[1] and Carvalho *et al.* [15] propose what might be called 'confined constant biochemistry' models, in which the microscopic behaviors of proteins remain the same throughout early development, but the organization of these proteins adjusts to the changing size of the cell. Support for this class of model comes from perturbation experiments: the same relationship between cell size and spindle behavior [1] or cortical contraction dynamics [15] holds when embryo size is artificially altered, suggesting that it is really cell size that is important, not development stage. Hara and Kimura [1] account for their data by a model in which spindle elongation is caused by cortical forces pulling on astral spindle microtubules, with some forces being proportional to the square of the microtubule's length, which they claim is an approximate way to represent the effect of a limited number of cortical force generators [16], and some forces being length independent. The authors use computer simulations to argue that this combination of forces naturally reproduces the cell size dependence of spindle elongation, and they use RNAi experiments to suggest a molecular basis for the length-dependent forces.

However, it is still too early to rule out an alternative class of model for how the division machinery changes over the course of embryogenesis: 'developmental regulation' models, in which the activities of cytoskeletal proteins are modified in different cells through post-translational modifications, degradation, selective division, or some other mechanism. After all, at every stage of *C. elegans* development there are large differences between cells which have the same size [17,18], and even though artificially changing cell size can produce corresponding changes in cytoskeletal behaviors, this does not prove that those changes in the cytoskeleton are normally caused by changes in cell size. In addition to the mechanistic question of *how* cell division is modified at different stages of development, it will be equally crucial to ask *why* these changes occur from an evolutionary perspective. Are the spindle and the contractile ring perfectly optimized to function differently in different cell types, and if so, why are these particular scaling relationships optimal? Or, is the observed variation caused by non-adaptive processes [19]? Clearly much work remains, but these recent studies show that understanding the differences in how cells divide is just as interesting and important as understanding the similarities.

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Perceptual Decisions: From Sensory Signals to Behavior

Recent non-invasive studies in humans provide new insights into the timing of perceptual decision making and show that integrated sensory evidence is represented in motor areas well before a behavioral response.

Joachim Gross[1] and Markus Ploner[2]

Imagine you are driving down a road in the evening twilight looking for a certain house number. The darker it gets the longer it takes you to identify the numbers. The correct perceptual decision is relevant for selecting the appropriate behavioral response. What is the time course of processes in the brain leading to the decision? A study reported by Donner *et al.* [1] published in this issue of *Current Biology* provides new insights into the timing of perceptual decision making. Specifically, they demonstrate that the temporally integrated sensory information affects activity in motor areas well before movement onset.

The term 'perceptual decision making' refers to the process of transforming sensory signals into a percept and an appropriate behavioral response. Most of our knowledge about the mechanisms underlying this transformation and their neural substrates stems from seminal studies in monkeys carried out in the somatosensory domain by Romo and coworkers, and in the

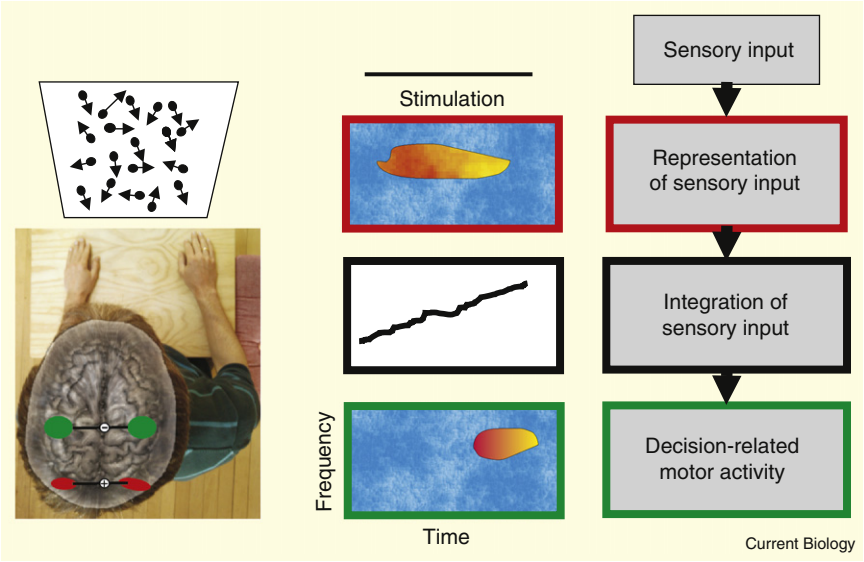

Figure 1. Neural activity related to perceptual decision making.

Left panel: randomly moving dots were displayed on a screen for two seconds. Participants were instructed to decide on the presence or absence of coherently moving dots and respond with left or right hand, respectively. Middle panel: schematic representation of neural activity time-locked to onset of visual stimulation. Motion coherence is represented in gamma activity in bilateral brain areas MT (red box and red dots in left panel). Task-relevant sensory information is temporally integrated (black box). Temporally integrated gamma activity averaged across bilateral MT areas correlates with lateralized gamma activity in primary motor cortex (green box and green dots in left panel). Right panel: sequence of processes in the perceptual decision task corresponding to the middle panel.

visual system by Newsome, Shadlen and coworkers (for reviews see [2–4]). These studies showed that perceptual decisions are based on sensory evidence that is represented by neurons in lower-level sensory brain areas. This sensory evidence is transmitted to higher level and more decision-related brain areas. In some of these brain areas, a gradual increase in neuronal activity indicates that the sensory evidence is integrated over time. The rate of accumulation of neural activity in these brain areas relates to the strength of the sensory evidence and the difficulty of the decision [3,4]. Intriguingly, there is a large overlap between these brain areas and areas that are involved in the preparation and execution of movements. These observations in monkeys lead to some interesting questions: Do these principles hold true in humans? And if so, how does the transformation of sensory evidence to motor output evolve over time?

Only very recently has the extensive research in monkeys been complemented with MEG/EEG studies addressing the questions non-invasively in humans. Philiastides *et al.* [5] performed single-trial EEG analysis to study the time course of processes leading to categorical decisions. They presented noisy images of faces and cars that differed with respect to the level of noise and, thus, the amount of sensory evidence and decision difficulty. They instructed the participants to perform a simple categorization task while EEG signals were recorded. Single-trial analysis revealed three components with different relations to sensory evidence and motor behavior. The first EEG component (170 ms after stimulus onset) seems to reflect early sensory processing (for example, see [6] for a detailed analysis of this component). The second component ($\sim$220 ms) is likely to represent a top-down influence of attention. The third component ($\geq$300 ms) is strongly related to the decision process as its amplitude predicts decision accuracy and its latency predicts decision difficulty [7]. These studies, thus, provided first insights into the dynamics of perceptual decision processes in the human brain.

The study by Donner *et al.* [1] opens a new window to the understanding of perceptual decision processes. The authors presented moving dots for 2 seconds in a large number of trials while recording MEG signals during two experimental conditions (Figure 1, left panel). In one condition, a fraction of dots was moving coherently either up or down. In the other condition, all dots were moving randomly. Participants were instructed to report, after a delay, on the presence or absence of coherently moving dots with button presses using the left or right index finger, respectively. Importantly, to successfully perform the task, information has to be integrated over time. The paradigm is, thus, well suited to study the temporal evolution of perceptual decisions.

Donner *et al.* [1] focused the analysis on lower-level sensory brain areas and on brain areas related to movement preparation and execution as the final output stages of the decision process. They particularly relied on results from a previous study by Siegel *et al.* [8], who demonstrated in a similar paradigm that sensory evidence is represented by high frequency neuronal oscillations in the gamma band (60–100 Hz) in brain area MT. This is consistent with a recent MEG study in the somatosensory domain [9]. In this study, the authors reported high-frequency gamma oscillations and low-frequency neuronal activity (corresponding to the evoked component) at the same latency in primary somatosensory cortex. Both components were closely related to the objective stimulus intensity but the gamma oscillations were particularly related to the subjective perception of the stimulus. Thus, evoked responses and gamma responses both represent sensory evidence but the representation by neuronal gamma oscillations may be particularly relevant for the perceptual decision process. In line with this evidence, Donner *et al.* [1] used single-trial estimates of gamma oscillations in MT as representations of sensory evidence (Figure 1, middle panel).

Next, Donner *et al.* [1] identified components in the MEG signal that were related to the behavioral response in their task. Because both choices — target present or target absent — were reported with different hands, the perceptual decision can be treated as a movement selection problem and response related components should be lateralized. The authors identified two frequency bands with lateralized

modulation: High frequency gamma activity was stronger in primary motor cortex contra-lateral to the responding hand (compared to ipsi-lateral motor cortex), whereas low frequency (<40 Hz) activity showed the opposite pattern. These results are consistent with previous studies that show movement related increases in high frequency bands and suppressions in low frequency bands [10–12].

Having identified these two 'markers', Donner *et al.* [1] could track the evolution of these markers during presentation of the moving dots. Interestingly, this novel approach revealed that the amplitude of both components during stimulus presentation — well before movement onset — predicted subsequent responses. The prediction accuracy of the markers increased towards the end of the stimulus presentation period. These findings indicate that the temporal dynamics of the decision process are reflected in motor areas.

To elucidate the mechanisms of the decision process in more detail, Donner *et al.* [1] analysed the two identified markers at the back-end stage of the decision process in more detail. They found that even in trials where participants did not perceive coherent motion predictive activity in the motor areas can be observed as early as in trials where participants did perceive coherently moving dots. This result argues against a simple decision process whereby subjects decide that they perceive the motion if the sensory evidence for the target surpasses a certain threshold. Finally, the authors related their gamma decision-marker at the output stage of the decision process to neuronal gamma oscillations at the sensory level — in the motion-sensitive area MT. Analysing single trials, they observed that the temporal integral of gamma-activity in MT was significantly correlated with the strength of lateralized gamma activity in motor cortex throughout the stimulation period (Figure 1, middle column). This finding provides compelling evidence (albeit only in four participants) for the temporal integration model outlined above in humans (Figure 1, right panel).

Taken together, these recent studies open a new window to the understanding of simple perceptual decision processes. However, several questions remain to be answered: To what extent are motor areas involved in decisions where no overt motor response is required? Where and how is the sensory evidence provided by lower-level brain areas integrated and transformed to a motor plan? To answer these questions future studies will likely combine sophisticated analysis techniques such as distributed source localization, spectral analysis, functional connectivity analysis, single-trial and machine learning analysis to optimally exploit the high temporal resolution of MEG/EEG.

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Meiosis: Making a Synaptonemal Complex Just Got Easier

In preparation for meiosis, chromosomes go through several massive structural transitions, including chromosome fragmentation, pairing and synapsis. A checkpoint factor and a SUMO ligase collaborate to keep things in order.

Andreas Hochwagen

Meiotic prophase is a busy period for chromosomes. Within a comparatively short time, chromosomes become duplicated, undergo controlled fragmentation and reshuffling during meiotic recombination, and finally end up paired and synapsed along their entire lengths by the synaptonemal complex [1–3]. Not surprisingly, the proper timing and coordination of these events is key to avoiding chromosome abnormalities and meiotic defects.

One particularly interesting problem is the formation of the synaptonemal complex. A favorite of cell biologists for many decades, the synaptonemal complex is an elaborate protein superstructure that apposes and links pairs of homologous chromosomes. By electron microscopy, the synaptonemal complex appears like a train track that assembles in a zipper-like fashion to keep chromosomes arranged at a set distance from each other (Figure 1) [1,3].