

Buildup of Choice-Predictive Activity in Human Motor Cortex during Perceptual Decision Making

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Summary

Simple perceptual decisions are ideally suited for studying the sensorimotor transformations underlying flexible behavior [1, 2]. During perceptual detection, a noisy sensory signal is converted into a behavioral report of the presence or absence of a perceptual experience [3]. Here, we used magnetoencephalography (MEG) to link the dynamics of neural population activity in human motor cortex to perceptual choices in a “yes/no” visual motion detection task. We found that (1) motor response-selective MEG activity in the “gamma” (64–100 Hz) and “beta” (12–36 Hz) frequency ranges predicted subjects’ choices several seconds before their overt manual response; (2) this choice-predictive activity built up gradually during stimulus viewing toward both “yes” and “no” choices; and (3) the choice-predictive activity in motor cortex reflected the temporal integral of gamma-band activity in motion-sensitive area MT during stimulus viewing. Because gamma-band activity in MT reflects visual motion strength [4], these findings suggest that, during motion detection, motor plans for both “yes” and “no” choices result from continuously accumulating sensory evidence. We conclude that frequency-specific neural population activity at the cortical output stage of sensorimotor pathways provides a window into the mechanisms underlying perceptual decisions.

Results

During flexible sensory-guided behavior, our brain maps interpretations of sensory information onto complex courses of action. A simple example is perceptual detection, in which a noisy sensory signal is converted into an arbitrary behavioral response (e.g., a verbal report or button press) indicating our sensory experience, or the lack thereof [3]. Although this is the most elementary perceptual task, our understanding of the neural mechanisms mediating this conversion is still incomplete [1, 5]. Here, we used magnetoencephalography

(MEG) to study the neural basis of perceptual choice in a visual motion detection task. Four human subjects searched for weakly coherent motion as a target signal, which was embedded in dynamic noise and presented on half the trials (Figure 1). If present, the target signal persisted throughout the stimulus interval, eliminating temporal uncertainty about its occurrence. Thus, subjects could benefit from integrating the sensory evidence for coherent motion across the stimulus interval [1, 6, 7]. After a delay, which dissociated the evolving motor plan from its execution, subjects reported “yes” if they had seen the target signal and “no” otherwise. The combinations of stimulus and perceptual report in this simple forced-choice procedure yielded four possible outcomes (Figure 1B): correct rejections, false alarms, misses, and hits [3].

Effector-Selective Activity during Behavioral Response

Cortical population activity exhibits rhythmic temporal structure [8]. Rhythmic activity carries information about sensory stimuli [4, 9], cognitive processes [10–14], or motor acts [15–21]. Specifically, limb movements are accompanied by suppression of low-frequency (<40 Hz) activity and enhancement of high-frequency (>40 Hz) activity, both typically stronger in the motor cortex contralateral than ipsilateral to the movement [15–21]. We exploited this contralateral bias of motor activity by associating subjects’ “yes” and “no” choices with button presses executed by different hands. Figures 2A and 2B show time-frequency representations of the MEG activity recorded over left and right motor cortices during the course of the trial. The contralateral bias was evident in a stronger enhancement of MEG power in the 50–100 Hz range (high “gamma band”) and stronger power suppression below 40 Hz contralateral to the button press. Thus, the MEG lateralization shown in Figure 2B provided a measure of effector-selective (left versus right hand) neural activity. In the gamma band, the effector-selective activity increased transiently at about 500 ms before and again around the button press. Below 40 Hz, activity exhibited a strong sustained, but no transient, effector-selective decrease, which also emerged long before button press. Modulations in this lower frequency range consisted of an “alpha band” (8–12 Hz) and a stronger “beta band” (12–36 Hz) component (see Figure S1 available online). Source reconstruction by means of adaptive spatial filtering (see [22] and Supplemental Experimental Procedures) showed that effector-selective activity before button press in the gamma and beta bands was expressed in motor cortex (Figure 2C). It peaked in the central sulcus, in the hand representation of primary motor cortex (M1), extending into the anterior part of dorsal premotor cortex (PMd). Thus, in accord with previous studies [16–18, 20], neural activity in human motor cortex exhibited robust lateralized effector selectivity of opposite polarity in beta and gamma frequency bands.

Buildup of Choice-Predictive Activity during Stimulus Viewing

A notable aspect of the effector-selective activity was that it gradually built up already during stimulus viewing (Figure 2B; Figure 3). To study this in more detail, we estimated single-trial time courses of band-limited activity in the M1 hand area and

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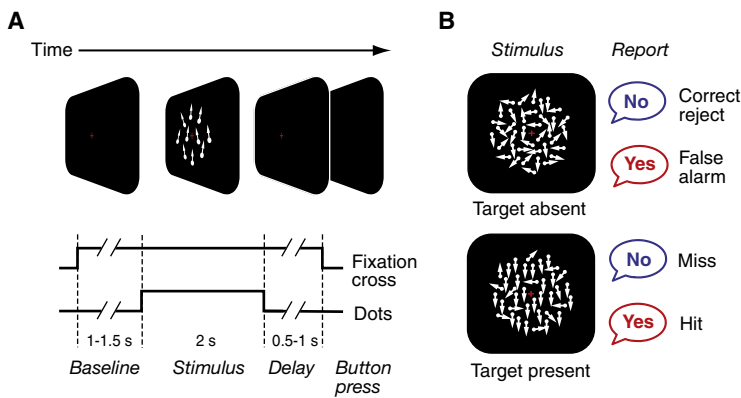


Figure 1. Visual Motion Detection Task

(A) Temporal sequence of trial intervals. Each trial consisted of fixation baseline, stimulus, and delay intervals, followed by a button press (left/right hand) indicating the subject's choice. (B) Trial categories according to signal detection theory. On "target absent" trials, the dynamic random dot stimulus consisted of pure noise (0% coherence). On "target present" trials (50% of the trials), the stimulus contained a weak coherent motion signal near detection threshold. If present, the target signal persisted throughout the stimulus interval. Subjects had to decide whether or not the target signal was present ("yes/no").

PMd, again via adaptive spatial filtering (Supplemental Experimental Procedures). We quantified how well an ideal observer could predict subjects' upcoming choices based on the lateralization of M1 and PMd activity during stimulus viewing (Supplemental Experimental Procedures). The resulting index ("choice probability") ranged between 0 and 1, with 0.5 being chance-level prediction. Significant upward deviations from 0.5 indicated that "yes" choices were preceded by larger lateralization toward the hemisphere contralateral to the hand indicating "yes," and vice versa for significant downward deviations.

Significant choice-predictive activity in both frequency bands emerged already during stimulus viewing (Figure 3A; $p < 0.01$ by two-sided permutation test), while subjects were forming their decision. As during movement execution, this activity also had opposite polarity in both bands during stimulus viewing: gamma-band activity showed more lateralization toward the hemisphere contralateral to the chosen effector (choice probability > 0.5), and vice versa for beta-band activity (choice probability < 0.5). These effects were specific to regions with a known contralateral motor bias; they were not found in a control region within dorsolateral prefrontal cortex (Figure S2). In the beta band, the choice probability in motor

cortex became significant in the first half of the stimulus interval and then increased toward the time of movement execution, with a similar time course before correct and incorrect choices (Figure 3A, upper panels). By contrast, in the gamma band, the choice probability reached significance earlier before incorrect than before correct choices (Figure 3A, lower panels), perhaps reflecting premature guesses on error trials.

The separate time courses of lateralization before "yes" choices (hits and false alarms) and "no" choices (misses and correct rejections) suggest similar processes underlying both kinds of choices (Figure 3B): the choice-predictive activity emerged similarly early during stimulus viewing before both kinds of choices. The early emergence of "no" predictive activity contradicts the notion that subjects chose "yes" if the evidence for target presence surpassed a certain threshold at the end of stimulus presentation and "no" otherwise [3, 5]. The predictive activity should then have evolved toward the "no" option only after stimulus viewing was completed and had not yielded a "yes" choice. Instead, the results are consistent with the existence of two, perhaps competing, neuronal groups involved in planning "no" and "yes" reports during stimulus evaluation [5].

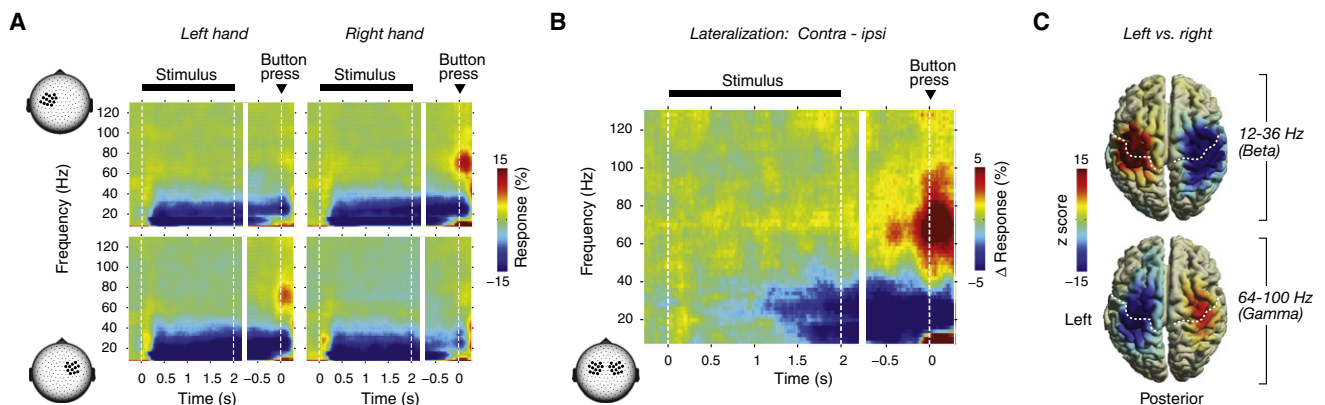


Figure 2. Effector-Selective Neural Activity

(A) Time-frequency representation of group average activity of two symmetric groups of MEG sensors overlying left (top) and right (bottom) motor cortices. The sensor groups are marked on schematic scalp projections. Time courses are aligned to stimulus onset (leftmost vertical dashed line) and to button press (rightmost vertical dashed line) and are shown separately for left-hand and right-hand button presses.

(B) Time-frequency representation of the MEG lateralization, i.e., the difference between the two sensor groups contralateral and ipsilateral to the button press, averaged across both kinds of button presses.

(C) Group average statistical z score maps of reconstructed effector-selective cortical activity (left- versus right-hand button press) during the 0.5 s before button press in the gamma and beta frequency ranges. The statistical maps are overlaid on a cortical surface representation of the MNI template brain. Opacity scales linearly with z score. The dashed lines indicate the central sulcus.

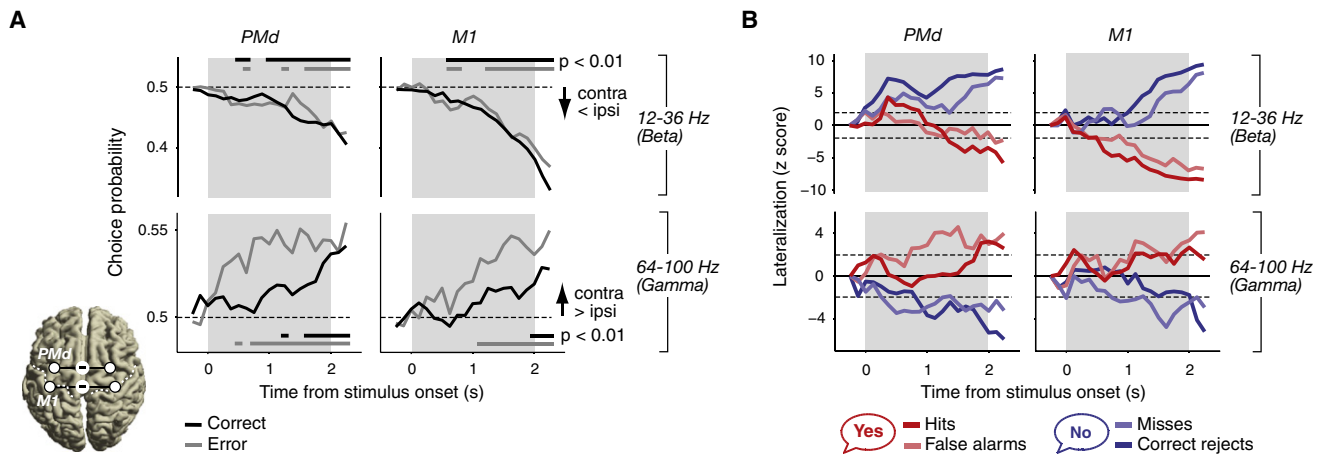


Figure 3. Buildup of Choice-Predictive Neural Activity during Stimulus Viewing

(A) Time courses of choice-predictive activity in PMd and M1. The choice probability quantifies the predictability of “yes” versus “no” choices from each region’s response lateralization (contralateral-ipsilateral to “yes” button). Time courses are aligned to stimulus onset and are shown separately for gamma and beta bands and for correct (black) and incorrect (gray) choices. The dashed line corresponds to chance level (choice probability = 0.5). The black and gray bars indicate significant deviations from chance level ($p < 0.01$ by two-sided permutation test). The gray shading indicates the stimulus interval. Lower left: anatomical locations of cortical regions of interest are displayed on a cortical surface reconstruction. The following abbreviations are used: PMd, anterior portion of dorsal premotor cortex; M1, hand area of primary motor cortex (see [Supplemental Experimental Procedures](#) for definition of these regions). The dashed lines indicate the central sulcus.

(B) Time courses of choice-predictive activity lateralization (contralateral-ipsilateral to “yes” button), expressed as z scores in PMd and M1 separately for the four trial categories. Time courses are aligned to stimulus onset and are shown separately for gamma and beta bands. The dashed lines indicate significance levels ($p = 0.05$ by two-sided t test).

Choice-Predictive Activity Reflects Integrated Sensory Evidence

A large body of evidence suggests that the decision variable underlying perceptual choices [3] results from the temporal accumulation in association cortex of evidence provided by sensory cortex [1, 6, 7]. If the choice-predictive activity in motor cortex was driven by this decision variable, it should have reflected the temporal integral of activity in the task-relevant sensory cortical area. The sensory evidence for coherent motion was (at least partly) provided by visual cortical area MT [1], whose gamma-band activity reflects motion coherence [4]. Thus, we hypothesized that the trial-to-trial fluctuations [23] of choice-predictive activity were predicted by the trial-to-trial fluctuations of the temporal integral of gamma-band activity in MT. Indeed, the integral of MT gamma-band activity across the stimulus interval exhibited a highly significant correlation

with the choice-predictive M1 lateralization at the end of this interval. This was true for the lateralization in both beta and gamma bands, again with opposite sign (Figure 4A), reflecting their opposite polarity of effector-selective activity (Figure 2; Figure 3). Thus, the level of choice-predictive activity in motor cortex at the end of stimulus viewing reflected the integrated sensory evidence provided by visual area MT.

This coupling between choice-predictive motor activity and the MT integral not only emerged at the end of the decision process but also was expressed throughout the course of stimulus viewing. Figure 4B shows the correlation between the gamma-band lateralization in M1 at each time point and the MT integral up to that time point, separately for trials ending with “yes” and “no” choices (Supplemental Experimental Procedures). The correlation was significant throughout the stimulus viewing until into the delay, regardless of

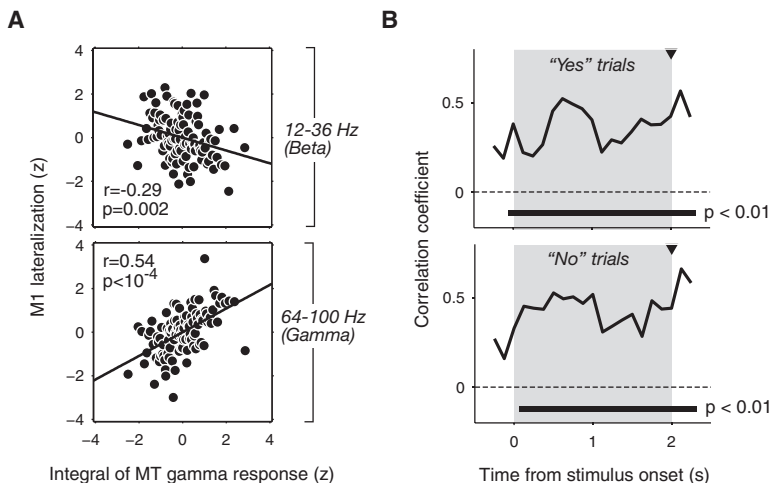


Figure 4. Choice-Predictive Neural Activity Reflects Integrated Sensory Evidence

(A) Linear regression between the temporal integral of gamma-band (64–100 Hz) activity in MT across the stimulus interval and the activity lateralization in M1 (contralateral-ipsilateral to “yes” button) in beta and gamma bands at the end of the stimulus interval. Responses were binned (100 trials per bin) by MT response integral and z transformed. The correlation coefficient, but not its significance, decreased with the size of binning (Supplemental Experimental Procedures).

(B) Correlation between the gamma-band lateralization in M1 (contralateral-ipsilateral to “yes” button) at each point in time and the temporal integral of gamma-band activity in MT from 0.25 s before stimulus onset up to that point in time. The correlation is evaluated throughout the course of the trial, separately for trials ending with “yes” and “no” choices (Supplemental Experimental Procedures). Responses were binned by MT response integral before correlation (100 trials per bin). The gray shading indicates the stimulus interval. The black arrowhead indicates the time point for the analysis shown in (A).

the final behavioral choice. Thus, the larger the integrated MT activity during stimulus viewing on each trial, the larger the choice-predictive lateralization toward the “yes” option; equivalently, the smaller the MT integral, the larger the lateralization toward “no.” This suggests that the motor buildup is continuously driven by accumulation of MT activity throughout the evaluation of the sensory evidence. In sum, our findings provide novel evidence for the temporal integration model of perceptual decision making by directly linking fluctuations of neural activity measured simultaneously at the sensory and motor stages.

Discussion

The observation that persistent MEG activity in the beta and gamma bands predicted subjects’ upcoming behavioral choices several seconds before movement execution is consistent with evidence from electrophysiological studies of motor preparation [15–21]. Beta-band suppression contralateral to the movement likely reflects a suppression of intrinsic rhythms by motor cortex activation [21]. Contralateral enhancement in the gamma band might reflect local neural oscillations on a faster time scale [16, 24]. In particular, the choice-predictive gamma-band activity during stimulus viewing and delay in the present task might reflect locally recurrent network interactions that help maintain the evolving motor plan [25].

Perceptual choices can also be predicted from functional magnetic resonance imaging (fMRI) responses in humans [26]. However, the limited temporal resolution of fMRI hampers a detailed characterization of the dynamics of decision making. When decision making is slow, choice-predictive activity of single neurons in motor cortical areas of the macaque monkey exhibits a buildup similar to the MEG activity in the present detection task, perhaps resulting from temporal integration of the sensory evidence [1, 27, 28]. Our finding that the motor buildup directly reflects the integral of the evidence provided by MT strongly supports this idea. Thus, as in monkeys [28], the temporal evolution of choice-predictive activity in human motor cortical areas provides a window into the dynamics of decision making.

One limitation of the present study is that only areas with a macroscopic contralateral motor bias were apt to signal subjects’ choices. Because this bias decreases upstream from M1 [29, 30], choice-predictive activity might have also been evident in other regions if assessed at a mesoscopic or single-neuron level. In other words, the present results do not show that the temporal integration of sensory evidence takes place within PMd or M1. Rather, they suggest that motor preparation in these areas is continuously driven by the outcome of this integration process.

Several studies in monkeys and humans suggest that the integration process takes place in parietal and prefrontal association cortex, that is, between MT and motor cortex [1, 2, 14, 26, 31–33]. Evidence from auditory discrimination suggests that gamma-band activity in prefrontal cortex might reflect this integration [33]. We have previously established that low-frequency (12–24 Hz) activity in parietal and prefrontal cortex predicts the accuracy of upcoming choices during the motion-detection task [14]. We speculate that the sensory evidence provided by MT might be integrated over time by long-range network reverberations in the 12–24 Hz range [34, 35] among visual, frontoparietal, and motor cortices and thereby transformed into motor plans.

In conclusion, the present results suggest that the motor output stage of simple sensorimotor tasks provides a window into the dynamics of the underlying decision process. Together with previous studies [2, 26, 31–33, 36], this links human neuroimaging studies of perceptual decision making to modeling and monkey neurophysiology. Specifically, by directly correlating neural activity between the sensory and motor stages of a simple decision process, our results suggest that the evidence delivered by sensory cortex (area MT) is integrated toward motor plans for both “yes” and “no” choices, expressed in frequency-specific population activity of motor cortex.

Experimental Procedures

All procedures are described in detail in [Supplemental Experimental Procedures](#); here, we provide a brief summary. The study was based on a reanalysis of data from a previous study [14]. The study was conducted with four healthy male subjects after informed consent and was approved by the local ethics committee. The dynamic random dot stimuli were presented in the center of the screen. “Target absent” stimuli consisted only of incoherently moving dots. “Target present” stimuli contained a small fraction of coherently moving dots, which was individually adjusted to the 71% correct detection threshold. Subjects reported their “yes/no” decision by pressing a button with their left or right index finger after the delay interval. The mapping between “yes/no” choice and response hand was counterbalanced across subjects. Each subject completed several thousand (≥ 3200) trials, distributed across multiple recording sessions. Despite the large number of trials, the small number of subjects might in principle have limited the sensitivity of the present study. While subjects performed this task, MEG was recorded continuously at a sampling rate of 1200 Hz with a 151-channel whole-head system (Omega 2000, CTF Systems). Electro-oculography and electrocardiography were recorded simultaneously for offline artifact rejection. Data were analyzed with the “FieldTrip” toolbox (<http://www.ru.nl/fcdonders/fieldtrip>) and custom-made software.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and two figures and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01543-7](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01543-7).

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