would not necessarily predict a impairment on their recognition task even if the pathology in SD did involve a human homologue of monkey PRh.

Which brings us finally to the issue of the putative functional homologies of cortical fields in human and non-human primates. Our statements pertaining to PRh in humans were accompanied by a great deal of qualification – both in the text and in our list of Outstanding questions – related to the question of homology and the location of pathology in SD. We therefore agree that the functional homology of human and monkey PRh is not well-established, and that conclusions based on homology must, for the moment, remain tentative.

To summarize, when all evidence is reviewed, there is probably more agreement than disagreement between the monkey lesion results and semantic dementia, and indeed between the position of Simons *et al*. and

our own. The hierarchical model we proposed can account for many of the effects of PRh lesions in the monkey and is also consistent with the pattern of deficits seen in SD patients. We and Simons *et al*. clearly agree that the question of functional homology of monkey and human PRh is unresolved, and is an important target for future study.

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High-frequency brain activity: perception or active memory?

Tallon-Baudry and Bertrand[1] make a strong case for the significance of non-stimulus-locked high-frequency brain activity for cognition. When coherent figures are processed, large-scale neurophysiological recordings demonstrate stronger spectral power in the 20–60 Hz range compared with control conditions where no coherent objects are being recognized. Furthermore, their most recent study[2] even indicates a role of high-frequency brain activity in short-term storage of coherent engrams, a view which can well be linked to data and theory about the role of memory networks in cortical active memory[3].

With their investigations, Tallon-Baudry and Bertrand venture substantially beyond animal studies that focussed on cortical responses to simpler stimuli like the arrangements of bars slowly moving across the visual field. These 'moving-bar studies', and other research on high-frequency activity related to physically simple stimuli such as gratings, light flashes and tone pips, have provided important insights in cortical binding mechanisms. However, these studies are at the level of elementary perceptual processes. To test a theory about object representations and other meaningful cognitive entities, it is mandatory to explore the brain's responses to the corresponding stimuli: illusionary figures versus comparable incoherent arrays, physically very similar pictures which do versus do not evoke the perception of an object, and words whose shape and meaning have been learned versus meaningless but physically almost identical letter combinations for whom no previously learned representation exists. In

demonstrating distinct modulation of high-frequency EEG and MEG responses to coherent and gestalt-like stimuli, Tallon-Baudry and Bertrand and their colleagues have made a major contribution to cognitive science.

We should, however, mention four issues raised in their article where, as to our view, data currently available call for modification and specification of their proposals.

Feature binding versus associative representations

Tallon-Baudry and Bertrand define their distinction between the binding hypothesis and a representational hypothesis in terms of bottom-up and top-down processes. Accordingly, top-down activation should apply to representations only. But one may well argue that top-down processes can also affect binding processes. It might be best to define the distinction in the following way: at the psychological level, 'feature binding' can be characterized as the linking of stimulus features *according to cognitive principles*[4]. The most important examples here are those proposed by Gestalt psychologists[5], for example proximity, similarity, continuity (e.g. the property that two bars are aligned) and common fate (e.g. stimuli that move together). Evidence that high-frequency responses reflect such gestalt principles comes from numerous EEG studies, for example those showing that bars moving in the same direction elicit stronger high-frequency responses than bars moving in opposite directions[4,6]. Tallon-Baudry *et al*.'s finding of stronger high-frequency responses to Kanizsa's triangle compared

with those to a non-triangle[7] can also be related to feature binding, because only their Kanizsa triangle included aligned lines and thus satisfied the criterion of continuity.

In contrast to the feature binding-view, one may posit that it is the individual's experience, not a general gestalt principle, which is crucial for high-frequency dynamics. Thus, high-frequency dynamics would be expected when learned associative representations are being activated. Tallon-Baudry and Bertrand's term 'object representation' is both too narrow and too wide: too narrow because stimuli other than objects, for example written and spoken words[8–10], apparently elicit the same type of phenomenon. And too wide, because objects presented in an unusual way, for example faces presented not upright but horizontally[11], can fail to elicit the high-frequency responses. Learned associative representations can be postulated for all entities that have been subject to learning. These include many objects, Tallon-Baudry and Bertrand's dalmatian dog pictures, written and spoken words, and, more generally, perceptions and actions linked by associative learning. Notice that there are no Gestalt principles or other a priori cognitive principles that would predict feature binding for coherent items such as 'USA', but not for 'SAU'. Choice of the letter combinations that are meaningful in a particular language is arbitrary. However, the frequent occurrence of certain stimulus forms during language acquisition guarantees that cortical representations are being built up for them. Thus, a learned representation would

become active if a stimulus fits the representation. An explanation based on associative learning also accounts for feature binding phenomena, because the coherent stimuli used in feature-binding-studies (e.g. bars moving together) are more common compared to stimuli used in the control conditions (bars moving in opposite directions).

In summary, we propose to reformulate the representational hypothesis as follows: activity of a neuronal representation formed by associative learning leads to induced high-frequency responses >20 Hz.

Periodic oscillations versus complex spatiotemporal patterns

The marked periodic oscillations that appear when animals are visually stimulated with coherently moving lines[4] do not warrant that the same phenomena are actually picked up in EEG and MEG recordings during higher cognitive processing. Although Lutzenberger *et al.*[12] and Müller *et al.*[13] demonstrated high-frequency dynamics in the human EEG similar to dynamics observed in the monkey, there is no conclusive evidence that these independent observations actually reflect the same phenomena. While dynamics in the high-frequency range of the EEG (>20 Hz) could be related to the modulation of rhythmic synchronizations, that is, coherent sine-like waves, it is equally well possible that they are caused by more complex spatiotemporal patterns of activity in large and distributed neuronal ensembles (see below). These spatiotemporal patterns can be periodic or aperiodic. There is certainly a range of electrophysiological phenomena that can underlie spectral dynamics.

Another important point is that stimuli activating representations of objects or words may produce physiological responses that differ in their nature from those induced by moving bars. The perceptual processes involving binding of elementary stimulus features and the activation of higher-level cognitive representations are not necessarily produced by the same brain mechanisms.

The influential neuropsychologist Donald Hebb[14] suggested that cortical representations are strongly connected cell groups in which neuronal activity can reverberate in a well-ordered fashion. Synchrony of neuronal responses is but one special case of well-ordered activity. Evidence for non-oscillatory well-timed reverberatory activity comes from analyses of neuronal activity during cognitive tasks performed by monkeys[15]. Stimulus-specific precisely timed activity patterns have been observed, for example, during delayed matching-to-sample tasks, when the animal has to keep a particular engram active in short-term memory[3,16]. It may well be that neuronal activity rapidly reverberates in the many loops of an assembly whenever a coherent visual stimulus has been perceived and is 'kept in mind'. Such multiple reverberations

are not necessarily periodic. Nevertheless, if they take place in a sufficiently large neuron population, they can cause fast changes of EEG or MEG activity. After filtering of the EEG/MEG signal, this change would emerge primarily as high frequencies dynamics. In essence, dynamics in high frequencies and changes of correlation coefficients obtained from large-scale recordings might be related to rapid complex spatiotemporal patterns rather than to oscillations in a narrow frequency band.

Are high-frequency cortical responses too late for perception?

There are early oscillatory phenomena reflecting elementary perceptual processes (latency <100 ms after stimulus onset). These include stimulus-locked (evoked) activity in the auditory system closely related to the so-called middle-latency components of the evoked potential[17], and oscillations in the retina and at later stages of the visual path that correspond to changes of physical stimulus features[18]. Furthermore, there are early high-frequency responses related to attention mechanisms[19]. Induced high-frequency activity, possibly reflecting the presence of learned associative representations activated by incoming stimuli, however, has been found at relatively late time intervals, usually >250 ms after onset of the stimuli[20].

Tallon-Baudry and Bertrand state that induced high-frequency brain activity reflects perceptual *and* memory processes. We fully agree with the latter view but do not share the former. Stimulus-specific changes in evoked potentials and other physiological correlates of perceptual processes have been reported to occur early, significantly earlier than the corresponding differences seen in high-frequency responses. Differences in evoked potentials reflecting the distinction of physically similar but cognitively distinct stimuli (words versus nonwords; words of different types) occur as early as 100–200 ms post stimulus onset[21,22]. In contrast, differences in high-frequency responses to coherent words and incoherent pseudowords emerge around 300 ms (Ref. 8), almost exactly at the same time when Tallon-Baudry and Bertrand find spectral dynamics to coherent/incoherent figures[7]. The same point can be made for other kinds of stimuli as well. Electrophysiological processes corresponding to the access to cognitive representations occur before induced high-frequency dynamics. The initial access to a cortical representation might therefore be reflected in evoked potentials, whereas induced high-frequency responses might mirror processes related to active memory in reverberating cell assemblies following their stimulus-triggered initial activation.

Ruling out models of cortical arousal and attention

If a stimulus activates a piece of cortex, many things can happen there. A

stimulus-specific representation might become active, but a more global increase of activity and of neuronal crosstalk is equally likely. Peter Milner[23] proposed that sensory stimulation leads to non-specific activity increase in sensory cortices accompanied by oscillatory phenomena. At the cognitive level, this general activity increase could be related to an increase in arousal or attention to a particular modality, or even to one part of the visual field. A similar proposal has been made by Kirschfeld and colleagues[24]. Focussing of attention may correspond to an increase of the gain of a feedback regulation mechanism controlling cortical excitation. Such gain increase makes oscillations more likely[24]. Sheer had suggested earlier that focussed arousal is reflected in 40-Hz EEG activity[25]. Results summarized in Tallon-Baudry and Bertrand's review[1] can largely be explained by a focussed arousal or attention model. Enhanced high-frequency activity to Kanizsa's triangle[7] was maximal at occipital sites, thus nicely fitting Milner's model[23], while the more anterior maximum of high-frequency activity during the memory interval[2] would not confirm Milner's view, but could be accounted for in Kirschfeldt's framework[24]: areas more distant from the primary cortices might take more time to adjust their gains.

Is there empirical evidence that dynamics of high-frequency cortical activity actually relates to cognitive representations, rather than to arousal or attention? One possibility is to use stimuli whose cortical representations might be distributed over different cortical areas.

Consider visual stimuli that have been linked, by associative learning, to somatosensory perceptions in the left versus right hand. High-frequency dynamics and synchrony in visual and the respective somatosensory areas would be expected if these stimuli are being processed. Recently, Miltner *et al.*[26] reported that increased coherence of EEG signals can reflect associative learning. After visual stimuli had been co-presented with somatosensory stimulation of the left or right hand, coherence increased between electrodes above visual areas and somatosensory areas contralateral to the hand stimulated. In this case, the associative links were reflected in a stronger correlation of high-frequency signals recorded over the cortical areas likely involved in association storage. This experimental outcome cannot be explained by an attention model, because correlation of activity at distant cortical sites were systematically related to learned contingencies.

In complementary studies on language processes, we used words reminding experimental subjects of actions or of visual stimuli[27]. Perception of these words, flashed on a computer screen, changed high-frequency EEG responses recorded over visual and motor areas. While over visual areas,

stronger high-frequency activity was seen when visually-related words were processed, action words elicited stronger activity over motor and premotor areas. Similar topographic specificity was seen in evoked potentials, but these occurred before high-frequency dynamics. Semantic associations of the words were reflected in topographies of both evoked potentials and high-frequency responses.

In essence, physically similar stimuli that primarily differ in their learned associations elicited high-frequency dynamics and correlations at different recording sites, and likely in different cortical areas. These results can not be explained by a global attentional mechanism building upon stimulus-evoked neuronal excitation. How should such an attention mechanism direct neuronal activity to different areas, based on cognitive properties of the stimuli? A theory of associative learning is necessary to explain that topographically specific high-frequency dynamics are a function of cognitive properties of incoming stimuli. Based on associative learning leading to the formation of distributed cortical-cell assemblies that include neurons in distant areas and produce reverberatory activity, it is possible to explain recent findings about induced high-frequency dynamics picked up in the EEG and MEG (Ref. 20).

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Reply

Are representations necessarily learned?

We proposed that high-frequency gamma activity could reflect the activation of object representations, an 'object' being any coherent entity (including words)[1]. This activation could result from bottom-up mechanisms as well as higher-level cognitive processes. Pulvermüller and his colleagues[2] reformulate this proposal thus: high-frequency activity would reflect the activation of learned associative representations, based on either individual's experience or Gestalt principles. This implies that any representation would necessarily be learned (during development as for language, or within an experimental session as for the Dalmatian dog image). In our view, a representation of a coherent entity could also emerge from the basic neural connectivity (causing stimuli to 'pop out', like an illusory triangle), without any learning requisite. Nevertheless, both views agree upon the existence of a relationship between gamma activity and coherent representation.

Periodic oscillations versus complex spatiotemporal patterns

As proposed by the authors, high-frequency EEG spectral variations could be related either to oscillatory spike synchronization or to complex reverberating spatiotemporal patterns of neural activity. To address this issue, recordings at different levels (from spike discharge to electro-corticogram) should be performed, and analysed with comparable timescales to allow the detection of high-frequency events as transient as those observed in human EEG.

Global cortical arousal and attention

Pulvermüller *et al.* have nicely shown that the topography of induced gamma depends on the semantic properties of the stimulus[3]: therefore, high-frequency activity does not originate solely from global cortical arousal. Likewise, selective attention cannot be considered as underlying gamma oscillations either. Indeed, during anesthesia, an induced gamma response, with the same time-course as in humans, has been observed in the electro-corticogram over the rat auditory cortex[4]. Gamma oscillations thus do not correspond to selective attention itself, but still could be modulated by attentional processes as many other stimulus-evoked components.

Induced gamma can be the earliest expression of perceptual differences

The authors claim that gamma activity cannot reflect perceptual processes because it appears later than stimulus-specific changes in evoked potentials. Indeed, in their noun–verb experiment[5], they found the earliest effect in the evoked response. Nevertheless, this contradicts other experimental findings: in