience, University College London, 17 Queen Square,*
London WC1N 3AR, UK
[6]*Wellcome Trust Centre for Neuroimaging, University College London, 12 Queen Square,*
London WC1N 3BG, UK

Few phenomena are as suitable as perceptual multistability to demonstrate that the brain constructively interprets sensory input. Several studies have outlined the neural circuitry involved in generating perceptual inference but only more recently has the individual variability of this inferential process been appreciated. Studies of the interaction of evoked and ongoing neural activity show that inference itself is not merely a stimulus-triggered process but is related to the context of the current brain state into which the processing of external stimulation is embedded. As brain states fluctuate, so does perception of a given sensory input. In multistability, perceptual fluctuation rates are consistent for a given individual but vary considerably between individuals. There has been some evidence for a genetic basis for these individual differences and recent morphometric studies of parietal lobe regions have identified neuroanatomical substrates for individual variability in spontaneous switching behaviour. Moreover, disrupting the function of these latter regions by transcranial magnetic stimulation yields systematic interference effects on switching behaviour, further arguing for a causal role of these regions in perceptual inference. Together, these studies have advanced our understanding of the biological mechanisms by which the brain constructs the contents of consciousness from sensory input.

Keywords: functional magnetic resonance imaging; voxel-based morphometry; perceptual awareness; binocular rivalry; ongoing brain activity; predictive coding

1. CONCEPTUAL AND EMPIRICAL RELEVANCE OF MULTISTABILITY FOR SENSORY NEUROSCIENCE

Conscious perception of the sensory environment relies on neural processes that can be thought of as a 'handshake' between the representation of physical stimulus properties and an endogenously generated inference. Inference is a hypothesis about what in the physical environment caused the activity pattern that is generated at sensory receptors for instance in the retina or cochlea. Inference carries information related to the 'meaning' or the semantic properties of a stimulus. Usually, we experience the perceptual 'handshake' to be rapid, firm and stable, and inference is then considered to be an unconscious process requiring no volitional allocation of cognitive resources. Though in itself unconscious, inference determines the contents of perceptual awareness. Also, there may be situations when for inference to be successful, it does need to call upon cognitive processes of which one is conscious. Impoverished sensory input, for instance, is a way of slowing down or even preventing locking into a 'handshake' that may engage conscious search processes, but once a grip is established, it remains firm without any apparent effort and despite degraded sensory input [1]. A different situation arises when sensory input is not degraded but when the 'handshake' is transiently destabilized because more than one perceptual inference provides firm locking. This situation arises when a given sensory input is ambiguous from the observer's perspective. Only one hand can be shaken at a time and this determines the contents of perceptual awareness, but the 'handshake' then wavers between these different stretched out options of inference [2,3].

Ambiguous figures provide the experience of having one's perceptual awareness switching between different options while at the same time remaining fully conscious that no physical stimulus change whatsoever underpins these vivid perceptual changes. Such multistable

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* Author for correspondence (andreas.kleinschmidt@cea.fr).

One contribution of 10 to a Theme Issue 'Multistability in perception: binding sensory modalities'.

stimuli disrupt and hence question our usually uncontested confidence in veridically deriving the properties of our physical environment from the information received by our senses. In the scientific community, perceptual multistability has been popular for two reasons. At a conceptual level, multistability highlights the importance of inference in the emergence of conscious perception [4]. At a more pragmatic level, the use of multistable stimuli permits behavioural or neurophysiological recordings for which the observed dynamics can be unequivocally assigned to the changes and the contents of perceptual awareness rather than to sensory input representation, as the latter remains constant throughout [5].

It would be misleading, though, to consider these two aspects, inferential processes and multistability, as equivalent. For example, the presentation of discrepant input patterns to the two eyes can lead to binocular rivalry, and in this case competitive interactions between low-level monocular channels may be one of the driving forces of multistability [6]. Thus, the temporal dynamics of perceptual awareness in binocular rivalry are not necessarily identical with fluctuations in perceptual inference in the sense of changing interpretations of a single but ambiguous meaningful input pattern. Neural findings from binocular rivalry may hence to an unknown extent also reflect different mechanisms than in paradigms where the dynamics of perception depend exclusively on inference, as for instance ambiguous figures and bistable motion stimuli. Whether such distinctions are important depends on the type of question a given experiment seeks to address. For example, it is perfectly legitimate to use binocular rivalry as a model for studying the correlation of brain activity patterns with perceptual dominance. However, it would be difficult to derive the mechanisms underpinning perceptual inference from a paradigm where lower level mechanisms other than those related to perceptual inference may interfere with and in fact enslave perceptual awareness.

A generalized account of the neural architecture underpinning perceptual multistability must address not only effects that are related to differences between stimuli but also differences that are related to neural mechanisms. Although some progress has already been achieved over the last decade (for a recent review see Sterzer *et al.* [7]), it cannot yet be considered satisfactory. If we require that a neurophysiological account of perceptual multistability should be able to predict our actual perceptual experience when presented with ambiguous stimuli, we are still some distance from such a goal. One persistent problem is illustrated by the following comparison. Functional neuroimaging during dynamic sensory stimulation (e.g. watching a film) can be used to predict the time courses of activity in many brain regions of one observer from those recorded in other observers [8]. In this situation, there is a fairly reproducible entrainment of brain activity across observers. However, if we were to apply the same procedure to participants in an experiment with ambiguous sensory input, any attempt at transferring the actual time course of perceptual experience between them would most probably fail. The reason is that although the experience of multistability in its general form is shared between observers, its actual dynamics are subject to considerable variability between individuals. And even for a single given individual who experiences multistability, our current prediction of the real-time dynamics of conscious awareness does not yet go beyond an overall fit of the distribution of perceptual epoch lengths (for instance, to a gamma function), and the fitted parameters vary vastly between individuals.

The present review will first briefly outline the neuroanatomical framework within which perceptual multistability can be related to variations of neural activity. It will then explore two approaches to the understanding of mechanisms, chronometric studies that analyse precedence of neural responses across different regions and stimulation studies that produce interference with activity in a given region. As its final main theme, it will address the two aforementioned issues, inter-epoch (or inter-trial) and inter-individual variability, and discuss some recent findings that may pave the way towards a more complete understanding of the neural determinants of perceptual multistability.

2. THE FUNCTIONAL NEUROANATOMY OF PERCEPTUAL MULTISTABILITY

The use of multistable stimuli in neurophysiological recordings runs counter to the classical approach of sensory physiology, which establishes stimulus-response functions. It requires obtaining reports of perceptual dominance which can then be used to explore the data for a neurophysiological modulation associated with perception, but in the absence of any confounding change in sensory input. Functional magnetic resonance imaging (fMRI) has proven particularly useful for determining the functional neuroanatomy of perceptual multistability. There are two reasons for this. First, in contrast to positron emission tomography, which accumulates signals originating from externally timed radiotracer injection, fMRI relies on signals associated with the concentration of deoxyhaemoglobin, a permanently present endogenous tracer that allows fMRI to record a blood oxygenation level-dependent (BOLD) signal [9]. This technique can thus provide continuous recordings of neural activity convolved by the temporal low-pass-filter properties that couple synaptic activity to BOLD signals. Second, and different from invasive electrophysiological techniques that require an *a priori* selection of recording sites (and hence spatially undersample brain activity), this technique provides coverage of the entire brain with good spatial resolution and very high fidelity of localization.

Functional neuroimaging of observers reporting multistability has allowed two important questions to be addressed; where does brain activity reflect perceptual dominance; and where does brain activity reflect perceptual alternations? Regarding the first question, a range of studies have provided evidence for a rather intuitive answer, namely that visual perceptual dominance is reflected in activity levels of those brain regions that are functionally specialized for the sensory properties of the percept in question [10–14]. Equivalent observations have been reported for the auditory modality [15,16], and it has been suggested that across different senses similar principles govern perceptual multistability [17]. These findings have also expanded the notion of functional specialization in the brain. Previously, a given brain region was considered functionally specialized if its response properties were tuned to specific sensory features or categories, or if selective perceptual deficits followed focal lesions. But the aforementioned studies establish that a functional specialization of brain regions can also be demonstrated for the perceptual outcome of a given stimulus, over and above the specialization related to the processing of its sensory properties. In addition to these findings, where the dominant percept can be tied to mean regional activity levels, traces of the suppressed percept have also been demonstrated, e.g. neural activity in the amygdala [18–20] and in functionally specialized visual areas of the 'dorsal stream' [21]. Using multi-voxel pattern analyses of high-resolution fMRI and magnetoencephalography, such traces of the suppressed percept even persist in correspondingly specialized sensory brain regions of the 'ventral stream' [22,23]. Together, these studies have hence shown neural signatures both for the continuous sensory representation of the two rivalling stimuli and for the moment-by-moment dominance of one over the other.

One exception from the general pattern of observing strong effects of perceptual dominance in specialized sensory brain regions has been found with visual motion stimulation. If visual motion input is coherent across a wide part of the visual field it can elicit perceptual alternations between object-motion (veridical) and illusory self-motion, also referred to as vection. The sensation of vection occurs along the same direction of motion that would be associated with the given visual input. The anterior pole of the human middle temporal complex, a likely homologue of the dorsal medial superior temporal area (MSTd) in monkey, is arguably most specialized for the type of visual motion input that arises from self-motion. During exposure to a bistable wide-field visual motion stimulus, activity levels in this brain region were not notably different between epochs for each of the two percepts, object- and self-motion [24]. Instead, perceptual dominance of vection was reflected in a decrease of activities throughout the whole chain of lower level motion-sensitive visual areas. One explanation of this could be that processing in the human MSTd homologue is equally important for both percepts, self- and object-motion. From a functional perspective, the effects in lower level motion-sensitive areas could indicate that when computation of one's self-motion relies on wide-field visual motion processing, as in vection, motion of intervening objects in the visual field becomes distracting. It is conceivable that the impact of such distraction is attenuated by inhibiting earlier visual areas, where receptive fields are smaller and therefore also sensitive to motion of objects in a scene. Consistent with this, electrophysiological investigation has shown that vection (as opposed to perceiving the identical sensory input as object-motion) is associated with a reduction in event-related potentials elicited by other visual stimuli [25].

This finding suggests that perceptual multistability not only determines the contents of awareness but also gates the processing of afferent input, an effect that is usually tied to the exertion of voluntary attentional control. Further support for percept-dependent attentional gating comes from experiments with bistable apparent motion stimuli. Under certain conditions, a sequence of two frames showing a dot at one and then another position will yield the illusion of perceiving this dot move along a trace. If both frames contain two dots and are presented in regular alternation, perception can become multistable, with different possible directions of apparent motion. Interestingly, apparent motion is quite robust against feature changes of the dots between successive frames, for instance, in colour or in shape, which then appear to change in mid-flight. In situations where only one of two rivaling directions of apparent motion is compatible with chromatic object cues, epochs of the percept that violate these chromatic cues are associated with lower activity in early visual areas, where colour information is processed [26]. This might hence be a case of perception overruling those facets of sensory information that conflict with the dominant inference instead of being destabilized by them.

Percept-dependent attentional gating of afferent processing may also be important for interpreting findings from binocular rivalry. Several studies have shown that activity alternates between separate afferent monocular pathways as a function of perceptual dominance, even as early as the lateral geniculate nucleus [27,28]. Yet, these observations do not necessarily imply that rivalry between these monocular channels is at the origin of perceptual multistability. Instead, an alternative explanation could be that top-down (eye-independent) modulation controls switches between those lower level afferent processes that are tied to a given percept. This explanation may also hold for figure-ground reversals [29] or even when top-down attention may be deployed without any actual sensory input, for instance retinotopically along the trace of an apparent motion [30,31].

Greater activity associated with one of two rivaling percepts has also been found in higher level cortical areas that one would not traditionally associate with a preference for one percept over another. The reason for such observations could be that the two percepts differ not only with respect to the contents of awareness, but also with respect to salience, perceptual or task difficulty, i.e. factors that in a less specific way than perceptual content might account for greater activity or indicate that one percept but not the other calls on higher order mechanisms [32–34].

In summary, functional neuroimaging studies have outlined a plausible anatomy of perceptual multistability but the specific results vary as a function of the perceptual domain and probably also with the mechanisms underlying changes in perceptual dominance. Overall, neural processing of the sensory input underpinning the rivaling percepts is maintained throughout alternations of dominance and suppression. Perceptual dominance is associated with greater overall activity in brain regions that are accordingly functionally specialized, e.g. for visual objects or motion. However, similar effects can occur both upstream and downstream of the region that is most closely tied to the perceptual content. As a consequence, the neuroanatomical location where activity correlates with perceptual dominance does not make it possible to clearly determine the mechanism that underpins perceptual multistability.

To better understand mechanisms of multistability, it may be useful to turn to the second of the two questions introduced above, the functional neuroanatomy of perceptual alternations. Functional neuroimaging studies show that transient event-related signal changes time-locked to changes in perceptual dominance occur in those functionally specialized areas that are sensitive to the perceptual content that is perceived to change [35–40]. This general rule has been confirmed even for the aforementioned case of wide-field visual motion stimulation with alternations between object- and (illusory) self-motion. In other words, every time motion perception flips, this is associated with transient activation in the brain regions specialized for processing wide-field coherent visual motion, but neither the amplitude of this phasic response nor the tonic level of activity differ between percepts [24].

Event-related activation during perceptual reversals is not confined to brain regions representing the sensory properties of the visual stimuli undergoing perceptual alternations. The most robust finding in this respect is that perceptual alternations are associated with transient activity increases in focal regions of the parietal cortex and lateral prefrontal cortex. These regions are similar to those which have been implicated in attentional processes such as selection. Transient activity increases in frontoparietal regions associated with spontaneous alternations during perceptual bistability are greater than those produced by stimulus-driven changes in perception [35,41]. This could imply that supra-modal brain regions are involved in generating perceptual inference and thereby inducing perceptual alternations. Yet, such an interpretation cannot be based solely on the analysis of the amplitude of transient activity increases during switches. Alternatively, enhanced activity increases in frontoparietal regions could reflect greater salience of spontaneous perceptual reversals determined in a remote neural substrate, relative to stimulus-driven perceptual changes. Furthermore, increased perceptual uncertainty and longer transition phases may also contribute to greater activity increases during spontaneous versus stimulus-driven perceptual changes [42]. In the following two sections, we discuss recent evidence from chronometry and interference that indeed suggest a causal role of higher order areas in the parietal and frontal lobe in determining perceptual alternations.

3. THE NEURAL CHRONOMETRY OF PERCEPTUAL MULTISTABILITY

Chronometric analyses of fMRI signals show that the temporally dispersed BOLD response is reliable enough to resolve onset latency differences between distinct BOLD responses in the range of a few hundred milliseconds [43–46]. The comparison of response onset latencies between experimental conditions can thus provide insights into the relative timing of the underlying neural events. Spontaneous perceptual reversals during continuous viewing of a bistable apparent motion stimulus are associated with transient increases in the fMRI signal in the human motion complex V5/MT+ in visual cortex [12,26,38,39] and in supra-modal frontal and parietal regions [38,39,41]. Chronometric analyses of fMRI signals showed that transient responses in right inferior prefrontal cortex occur approximately 800 ms earlier during spontaneous perceptual reversals than during stimulus-driven perceptual changes in a matched control condition [41]. Importantly, in the absence of a valid time marker for spontaneous perceptual switches, such temporal precedence was observed relative to the timing of event-related activation in V5/MT+ and to externally induced perceptual switches, suggesting that the earlier onset of transient activity increases in prefrontal cortex reflects a role of this region in an inferential process that triggers spontaneous reversals during bistable as opposed to purely stimulus-driven perception.

The notion that prefrontal structures contribute to perceptual inference is supported by the finding that perceptual alternations are slowed in patients with focal damage to prefrontal and parietal cortex [47,48]. Nonetheless, it should be noted that conclusions based solely on chronometric analyses of fMRI signals—even when appropriately grounded in tests of region-by-condition interactions that remove effects of local variations in neurovascular coupling—are still limited by our incomplete understanding of the relationship between neural and haemodynamic responses. The use of neurophysiological measures with a higher temporal resolution, such as electroencephalography (EEG) or magnetoencephalography, may help to overcome this limitation.

One problem with the measurement of neurophysiological signals related to spontaneous perceptual switches is that the analysis of these signals has to rely on subjective reports of the participants. Thus, the exact timing of the perceptual transitions—with respect to both their onset and duration (transitions may not always be instantaneous)—remains uncertain. It has been attempted to circumvent this problem by presenting bistable stimuli not continuously but intermittently, and requiring participants to report their percept for each stimulus presentation. If the stimulus presentations are brief enough (500–1000 ms), the change in perception will, to a first approximation, be time-locked to the onset of a given stimulus presentation. Neural activity can thus be analysed in relation to the known time of stimulus onset, rather than a behavioural report.

Electrophysiological studies with discontinuous, regularly repeated presentation of ambiguous stimuli show differences between potentials elicited by the first trial in a sequence for which reversal of perception was reported and potentials elicited in trials where perception stayed the same. These differential stimulus-locked electrical signals hence indicate neural processes associated with a perceptual reversal, although it is not clear whether the mechanisms are truly identical to those observed during bistability under continuous stimulus presentation. Given the short latencies of the observed effects, these event-related responses have been taken to suggest a bottom-up (or low level) origin of perceptual reversals [49]. The problem with this interpretation is that an early response difference in a trial on which participants report a change compared with the preceding ones might in turn reflect a neural process that was already active before stimulus onset on that trial. In other words, it could be that the fate of a given trial to be reported as a reversal is already determined by neural activity preceding the actual stimulus onset that will result in this report. Evidence in favour of this view comes from a recent EEG study using intermittent presentation of a Necker cube variant [50]. This study compared electrophysiological microstates preceding stimulus presentations with reversals to those where the percept remained stable. Activity in right inferior parietal cortex increased 50 ms before stimulus onsets associated with perceptual reversals. In a subsequent study from the same laboratory, EEG was recorded during intermittent presentation of stimuli producing binocular rivalry, namely between orthogonally oriented grating stimuli [51]. Again, an increased EEG signal in right inferior parietal cortex was observed to precede perceptual reversals. In addition, pre-reversal activity was reduced in bilateral ventral temporo-occipital cortex. Importantly, no such effects were found for physical alternation of the same grating stimuli, indicating that the observed pre-reversal signal is specifically associated with spontaneous perceptual reversals. The findings from these two studies suggest a causal role for right inferior parietal cortex in generating perceptual reversals, regardless of the mechanism underlying perceptual multistability.

The apparent discrepancy between the above-mentioned chronometric fMRI study showing temporal precedence of activity in right inferior frontal cortex [41] and the two EEG studies [50,51] suggesting a causal role of right inferior parietal cortex could potentially be explained by differences in temporal resolution. The BOLD signal is characterized by relatively poor temporal resolution and it is conceivable that short onset differences in parietal activation between spontaneous and stimulus-driven reversal were simply not detectable in fMRI signals. Conversely, the EEG studies of Britz and colleagues limited their analyses to the time window 50 ms before stimulus onset. Earlier activity possibly occurring in prefrontal regions may therefore have been missed in these analyses. The two findings in right prefrontal cortex (fMRI) and right parietal cortex (EEG) may thus reflect parts of a cascade of neural events that precedes spontaneous reversals.

While temporal precedence is widely used as an indicator of causality, it does not provide direct evidence for a causal relationship between frontal and parietal activations and perceptual reversals. For instance, these activations could signal perceptual uncertainty owing to a breakdown of perceptual stability at the sensory level, which then might, or might not, play a causal role in triggering a perceptual reorganization. It is therefore as difficult to deduce mechanisms from effects 'early' in time as it is to do this from effects 'early' or low in the anatomical visual hierarchy, as discussed earlier. Complementary evidence, at least for a causal role of parietal cortex in controlling the rate of reversals during perceptual bistability, comes from experiments where transcranial magnetic stimulation (TMS) was used to interfere with cortical function.

4. INTERFERING WITH THE NEURAL ARCHITECTURE OF PERCEPTUAL MULTISTABILITY

TMS transiently disrupts neuronal activity below the targeted area on the scalp, and can thus be used to address questions of whether a cortical area whose activity is correlated with perceptual reversals in fact plays a causal role in such reversals. If disruption of a cortical area with TMS affects the dynamics of perceptual reversal, then a causal role for that cortical area can be inferred in determining the perceptual dynamics.

TMS applied over early retinotopic visual cortex during binocular rivalry produces phosphenes and interferes with the dynamics of rivalry in a retinotopically specific fashion [52]. Thus, interfering with visual processing in a retinotopically specific location can interfere with rivalry occurring between stimuli presented at that location, indicating that the neuronal dynamics at retinotopically localized cortical locations are involved in binocular rivalry. This effect does not appear to be simply due to the TMS inducing a phosphene, because presenting perceptually similar flashes without TMS did not replicate the effect. Importantly, such changes to the dynamics of binocular rivalry are not seen when the binocular rivalry stimuli are rapidly swapped between the eyes, producing stimulus rivalry that does not depend on monocular representations. The retinotopic effect of TMS on rivalry therefore reflects an effect of TMS on interacting monocular populations of neurons. Interestingly, the effects of TMS on rivalry dynamics are delayed by between 600 and 1800 ms after the pulse, which is a relatively long duration relative to processing speeds in visual cortex. The effect of TMS may therefore be to perturb the ongoing nonlinear dynamics of rivalry rather than to directly interfere with the feed-forward processing of visual stimuli.

Outside striate and extrastriate visual cortex, several studies have targeted cortical locations in dorsal and ventral visual pathways. TMS applied to the left temporo-parietal cortex can reverse a perceptual switch when applied at or close to the timing of the switch [53]. The interpretation of this finding is somewhat unclear, because rivalry with comparable perceptual dynamics can be seen when stimuli are presented to either the right or left hemispheres of split brain observers, where no interhemispheric connections are present [54]. Stronger evidence comes from studies that have targeted parietal cortex. For a range of different paradigms, including binocular rivalry and bistable structure-from-motion, stimulation with different types of TMS protocols at several different locations in superior parietal cortex can alter the dynamics of perceptual multistability [55–58]. Thus—and in accord with the aforementioned EEG results—parietal cortex seems to play a causal role in the dynamics of multistability, but despite dedicated attempts equivalent evidence is lacking for prefrontal cortex [59].

Comparing different studies is difficult owing to differences in stimulation protocol and stimulus. One study has directly compared two different stimulation sites in parietal cortex with the same bistable visual stimulus and identical TMS protocols and shown that different locations can produce opposing effects on perceptual alternations [58]. While TMS at one location in parietal cortex can increase the rate of perceptual alternations, TMS applied to a closely related but more anterior stimulation site leads to a *decrease* in the rate of alternations. Thus, different regions of parietal cortex show functionally distinct causal roles in bistable perception.

5. UNDERSTANDING MULTISTABILITY FROM THE PERSPECTIVE OF PERCEPTUAL DECISIONS

In the previous sections, we have presented evidence suggesting that higher order brain regions are causally involved in generating alternations occurring during perceptual multistability. The techniques that provided this evidence are unfortunately less suitable for addressing the role of the specific sensory areas in this respect. Negative TMS results are difficult to interpret but even positive results can pose problems when they were obtained for regions that are very directly involved in the representation of sensory content since non-specific or generic effects might come into play. And for chronometric studies of rivalry, the timing of reversal-related activation in sensory cortex has to serve as an endogenous marker of perceptual alternations because no external stimulus change can be used to create a timeline. Moreover, neural processes associated with a perceptual reversal are ambiguous in the sense that appearance of one percept is inherently linked to disappearance of another (with the exception of stimuli involving more than two possible percepts or ill-defined intermediate states). That was our reason for discussing findings from some of the studies that discontinuously presented ambiguous stimuli. These studies have highlighted the difficulties in interpreting neural signals associated with reversals as either causes, correlates or consequences of a change in perceptual experience. At least for the studies reporting neural signal changes that precede actual sensory input it is safe to conclude that these signals are good candidates for a causal function in governing perceptual multistability. But what exactly could this causal role be and can it account for variability between successive trials?

Some evidence comes from recent neuroimaging studies that did not repeat multistable stimuli at regular and short intervals but instead left long and variable delays between successive stimulus presentations. In such paradigms, no trace of any carry-over effects between successive trials can be recovered and they therefore uncouple the appearance of one percept from the disappearance of the other. In other words, each trial corresponds to a de novo perceptual decision which has to be reached when confronted with the same ambiguous stimulus. Perceptual decisions have usually been studied in a trial-based fashion with time-locking to stimulus onset [60], but it is interesting to extend their proposed mechanisms to the continuous dynamics evoked by perceptual multistability. Interrogating this relationship is especially appealing since many studies of perceptual decisions have used ambiguous or near-threshold stimuli. That is because with such stimuli there are two qualitatively different trial outcomes, one percept or another and detection (hit) or not (miss), respectively, instead of a single and always identical percept where variability can only be captured in quantitative parameters as reaction time. Obtaining qualitative differences facilitates the read-out of mechanisms from neurophysiological signals.

Many current models of perceptual decision-making share in common the idea that sensory input is analysed with respect to the evidence it provides in favour of a given perceptual interpretation. They posit that such evidence is accumulated over time, and that upon passing a given threshold, it will entail a decision in favour of that perceptual interpretation [61,62]. When the sensory input contains evidence in favour of more than one perceptual interpretation, the evidence accumulation for the two alternative percepts competes and the winner of this race, passing threshold first, determines the perceptual outcome on that trial.

Electrophysiological experiments have shown that perceptual decisions can be influenced by micro-stimulation of neural populations with response properties related to a given percept [63]. Yet, it has never been reported that such effects could be elicited in time intervals preceding the neural accumulation of stimulus-driven evidence. Externally applied electrical stimulation is non-physiological and this might account for the failure to establish a link between the outcome of perceptual decisions and pre-stimulus activity levels in sensory areas. Despite this lack of evidence for a role of activity preceding the stimulus-driven neural response, mathematical models of perceptual decisions can only fit behavioural data well if they allow for variability of the initial signal even before stimulus-driven evidence becomes available. Some studies have therefore pursued a different approach to this question by testing whether spontaneous trial-by-trial fluctuations of pre-stimulus ‘baseline’ activity influence perceptual decisions on ambiguous sensory input, as suggested by computational studies of the effect of noise on rivalry [64,65].

Using two different visual paradigms, one in the face and object domain and the other in the motion domain, it was shown that pre-stimulus activity does indeed bias perceptual decisions upon subsequent presentation of ambiguous stimuli (figure 1*a*,*b*) [66,67]. Comparable results have been obtained for detection of near-threshold stimuli in the somatosensory and auditory domains (figure 1*c*) as well as for settings such as a Stroop paradigm, which involves interference from task-irrelevant conflicting sensory information (figure 1*d*–*f*) [68–70]. The neuroanatomical pattern of the pre-stimulus activity fluctuations that can be linked to perceptual performance reflects the specific task requirements in these various paradigms. In the case of ambiguous visual stimuli, the effects are limited to those visual areas that are specialized for the possible percepts. For the simple detection of stimuli embedded into a noisy background, the effects are found in the early sensory cortex of the

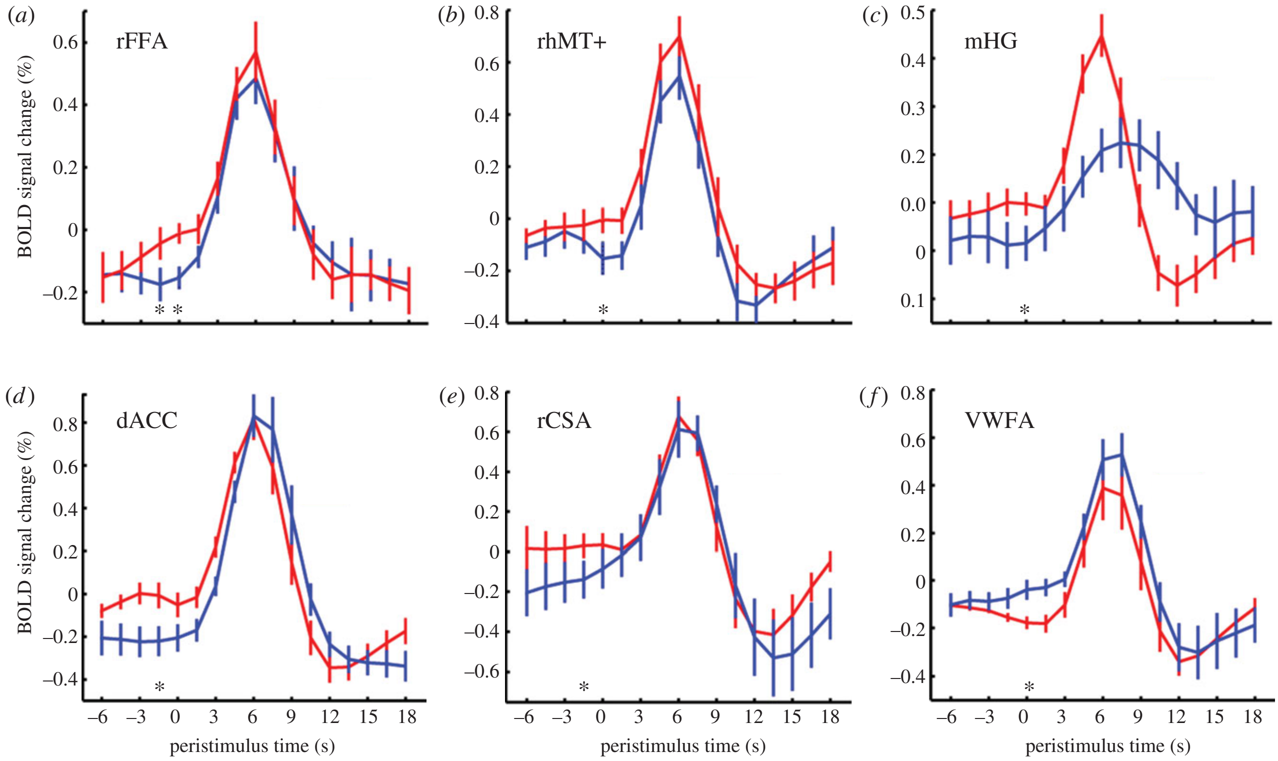

Figure 1. Effects of spontaneous variations of ongoing regional brain activity on perception and behaviour. The plots show event-related fMRI signal changes from paradigms involving ambiguous, periliminal or conflicting sensory stimuli. (*a*) In the case of perceptual decisions on ambiguous stimuli, pre-stimulus signal variations in the right fusiform face area (rFFA) bias the perceptual outcome for face (red)/vase (blue) ambiguity, and (*b*) activity fluctuations in the right occipito-temporal human motion complex (rhMT+) are related to the perceptual outcome of trials with a random (blue) dot motion kinematogram containing a periliminal amount of coherent (red) motion embedded into otherwise random motion. In both instances, perception is also but independently correlated with amplitude differences of the responses evoked in these brain regions. (*c*) An auditory paradigm where participants were instructed to detect near-threshold acoustic stimuli yields an even greater evoked response difference when comparing responses in medial Heschl's gyrus (mHG) and hence early auditory cortex during hits (red) and misses (blue). Again, perceptual outcome is biased by trial-by-trial variations of ongoing activity prior to stimulation. (*d–f*) Findings from three regions, dorsal anterior cingulate cortex (*d*; dACC) as well as independently localized colour-sensitive area (*e*; CSA) and visual word form area (*f*; VWFA). Signal time courses were split into two halves on the basis of reaction times for colour naming in incongruent trials with colour-word Stroop interference. While higher pre-stimulus activity in dACC and CSA facilitates response speed for upcoming stimuli, the opposite pattern is observed for activity levels in VWFA. Asterisks indicate time points with significant pre-stimulus activity differences depending on the perceptual or behavioural outcomes of the ensuing trials. For more details and further results from these experiments, see the original publications [66–69].

related modality (audition) but also in higher order neural systems maintaining alertness and task set. Finally, response speed in incongruent trials of a colour-word Stroop paradigm (when participants need to suppress reading the colour word for which they are to name the colour in which it is written) is accelerated by higher pre-stimulus activity in task-relevant, i.e. colour-sensitive, visual cortex but also by activity in brain structures serving cognitive control and interference monitoring, such as a region of dorsal anterior cingulate cortex. Such findings suggest that continuous perceptual decision-making, as is required during the perception of multistable stimuli, is probably also influenced by uncontrolled activity fluctuations, and that fluctuations anywhere in the network of brain areas mediating the contents of consciousness could become functionally relevant.

Another important finding with ambiguous visual stimuli is that ongoing activity levels in specialized sensory areas not only influence subsequent perceptual decisions but also interact with responses evoked by these stimuli [66,67]. This nonlinear interaction is such that, in regions of crucial importance for a given percept, for trials where this percept was reported (as opposed to the other possibility), the evoked response was smaller when the preceding level of ongoing activity was higher on that trial. This suggests two separable but complementary contributions to perceptual decisions, one related to ongoing activity, the other to stimulus-driven activity. The interaction of evoked and ongoing activity in determining perceptual decisions is synergistic, because, when pre-stimulus activity is high, even a small evoked increment seems sufficient to yield a given percept, whereas when pre-stimulus activity is low this increment must be very strong to result in this percept. These findings are therefore compatible with the aforementioned evidence accumulation framework. So, does that mean that the fMRI signal in sensory areas can be regarded as a proxy for sensory evidence?

That question may be answered by considering false alarms. For example, if a dot kinematogram is reported as containing coherent motion, although the directions of the various moving dots are random, then this false alarm represents a percept reported in the absence of supporting sensory input. If fMRI signals indeed represent the level of sensory evidence then fluctuations in ongoing activity could be sufficiently strong that with an inappropriate stimulus, or even in the absence of an actual stimulus, perceptual threshold might occasionally be reached. Such a hypothesis leads to the prediction that false alarms are preceded by especially high levels of ongoing activity. This prediction was recently falsified by the opposite observation, that ongoing activity preceding false alarms was significantly lower than that preceding hits or misses [71]. Instead, these findings are compatible with predictive coding, as explained below.

In general terms, predictive coding models posit that neural activity fed forward in a hierarchical system represents the mismatch between predicted and observed sensory input. Perception then involves the process of reducing this prediction error to zero, an 'explaining away' achieved by adjusting and refining top-down inference that is conveyed by feedback signals [72,73]. The predictive coding framework is compatible with several robust empirical observations, for instance, enhanced responses evoked by oddball or mismatch stimuli or reduced responses evoked by primed or adapted stimuli [1,74]. In the latter case, as the prime or the adaptation entails a prediction about the actual target content, prediction error upon stimulation is lower than if the same stimulus is presented without a preceding prime or adaptation.

To explain other empirical observations, however, this simple framework must be complemented because optimal predictions or expectations rest on two distinct processes. The first is predicting the content of a percept (e.g. what caused the stimulus) and the second is properly inferring the uncertainty or precision of that prediction (e.g. the probabilistic context in which a stimulus appears). The implementation of precision in the predictive coding framework is necessitated by the presence of noise in environmental states or sensory input. Prediction and precision are thought to be combined in that precision modulates the gain of prediction error responses [75]. When precision is high, this results in amplified prediction error responses upon stimulation.

The need for such a regulatory mechanism is immediately obvious from a functional perspective. For instance, a peripheral stimulus may be entirely unexpected and hence induce a prediction error signal but if this stimulation is irrelevant in the current context, preceding precision levels will have remained low and little amplification is assigned to the evoked response. Conversely, if a certain location or feature is cued to be task-relevant, this increases precision and results in an amplification of the prediction error signal upon stimulation which in turn permits a more fine-grained result when 'explaining away' this signal. This modulatory mechanism of precision may be shared with that employed by directed voluntary attention [76]. In other words, precision could constitute the substrate by which the effects of top-down attention are implemented in a sensory cortical area. Greater precision then accounts for enhanced neural responses to attended stimuli and higher accuracy of behavioural performance. By combining prediction error with precision it becomes possible to understand that two ways of improving performance, cueing and priming, can have divergent effects on evoked responses, increasing or decreasing them, respectively.

But how do these concepts relate to the findings discussed above? It has recently been suggested that fluctuations of ongoing brain activity, often treated as noise, express not only itinerant predictions about possible future perceptual contents and action needs but that the activity from this trajectory of predictions is convolved with fluctuations of precision [77]. This mechanism could explain why in experiments involving long and irregular inter-stimulus intervals, sagging levels in precision can lead to false alarms such as those described above. It is interesting to transfer this view to the case of continuous exposure to multistable stimuli, where sensory input remains the same and its bottom-up accumulation over time should therefore not contribute to perceptual dynamics. Accordingly, ongoing activity should then become the only component governing alternations in perception. Moreover, as perceptual rivalry involves an overarching knowledge of the predictions that are tenable given a sensory input, it can be speculated that the dynamics of perception are mainly determined by fluctuations in precision. We therefore suggest that predictive coding models can account in a single unified framework for diverse situations such as stimulus-triggered perceptual decisions and continuous multistability [78]. We further suggest that variability in both can be related to an inherent fundamental property of brain function that is expressed in ongoing activity. For perceptual multistability, this view additionally offers the possibility of embracing in a single framework contributions from fatigue/adaptation as well as those from spontaneous activity dynamics because both should be manifest in ongoing activity [79,80].

In summary, this section described intrinsic neural mechanisms that shape the individual experience and time-course of perceptual multistability. Variability across repeated presentations of ambiguous stimuli might be accounted for by ongoing brain activity fluctuations. Continuous exposure to multistable sensory input might obscure but is unlikely to obliterate the impact of intrinsic brain activity on multistability. Although multistability usually occurs for all observers, it is subject to variability that suggests influences from individual traits. One possibility is that multistability varies across individuals because the structure of their intrinsic brain activity is different. The following section addresses how the neural bases of individual variability in multistability can be investigated and what results have emerged from such studies.

6. NEURAL SUBSTRATES OF INDIVIDUAL DIFFERENCES IN EXPERIENCING PERCEPTUAL MULTISTABILITY

The most straightforward measure of individual variability in multistable perception is the rate of

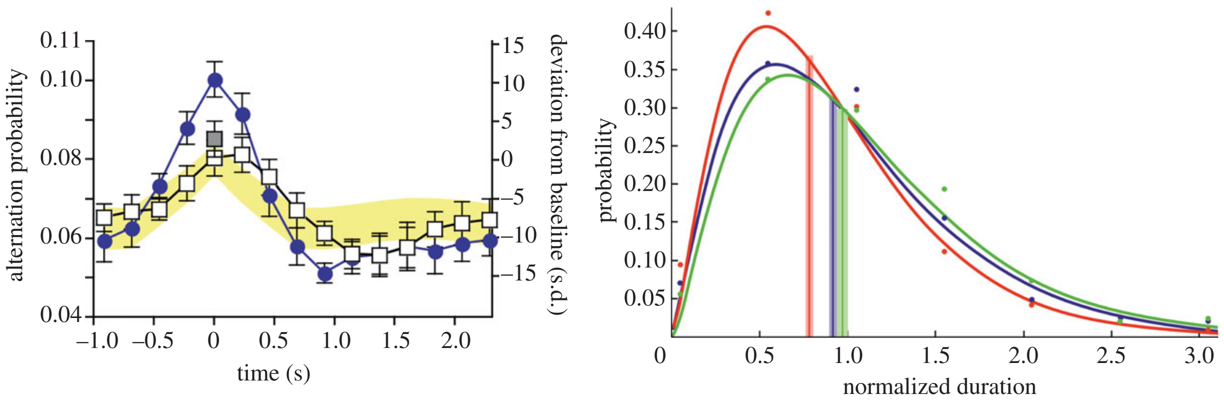

Figure 2. TMS-induced disruption of dynamics of perceptual bistability. (*a*) Plot of the probability of a perceptual alternation during viewing of a binocular rivalry stimulus when TMS is applied to cortical sites corresponding to the location of the stimulus (solid blue circles) or the visual periphery (unfilled squares). Adapted from Pearson *et al.* [52] and averaged over six observers. There is a clear peak in the alternation probability function for TMS applied to a cortical site corresponding to the location of the stimulus, indicating an effect of TMS on rivalry alternation. (*b*) Effect of TMS applied to right parietal location (corresponding to the aSPL location identified in figure 3) and the homologous region in left parietal cortex. Data corresponding to the histogram of dominance durations (seconds) are shown as a smooth gamma function fitted to data from six observers, taken from Carmel *et al.* [56]. Different colours indicate the gamma functions for right parietal TMS (red), left parietal TMS (green) or TMS applied to a control (vertex) site (blue). right parietal TMS leads to a decrease in the mean dominance duration while left parietal TMS has little effect.

perceptual alternations. The alternation rates for many forms of multistable stimuli show differences of up to an order of magnitude across large populations of individuals, for reasons that are not entirely clear. Although this has been known for many years [81], until recently there has been little investigation of the factors underlying such variability. A recent comparison of monozygotic and dizygotic twins found that about half of the variability in spontaneous switch rate in perceptual rivalry can be accounted for by genetic factors [82].

One way to explore the neural substrate of individual variability in behaviour is to attempt to relate it to individual variability in brain structure, using voxel-based morphometric analyses applied to structural MRI scans [83]. Because structural MRI scans are largely fixed context-invariant representations (at least over a short time period), unlike functional MRI scans, such an approach circumvents the need to find an appropriate fMRI paradigm to relate to the individual variability in behaviour of interest (cf. [57]). Studies using such an approach show that individual variability in perceptual switch rates for a bistable structure-from-motion stimulus is associated with variability in the grey matter density of remarkably focal regions of the bilateral superior parietal cortex, plus the microstructure of the white matter underlying these parietal regions [55,58]. As described above, such loci are causally linked to bistable perception, because targeting these regions with TMS leads to a reduction in switch rate. Moreover, not only does disruption of different regions in superior parietal cortex lead to different effects on the dynamics of perceptual bistability [58], but the association between cortical structure and individual variability in switch rate also differs between regions of the parietal lobe (figures 2 and 3) [55,58].

How differences in the structure of the superior parietal cortex arise remains unclear. As naive participants were included in the studies, perceptual learning owing to repeated exposure to bistable stimuli appears unlikely. The individual variability in superior parietal cortex structure may therefore arise through development and maturation of this cortical area during childhood and adolescence.

It is not certain how differences in the structure of superior parietal cortex lead to differences in perceptual switch rate. One possibility is that variability in parietal cortex structure leads to differences in the strength of top-down signals from superior parietal cortex to early sensory cortex that reset the neuronal activity supporting the current percept. Under such an interpretation, greater grey matter density in superior parietal cortex would lead to stronger and more effective top-down signals, which would therefore trigger perceptual switches at a higher rate. Such an account remains speculative but points the way to further empirical work examining the relationship between brain states and individual traits in multistable perception. Nevertheless, it should be acknowledged that alternative accounts cannot be entirely ruled out. For example, it is conceivable that individual differences in eye movements or fixation behaviour could be systematically related to switch rate, and this requires further investigation.

Another line of related investigation has also started to produce interesting results. There are individual differences not only in switch rates but also in preferences for one percept over another [26]. In the dynamic dot quartet, two frames are shown in alternation, each containing two dots at different locations. This stimulus can produce ambiguous apparent motion. In a typical arrangement, the dots will occupy positions in the four different quadrants and appear in diagonally opposite quadrants in each of the frames. The most likely percepts are vertical or horizontal apparent motion and the related trajectories implicitly involve receptive fields either within the same hemisphere (vertical) or across the two

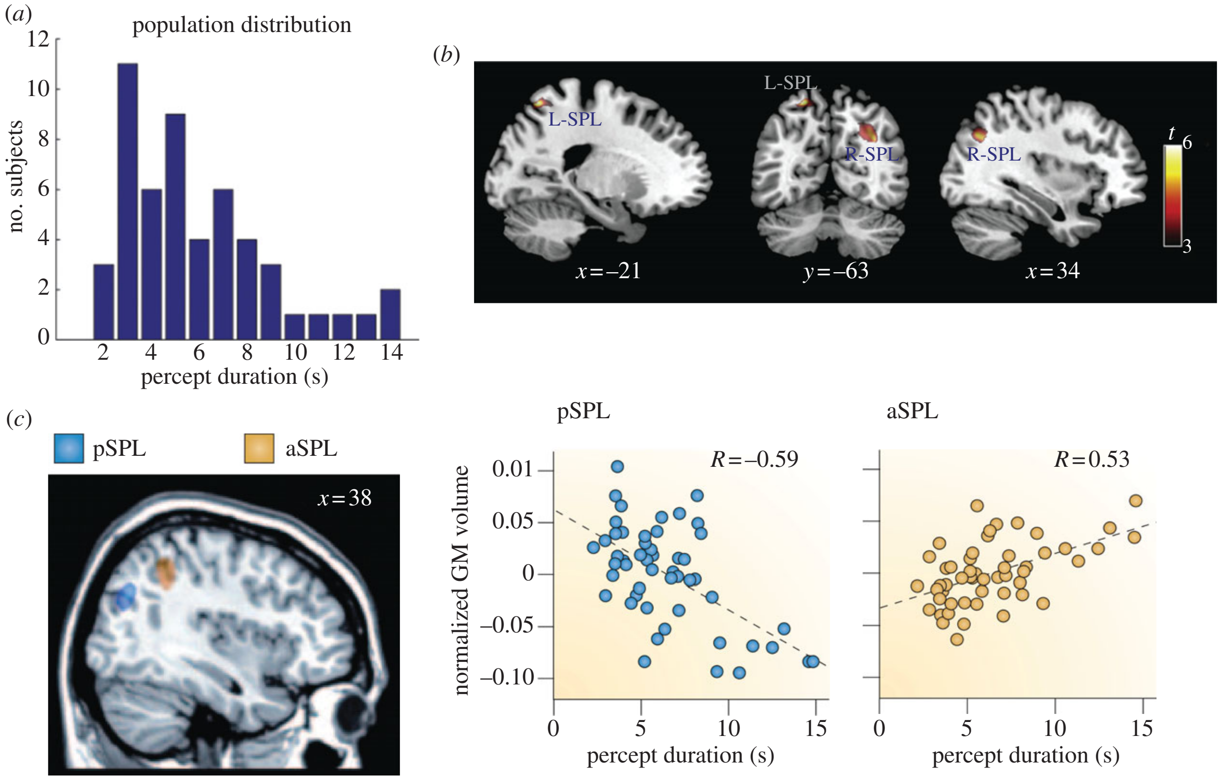

Figure 3. Individual variability in cortical structure and perceptual bistability. (*a*) A histogram of average percept duration for a bistable structure-from-motion stimulus across a large number of individual participants reveals substantial individual variability (data from Kanai *et al.* [55]). (*b*) Overlaid on sagittal, coronal and axial anatomical images of the brain are loci where grey matter density showed statistically significant correlations with inter-individual variability in bistable percept duration. Colour scale indicates *t*-value and coordinates are in standard Montreal Neurological Institute stereotactic space. Adapted from Kanai *et al.* [55]. (*c*) Further fractionation of the superior parietal lobe (SPL) [58] reveals that the more posterior anatomical location (labelled here as pSPL) depicted in the panel (*b*) is accompanied by a more anterior location (labelled here as aSPL) where grey matter density has an opposite relationship with inter-individual variability in percept duration during bistable stimulus viewing.

(horizontal). Individual differences in the likelihood of perceiving one percept rather than the other (expressed as overall time for which a given percept was perceived or as distance adjustments required for matched dwell time between percepts) have recently been related to microstructural properties of commissural fibres connecting the relevant portions of the human motion complex [84]. These findings highlight the importance of considering the connectivity of cortical structures mediating multistability and speak to the distributed nature of the underlying neural operations.

7. CONCLUSIONS

The neurophysiological findings reviewed here have led to a view of the neural architecture underlying perceptual multistability. We have established links with perceptual decision-making and discussed recent results pertaining to inter-trial and inter-subject variability in perceptual rivalry. Together with evidence from interventional approaches, such as TMS, these findings highlight the importance of higher order brain areas in determining the individual experience of multistability. Although these conclusions were derived mainly from studies in the visual modality, the anatomical substrates implied as major contributors are in themselves more supra- or polymodal than lower level areas in the sensory hierarchy. This in turn implies that their functional role may well extend to dealing with ambiguities within other modalities or across other senses. A close relationship between the neural correlates of consciousness and those of attention, working memory and decision-making appears especially intuitive if one considers that the stream of consciousness provides a powerful context for generating the appropriate inference for interpreting often noisy or ambiguous novel information received at the senses. In other words, efficient binding of physical information into coherent percepts can be supposed to rely not only on sensory integration but also on cognitive interpretation.

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