Analog, graded choices in the human brain

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Analog, graded choices in the human brain

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Decision-makers objectively commit to a definitive choice, yet at the subjective level, human decisions appear to be associated with a degree of certainty. Whether decisions are definitive—concluding in all-or-none choices, or whether the underlying representations are graded, has been unclear. To address this issue, we recorded neural signals directly from the brain while naive human subjects made perceptual decisions. The recordings revealed that each individual’s decisions formed within broadband gamma activity. The gamma activity was graded by decision evidence. Crucially, this analog, grading effect prevailed beyond the time of choice, instead of assuming a switch-like command. The effect was strongest in parietal and premotor cortex, brain regions traditionally implicated in decision-making. These data provide neural evidence for a graded nature of the decision process.

Many cognitive processes, including decision-making and memory recall, involve deliberation over a brief period of time. Psychology, neuroscience, and neuroeconomics have debated how the process of deliberation is implemented at the neural level and how the process concludes. It has frequently been suggested\textsuperscript{1–6} that choices are made in an all-or-none manner, when a neural signal that represents a forming decision reaches a defined bound (Fig. 1a). Nonetheless, the generality of these conclusions has been limited by the use of animals that are highly trained on a specific task. In nature, most decisions are made flexibly and in new scenarios, without involving extensive training. In these more general situations, our decisions and choices appear to be associated with a degree of certainty\textsuperscript{7,8}. Such introspective evaluations suggest a graded instead of an all-or-none process (Fig. 1b). This debate\textsuperscript{1–6,9–24} has been difficult to resolve at the general level because there has been no study that has i) recorded neural activity at high spatiotemporal coverage directly from the brain, and ii) in human subjects who make decisions without extensive training.
Figure 1. Nature of developing decisions. **a**, One class of models posits that choices are made when brain activity reaches a fixed bound (top), which results in defined, switch-like choices. The defined commands are passed on downstream effectors (bottom). **b**, An alternative view is that the choice process is generally graded. The LO (low), ME (medium), HI (high) levels indicate the amount of evidence for a choice.

**Results**

**Decision tasks and behavior.** To address this lingering issue, we recorded the neural dynamics of deliberation using intracranial electrodes (Fig. S1) while eight naive human subjects assessed temporally-defined quanta of decision evidence (Fig. 2). The evidence quanta constituted Poisson-distributed click sounds delivered into the right and left ears. The subjects communicated their choices using movements of two distinct choice kinds (a saccade or a button press) in two task contexts (congruent or reversed). In the congruent task context (Fig. 2b), the subject made a saccade to a left target (pressed a button with the right hand) if they heard more click sounds delivered into the left (right) ear. This contingency was flipped in the reversed task context. In both tasks, subjects were free to indicate their choice following the stimulus onset by making the respective movement. The stimulus ceased upon a choice. A total of 13 sessions were recorded in the two tasks (Fig. S1).

The temporally-defined quanta of evidence and each subject’s choices provided a decision variable (DV; Fig. 2c) that captured the subjects’ decisions, as in previous studies. The DV faithfully explained the subjects’ choices across the sessions. First, as expected, the polarity of the DV diverged over time according to each subject’s choices (Fig. 2d). Crucially, the DV at the time of choice captured the probability of choosing either alternative (Fig. 2e). Moreover, in line with chronometric predictions of the drift-diffusion model, the subjects’ reaction time (RT) was anti-correlated with the slope of the DV (Fig. 2f).

Throughout the deliberation, the subjects remained fixated on a central target. Moreover, the subjects responded with a single movement on each trial (i.e., a saccade or a button press). We validated this performance using EMG recording of hand muscles and continual recordings of the eye gaze. Indeed, in all valid trials, deviations in horizontal eye gaze were only observed during saccade choices (red in Fig. 2g), whereas increases in the hand EMG were only observed during button press choices (blue in Fig. 2h). This performance standard was maintained during the reversed task (Fig. S2).
Figure 2. Neural recordings, tasks, and behavior. a. We recorded intracranial activity of the human cortex during fixation, saccadic and manual responses. b. After acquiring a fixation cross, subjects listened to a binaurally presented auditory stimulus. Subjects decided whether they heard more click sounds in the left or right ear. In the congruent task context, subjects (specifically with electrodes implanted in the left hemisphere) made a saccade to the left side if they heard more clicks on the left, and pressed joystick buttons if they heard more clicks on the right. This sensorimotor contingency was flipped in the reversed task context. Subjects were free to indicate their choice following the stimulus onset by making the respective movement. The auditory stimulus ceased upon a choice. Overall, 7 subjects performed the congruent task and 6 subjects performed the reversed task (n = 13 sessions). 5 of the 8 subjects performed both tasks. c. Decision variable (DV) computation during an example trial. Red/blue dots indicate auditory clicks in the left/right ears. d, DV as a function of time, separately for trials that resulted in a saccade (red) and button press (blue) choices. One second following the stimulus onset, the DV reached 3.9 ± 2.4 and −3.4 ± 1.8 (mean±s.d., n = 13) for saccade and button press choices, respectively. e, Proportion of saccade choices as a function of the DV at the time of choice. Psychometric curve fits to the data of each subject explained 92.4 ± 3.2 % of the variance in the choice behavior (mean±s.d., n = 13). f, Reaction time as a function of the absolute value of the DV slope (see Methods) for saccade (red) and button press (blue) choices. The slope of this relationship was −7.4 ± 6.8 and −10.5 ± 8.5 (mean±s.d., n = 13) for saccade and button press choices, respectively. g–h, Mean±s.d. eye gaze and hand EMG signals for trials that resulted in a saccade (red) and button press (blue) choices, respectively. Around the time of the choice, the separation, measured by Cohen’s d, was 10.5 ± 3.3 and 3.0 ± 0.7 (mean±s.d., n = 13) for the eye gaze and EMG signals, respectively.
Broadband gamma activity reveals graded choices. We collected data in subjects with electrodes implanted into brain regions implicated in decision formation, including parietal, frontal, premotor, and motor regions (Fig. S1, Fig. S6). We recorded neural signals from these implanted electrodes throughout the decision process. We specifically evaluated broadband gamma (\(\gamma\)) activity, which has been shown to be tightly correlated with multi-unit spiking activity\(^{26-28}\).

We first identified task-related regions, which showed modulation of \(\gamma\) activity around the time of choice compared with baseline (see Methods). We assessed the regions in which a modulation was observed during both choice kinds (effector-independent, Fig. 3a, left) as well as regions that showed modulation during a specific choice (effector-specific, Fig. 3b, left). The cortical areas that were significantly modulated by the tasks are quantified in Fig. S6.

The high temporal resolution of the intracranial recordings, together with their broad cortical coverage, allowed us to investigate the spatial-temporal dynamics of the forming decisions. We investigated these dynamics by averaging \(\gamma\) activity across all task-related electrodes (Fig. S3c). We found that the average \(\gamma\) activity ramped up gradually (Fig. 3a–b, middle). This ramping activity is consistent with the drift-diffusion
However, we found that the γ signal was strongly graded by the DV immediately prior to choice (green bar in the plots). This finding is at odds with the drift-diffusion model, which posits that neural activity at the time of choice should reach a bound instead of being graded by the DV.

We quantified this graded effect at the time of choice (green bar) using the Spearman’s correlation (R) between the γ signal and DV for data of each session. We found that the effector-independent and the effector-specific regions were significantly graded by the DV (Fig. 3a–b, right). The effector-independent regions had an average $R = 0.12$ and $R = -0.12$ during saccade and button press choices, respectively ($t(12) = 3.2, p = 7.3 \times 10^{-3}; t(12) = -4.1, p = 1.5 \times 10^{-3}$; two-tailed t-tests). The effector-specific regions had similar significant result ($R = 0.12, t(12) = 3.2, p = 7.5 \times 10^{-3}; R = -0.13, t(12) = -3.5, p = 4.7 \times 10^{-3}$; two-tailed t-tests).

**Figure 4. Regression analysis rejects the null hypothesis of the signals reaching a common bound.** a. Modeled DV with a defined bound. The value of the modeled-DV ramps up linearly until it reaches a defined bound at the reaction time associated with each response. b, Regressed neural-activity graded by DV. In this analysis, the broadband gamma (γ) activity of all task-related electrodes (Fig. 3b) was regressed on the modeled-DV. The regressed γ is plotted on the ordinate as a function of time, and averaged over the individual sessions (mean±s.e.m, $n = 13$). The signals are aligned to stimulus onset (left dashed line) and movement onset (right dashed line). The top (bottom) panel shows regressed γ activity for trials that resulted in a saccade (button press) choice. c, Same format and analysis as in the histograms in Fig. 3. The shaded distribution results from a randomization test.

**Specific test of the bounded hypothesis.** We specifically tested the hypothesis that the neural signals that encode the forming decisions reach a defined bound at the time of choice. The null hypothesis was set by a modeled-DV that reaches a defined bound at the time of each choice (Fig. 4a). We regressed the recorded γ activity from all task-related electrodes (same as Fig. 3a–b-right) on this modeled DV (Fig. S3d). If the null hypothesis was true, we would not expect a significant correlation between the regressed γ and the raw DV at the time of choice. Yet, the graded effect was prominent also in this analysis (Fig. 4b). Specifically, we found that the regressed γ activity ramped up as a function of time, but was strongly graded by the DV around the time of choice (green bar). We again quantified this graded effect by plotting the histogram of R values over the individual sessions (Fig. 4c). The effector-independent regions showed a significant session-average $R = 0.14$ and $R = -0.12$ for saccade and button press choices, respectively.
Fig. 5. Individual brain regions modulated by the decision variable and the decision dynamics. a, Top panel: The yellow symbols indicate electrodes with broadband gamma (γ) significantly (p < 0.05) modulated by the DV at the time of choice for both saccade and button press choices (effector-independent). The bars show the proportion of electrodes within individual Brodmann areas (BA). The numbers above each bar indicate the number of sessions (numerator) and number of subjects (denominator). Bottom-left panel: Mean±s.e.m. γ activity within all effector-independent DV-modulated electrodes (n = 12). Bottom-right panel: Single-trial effects. The mean γ activity around the time of choice on each trial (green bars) is plotted against the corresponding DV value. *: Spearman’s correlation significant at p < 0.01. b, Top panel: Same format as in (a) but for electrodes with γ significantly (p < 0.05) modulated by DV at the time of choice during saccade (red) and button press (blue) choices. Bottom panel: Same format as in (a), but for signals specifically modulated by the DV during saccade (top) and button press (bottom) choices. The plots represent mean±s.e.m. over the individual sessions (n = 13). c, Same format as in (a), but for parietal (BA 40) electrodes significantly (p < 0.05) modulated by DV during both choices (n = 6).
Graded signals across brain regions. Thus far, we have found that the graded effect was observed across task-related regions. We next investigated the specific brain regions that contributed to the effect. In particular, we identified the brain regions that exhibited a graded modulation of $\gamma$ activity by the DV around the time of choice. The graded modulation during both choice kinds (effector-independent, Fig. 5a-top) was strongest in the parietal cortex (BA 40), while the graded modulation during each choice (effector-specific, Fig. 5b-top) was most prominent over parietal (BA 40) and premotor/supplementary motor areas (BA 6).

The graded effect was apparent in averaged $\gamma$ activity across all the DV-modulated electrodes (Fig. 5a–b, bottom). This prominent effect was not due to an averaging artifact because it was observed also in individual trials (see scatter plots). All $R$ values shown in the scatter plots were highly significant for saccade and button press choices (Effector-independent regions in Fig. 5a: $R = 0.17, p = 4.3 \times 10^{-13}$ and $R = -0.15, p = 7.8 \times 10^{-12}$; Effector-specific regions in Fig. 5b: $R = 0.26, p = 3.3 \times 10^{-28}$ and $R = -0.19, p = 2.0 \times 10^{-21}$; Effector-independent parietal region (Fig. 5c): $R = 0.17, p = 2.9 \times 10^{-6}$ and $R = -0.16, p = 1.3 \times 10^{-6}$; Spearman’s correlation).

Graded choices in the brain and the periphery. The graded modulation of $\gamma$ activity by DV at the time of choice suggests that subjects make their choices in a probabilistic manner, with varying levels of supporting evidence or certainty. To test this, we investigated how the subjects’ choice probability was modulated by the DV at the time of choice from the perspective of each fixed choice (Fig. 2e). We found that the level of evidence substantially modulated the choice probability (Fig. 6a), and this graded modulation effect was significant for saccade and button press choices ($F(2, 36) = 27.9, p = 4.8 \times 10^{-8}$; $F(2, 36) = 43.1, p = 2.8 \times 10^{-10}$; one-way ANOVA). Thus, the graded $\gamma$ signals represent the amount of accumulated decision evidence (Fig. 6b) and the probability of producing the respective choice (Fig. 6a), indicating a continuum between the neural activity and behavior during decision-making.

Figure 6. Summary: The human brain makes analog, graded choices. a, Choice probability for the individual levels of decision evidence. *: $p < 0.05$, one-way ANOVA. b, Graded cortical signals. Left panel: Fig. 3a-right. Right panel: Fig. 1b-top. c, Graded peripheral signals. Left panel: Same analysis and format as in (b), for eye gaze (top, red) and hand EMG (bottom, blue). Right panel: Fig. 1b-bottom.
This finding opens the possibility that these graded modulation effect could be also identifiable within the effector systems that execute each choice. The EMG activity of the hand muscles was significantly graded by the DV at the time of choice, and so was the amplitude of the saccades made to the choice target ($t(12) = 4.0, p = 0.0017$; $t(12) = 3.1, p = 0.010$; two-tailed t-test). This result suggests a continuum between the signals in the brain and the effector systems.

Together, these data reveal that the human brain represented choices in an analog, graded manner (Fig. 1b) instead of an all-or-none switch-like fashion (Fig. 1a).

**Discussion**

In this study, we recorded neural activity at high temporal resolution and broad coverage directly from the human brain. The recordings revealed that the human brain encodes developing perceptual decisions within broadband gamma activity. Across tasks, analyses, and response types, we found that the gamma modulation by decision evidence persisted beyond the time of choice, suggesting a graded instead of a definitive process.

These data provide evidence for a generalized drift-diffusion model that is not limited by a bounded termination rule (Fig. 1b). Within the traditional drift-diffusion model, a subject could meaningfully set a putative bound (Fig. 1a) only after having learned the statistics of the given decision task. This would require an extensive exposure to the particular task. Therefore, the bounded model (Fig. 1a) likely only applies to a subset of decisions performed by highly trained animals or operators. In natural settings, most decisions are novel. We emulated this more general scenario by involving naive decision-makers without extensive training. Indeed, the decision-makers found the decisions to be challenging (Fig. 2e), with 55.2% trials classified as valid under our stringent acceptance criteria. Thus, the design and execution of this study instantiate the novelty of choice situations generally encountered by decision-makers in nature. In this case, we have found robust evidence for a graded nature of the decision process (Fig. 1b).

The intracranial electrodes covered a large portion of the cortex, which enabled us to inspect the regions contributing to the decision formation. The decision evidence was found to be encoded across multiple areas of the cortex, in particular parietal, frontal, and premotor regions (Fig. 5). This multi-regional representation is expected, given that the tasks required subjects to assess and integrate sensory evidence, compare it across two accumulating systems, and accordingly plan a movement. These aspects of the tasks have been shown to map onto the respective brain regions. Moreover, the broad engagement of the nervous system during deliberation suggests that sensory, cognitive, and motor processes do not function in isolation but as a spatiotemporal continuum.

The decision-related effect reported in this study cannot be explained by a potential confound of sensory activity throughout the task, for two reasons. First, we tested two distinct task contexts—congruent and reversed (Fig. 2a), thus swapping the mapping between stimulus and response (Fig. S2). And second, prior to performing the analysis, we excluded electrodes that were modulated by sound clicks (Fig. S1d), thus avoiding the potential confound of sound-induced neural signals.
The decision-related effect reported here cannot be explained by a potential confound of motor activity, for four reasons. First, the effect was observed when the specific choice was fixed (sorting trials by the saccade or button press choices), indicating that the graded effect was not an averaging artifact of potential purely motor signals (Fig. 3, Fig. 4). Second, in several brain regions, the effect was effector-independent and thus not tied to specific movement (Fig. 3, Fig. 4). Third, the γ activity ramped up gradually (Fig. 3), reminiscent of similar findings in the parietal reach region and the lateral intraparietal region of non-human primates. And fourth, the decision-related grading was strongest over parietal cortex (Fig. 5), which is involved in deliberation during perceptual tasks rather than solely encoding movements.

We found that the grading of the task-related neural signals (Fig. 6b) was accompanied by graded probability of producing the respective choice (Fig. 6a). This suggests that the grading may reflect a subject’s certainty in their choice. Indeed, previous studies found that the signals that represent accumulated evidence also encode a subject’s certainty or confidence in their decisions. This notion is supported also by our previous use of this task, in which subjects reported the level of certainty in their decision.

In summary, we report neural evidence for a graded nature of the decision process. Intracranial recordings in naive humans suggest that the brain possesses the capacity for processing evidence and making decisions in a flexible, analog manner. The analog decision signals enable decision-makers to directly act on the analog representation of the available evidence. This mechanism circumvents an all-or-none conversion and may thus contribute to more flexible and accelerated cognitive processing.

References


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**Data and materials availability:** De-identified sessions and analysis code will be available upon reasonable request.
Materials and Methods

Subjects. Neural activity was recorded using intracranial electrodes implanted in 8 humans (5 males, 3 females, 6 right-handed, 2 left-handed, aged 15 to 57, recorded during July/2012 to February/2020; Fig. S1). The subjects underwent surgery for temporary placement of subdural grid electrodes (7 subjects) or intracerebral stereotactical electrodes (1 subject) to localize their epileptogenic focus. All subjects had normal cognitive capacity (mean±s.d. IQ of 94.5±17.2), normal hearing, normal or corrected-to-normal vision, and were able to perform the highly controlled task. The grid electrodes consisted of platinum-iridium contacts, were 4 mm in diameter (2.3 mm exposed) with an inter-electrode distance of 6 or 10 mm; The stereotactical electrodes consisted of platinum/iridium contacts with 0.8 mm in diameter, spaced 3.5 mm apart (contact length 2 mm, insulation length 1.5 mm). Electrode contacts distant from epileptic foci and areas of interest were used for reference and ground. The study was approved by the Institutional Review Board of Albany Medical College. All subjects gave informed consent to participate in the study.

Data Collection. The subjects were placed in front of a flat-screen monitor that presented the visual stimuli (17” diagonal size, 60 cm distance). The auditory stimuli were delivered using headphones (MDR-V600, Sony). The stimuli consisted of a train of brief (0.2 ms) click sounds drawn from a homogeneous Poisson distribution. Each train lasted for up to 2 s. The number of presented stimuli to the left and right ear ranged from 4 to 64 clicks. Consecutive clicks were spaced by at least 5 ms, and the initial click in each trial occurred in both ears simultaneously. For each train, the subjects determined whether they perceived more clicks in the ear contralateral or ipsilateral to the recorded hemisphere. They were free to indicate their choice during any time of the auditory presentation via the joystick or saccade. The hand contralateral to the recorded hemisphere rested on a pillow placed on a fixed table while holding a joystick (Logitech Attack 3). Subjects were instructed to simultaneously press the front and top buttons using their index finger and thumb, respectively. We used the two-finger response to potentially engage a wider network of the movement planning circuitry compared to if we had only used the response of a single digit. Additionally, we recorded electromyographic (EMG) activity from anterior forearm muscles to track the muscle activity during each decision. In total, we placed five surface electrodes (pre-gelled disposable Ag/AgCl sEMG electrodes) on the forearm muscles. Four electrodes were arranged as a 2×2 grid with an inter-electrode distance of 2 cm horizontally and vertically. They were placed on the flexor digitorum superficialis muscle. One electrode was placed on the first dorsal interosseous muscle. An additional sEMG electrode was placed on an electrically neutral tissue as the ground for EMG recording. The eye gaze position of each eye was measured 60 times/second using an eye tracker (Tobii T60, Tobii Technology) integrated into the flat-screen monitor. Neural signals and EMG signals were simultaneously amplified and sampled at 1200 Hz in a manner that prevents aliasing (g.USBamp/g.HIamp biosignal acquisition devices, g.tec). Synchronized acquisition of neural signals, EMG signals, eye gaze, joystick responses, and task control (Fig. 2a) was accomplished with BCI2000.
Task. Each trial started with the visual presentation of a red fixation cross, 2 visual degrees in size (Fig. 2b). Subjects had to maintain fixation within 2 visual degrees. After acquiring fixation, two icons appeared 15 visual degrees to the left and right to the fixation cross. The icons and auditory stimuli were presented on the sides contralateral and ipsilateral to the recording hemisphere. The icon at the contralateral side was a sketch of a joystick. The icon at the ipsilateral side was a sketch of an eye. At the same time, subjects listened to a binaurally presented auditory stimulus with a maximum duration of 2 s. Subjects had to determine whether they heard more clicks in the contralateral or ipsilateral ear. Subjects were free to indicate their choice during any time of the auditory presentation via the joystick or saccade. In the congruent task context (Fig. 2b, top), if subjects heard more clicks in the contralateral ear, they simultaneously pressed the front and the top buttons of the joystick. In contrast, if subjects heard more clicks in the ipsilateral ear, they directed a saccade to the eye icon on the ipsilateral side of the monitor. This contingency was flipped in the reversed task context (Fig. 2b, bottom). The auditory stimulus ceased upon a choice. Hand movement onset was taken as the time at which the first button was pressed. The eye movement onset was taken as the time at which the eye gaze started moving away from the fixation target with a certain velocity criterion (2% of the maximum velocity). We further corrected the eye movement onset with 33 ms relating to the limited resolution of the eye tracker. If subjects broke fixation for more than 150 ms, pressed any button before the auditory stimulus onset, responded with both button press and eye movements, or failed to indicate a response within 2 s following the stimulus onset, the trial was aborted and excluded from analyses. We collected $n = 7$ sessions in the congruent task and $n = 6$ sessions in the reversed task. Five of the 8 subjects performed both tasks. Overall, an average of 212 (84–490) and 245 (90–434) trials per subject were analyzed during saccade and button press choices, respectively (mean (min–max), $n = 13$, Fig. S1). Across the subjects, valid trials constituted $55.2 \pm 18.1\%$ (mean±s.d) of all trials. This modest proportion reflects the highly controlled nature of the task. The type of error was indicated to the subjects in a red and large-font text (fixation break: TOO EARLY; no response: TOO LATE; response with both movements: MOVED BOTH). A successful choice was communicated to the subject by shrinking the icon corresponding to the choice (the eye icon or the joystick icon) from 2 visual degrees in size to 1 visual degree in size. After subjects re-acquired fixation and released all buttons, they were given visual feedback for 0.6 s indicating whether they were correct or not. A correct response was indicated by a green text (+10c, +20c, +30c, +40c, or +50c; in the order of increasing stimulus difficulty), while an incorrect response was indicated by a red text (−50c, −40c, −30c, −20c, or −10c). The offset of feedback was followed by a variable inter-trial interval, 0.6–1.2 s in duration. The error trials were further excluded to eliminate the potential confound related to error response.

Decision variable. To capture the choice behavior of subjects in this task, we devised a decision variable (DV) according to signal detection theory\cite{3, 8}. In particular, a simple DV constructed from discrete, independent pieces of evidence (click sounds) can be evaluated using the logarithm of the likelihood ratio of either
choice (Fig. 2c):

\[ DV(t) = \log LR(t) = \sum_{i=1}^{i(t)} \log \frac{P(e_i|\text{saccade})}{P(e_i|\text{button})}, \]

where the sum runs from the first click up to the last click \(i(t)\) occurring prior to or at time \(t\), \(e_i\) is the \(i\)-th click (left_click or right_click), and \(P(\text{left_click}|\text{saccade})\) is the probability that a click is a left_click given a saccade choice (and analogously for the 3 other combinations of the arguments of \(P\)). These probabilities were computed from the frequencies of the summed left (or right) clicks over all trials of a given choice\(^8\).

We define the DV at time of choice as the DV value 100 ms preceding movement onset (Fig. S3b), and grouped the data for a given correct choice into terciles of growing evidence for that choice, i.e., LO (low), ME (medium), HI (high). We further calculated the DV slope by using a linear fitting of DV within the range of 200 ms after stimulus onset to the time of choice.

**Signal processing.** Prior to performing analyses, we visually inspected the signals recorded from all electrodes and excluded those that exhibited epileptic and artifactual activity (228/799). Together, 571 electrodes in eight subjects were included in the analyses (Fig. S1). We established the anatomical locations of the implanted electrodes by co-registering the post-operative computer tomography image (CT) with a pre-operative magnet resonance imaging (MRI) T1 image. We used Freesurfer\(^{47}\) to generate a 3D model of the cortical surface. Next, we projected the electrodes of all subdural grid subjects onto the surface of the cortex, accounting for eventual brain shifts caused by the craniotomy. To determine the Brodmann areas (BA) in which the electrodes are located, we first transformed the electrode locations into Talairach space, using a standard AC-PC alignment approach\(^{48}\). Next, we labeled each electrode based on annotations provided by Talairach Demon\(^{49}\). We analyzed the EMG signals using the bipolar configuration, notch filtering the signals at 60 Hz, 120 Hz, and band-pass filtering them between 20 and 170 Hz. Finally, we computed the envelope by taking the absolute value of the Hilbert transform applied to the signals. We used Hamming-windowed sinc FIR filters for all the filtering processes (pop_eegfiltnew(), EEGLAB). This script performs forward-backward filtering to avoid time shifts, using the filtfilt() function in Matlab.

**Extracting the broadband gamma (γ) signals.** The neural signals recorded from the brain were high-pass filtered at 0.5 Hz. Spatially distributed noise common to all electrodes was removed using a common average reference filter. We applied notch filters to remove line noise at 60 and 120 Hz. We analyzed brain signals within canonical broadband gamma (γ) range (Fig. S3a). Specifically, we filtered the neural signals from each electrode at 70-170 Hz, and computed the envelope by taking the absolute value of the Hilbert transform of the resulting signal. We further z-scored the γ signals of each electrodes.

**Extracting the auditory-related electrodes.** To determine auditory selective locations, subjects listened to short stories presented with computer speakers, while neural activity was recorded. In each trial, BCI2000 cued the subject visually to the task by presenting the words "listen carefully" or "stop and relax". Each short story lasted for 17–36 s, and was followed by a resting period of 15 s. Overall, an average of 32
(15–53) trials per subject were analyzed. We performed the same procedure as above to obtained the \( \gamma \) signals.

We assumed that the auditory-related electrodes should show significant \( \gamma \) increase for both the decision task (Fig. 2b) and the passive listening task. For the decision task, we computed the mean \( \gamma \) during the baseline period (250 ms window preceding stimulus onset) and stimulus period (50 ms to 300 ms following stimulus onset) for each trial. For the passive listening task, we computed the bin mean (1 second bin) of the \( \gamma \) during the baseline period (14 s preceding stimulus onset) and stimulus period (14 s following stimulus onset) for each trial. To determine whether an electrode had a significant auditory response, we correlated the obtained mean values with a vector of condition labels (baseline period = −1, stimulus period = 1), and performed a biserial rank correlation, which provided a Spearman’s \( R \) value for each electrode. We tested the significance of the obtained \( R \) values against a shuffled null distribution of \( R \) using a randomization test. Specifically, the condition labels vector was randomly reordered (without replacement) and a new \( R \) value computed, and this process was repeated 1000 times. In all cases, we tested for the normality of the null distribution using the Kolmogorov-Smirnov test (ks-test). We then determined the probability that a given tested \( R \) originated from the respective null distribution. This probability constituted the resulting \( p \) values. We corrected the resulting \( p \) values for the number of electrodes in each subject using false discovery rate (FDR). Electrodes with significant (\( p < 0.05 \)) \( \gamma \) increase for both decision task and passive listening task were defined as auditory-related electrodes.

To further eliminate the possibility of a purely auditory response, we excluded 79/571 auditory-related electrodes from eight subjects (Fig. S1d). This has provided 492 electrodes in eight subjects for analysis.

**Identifying the task-related regions.** To identify the task-related electrodes, for saccade (button press) choice trials of each electrode, we computed the mean of the \( \gamma \) during the baseline period (50 ms to 300 ms following stimulus onset) and task-related period (200 ms preceding to 50 ms following movement onset). Next, we correlated the obtained mean values with a vector of condition labels (baseline period = −1, task-related period = 1), which provided a Spearman’s \( R \) value. We performed the same randomization test as above and obtained a \( p \) value (FDR corrected for the number of electrodes in each subject).

Electrodes showing significant (\( p < 0.05 \)) \( \gamma \) modulation for both saccade and button press choices were defined as effector-independent task-related electrodes (Fig. 3a). Electrodes showing significant (\( p < 0.05 \)) \( \gamma \) modulation for saccade (button press) choices were defined as saccade (button press) effector-specific task-related electrodes (Fig. 3b). The task-related \( \gamma \) modulation responses were independent with the DV.

**Model-free analysis.** The key test in this study was the evaluation of neural signals graded by DV at the time of choice. To evaluate the effector-independent graded effect, we averaged the \( \gamma \) of the effector-independent task-related electrodes, and computed the correlation between the averaged \( \gamma \) with the DV at time of choice (Fig. S3c, Fig. 3). Specifically, we calculated the mean value of the averaged \( \gamma \) over a 100 ms window preceding movement onset for each trial. Next, we correlated the obtained saccade (button press) mean values with the saccade (button press) DV at time of choice (Fig. S3b), resulting in a Spearman’s \( R \)
value. We assessed the significance of this $R$ value using a randomization test. In this test, the obtained mean values were randomly reordered (without replacement) and a new $R$ value was computed, and this process was repeated 1000 times. We assessed the significance of correlation using the same procedure as above (results showed in Fig. 3a-b, right panel bar). To evaluate the effector-specific graded effect, we averaged the saccade and button press task-related electrodes, respectively, and performed the same correlation analysis.

**Model-based analysis.** Based on the drift-diffusion model in which the cognitive processes terminated towards a choice when the decision-related neural activity hit a fixed bound, we made a null bounded hypothesis that the DV would reach a bound for each decision Fig. 4a. We further validated the DV graded effect using a linear regression model based on this null hypothesis (Fig. S3D). Specifically, we generated a modeled saccade (button press) DV with the value linearly ramped from 0 to 1 (-1), spanning between 100 ms following the stimulus onset to 100 ms preceding movement onset. Additionally, the modeled saccade (button press) DV value during the 100 ms window preceding the movement onset was 1 (-1), and all the rest part of was 0. We down-sampled (pop_resample() in EEGLAB) the $\gamma$ signals to 100 Hz and regressed (regress() in Matlab) the $\gamma$ from task-related electrodes onto the modeled saccade (button press) DV. If the null hypothesis is true, then we would not expect a significant correlation between the regressed $\gamma$ (i.e., the predicted values from the regression model) and the raw DV at the time of choice. However, if we rejected the null hypothesis, we could confirm the DV graded effect.

To evaluate the effector-independent graded effect, we regressed the $\gamma$ from effector-independent task-related electrodes onto the modeled saccade (button press) DV. The time window used for the regression spanned the period from 200 ms preceding the stimulus onset to the onset of a movement. This regression provided a set of weights, which enabled us to predict the modeled saccade (button press) DV inferred from the $\gamma$ at each moment in time. Next, we calculated the mean value of the regressed $\gamma$ over a 100 ms window preceding movement onset for each trial, and correlated the obtained saccade (button press) mean values with the raw saccade (button press) DV at time of choice (Fig. S3b), resulting in a Spearman’s $R$ value. We assessed the significance of this $R$ value using a randomization test. In this test, the $\gamma$ from all task-related electrodes were simultaneously circular-shifted in time by a randomly selected amount, and a new $R$ value was computed. We repeated the process 1000 times, obtaining a null distribution of $R$. We assessed the significance of correlation using the same procedure as above (results showed in Fig. 4c). Notably, the circular-shift is a more stringent test than random shuffling as it leaves the temporal structure of the $\gamma$ intact (it only abolishes the temporal relationship between the $\gamma$ and the DV). To evaluate the effector-specific graded effect, we regressed the $\gamma$ from saccade and button press effect-specific task-related electrodes onto the modeled saccade-DV and button press-DV, respectively.

**Extracting DV-modulated electrodes.** We found a graded effect for both saccade and button press choices in both effector-independent and effector-specific task-related regions (Fig. 3, Fig. 4). Specifically, the $\gamma$ signals were positively modulated by the DV at the time of choice. To further evaluate the individual brain areas that contributed to this graded modulation effect, we calculated the mean value of the $\gamma$ over a
100 ms window preceding movement onset for each trial and each task-related electrode. Next, we correlated the obtained saccade (button press) mean values with the saccade (button press) DV at time of choice (Fig. S3b), and performed the same randomization test as the "Model-free analysis section". Electrodes with the γ significant ($p < 0.05$) positively graded by saccade (button press) DV at the time of choice were defined as saccade (button press) effector-specific DV-modulated electrodes (Fig. 5a). Electrodes positively graded by both saccade and button press DV were defined as effector-independent DV-modulated electrodes (Fig. 5b).
**Figure S1. Subjects information.** a, Electrode coverage for all subjects. The black dots show the locations of all 799 electrodes (prior visual inspection) inferred from CT scans. b, Electrode locations pooled across the subjects and projected onto a template brain (Methods). For visualization purposes, we projected the left hemisphere electrodes of subjects S2, S4, S6, and S7 onto the right hemisphere. Solid/hollow circles indicate the location of all 571 electrodes (after visual inspection) across all subjects engaged in the congruent/reversed tasks, respectively. c, Information of individual subjects. d, Auditory-related electrodes that were excluded. Electrodes with significant ($p < 0.05$) broadband gamma increase for both decision task and passive listening task were defined as auditory-related electrodes (see Methods). We extracted 79/571 auditory-related electrodes from eight subjects and these electrodes were excluded. Together, 492 electrodes in eight subjects were included for further analyses.
Figure S2. Choice behavior in the two task contexts. a, Congruent task context (n = 7 sessions). b, Reversed task context (n = 6 sessions). Panels from left to right: Mean±s.d. DV during the stimulus interval; Mean±s.e.m. proportion of saccade choices as a function of the binned DV at time of choice (100 ms preceding movement onset); Mean±s.e.m. reaction time as a function of the absolute value of the DV slope; Mean±s.d. eye gaze across subjects, aligned to saccade onset; Mean±s.d. EMG across subjects, aligned to button press onset. The data are shown separately for trials that resulted in a saccade (red) and trials that resulted in a button press (blue).
Figure S3. A graphical rendering of the analyses. We use saccade choice trials as example here. 

a, Procedure of signal processing. The decision variable (DV, red trace) was derived from the presented evidence (black dots indicating time and laterally of click sounds) in the same way as many previous studies. We define the DV at time of choice as the DV value 100 ms preceding movement onset. c, Model-free analysis. We averaged the broadband gamma ($\gamma$) from task-related electrodes (black traces), and calculated the mean value of the averaged $\gamma$ over a 100 ms window preceding movement onset for each trial ($y$). Next, we computed the correlation between $y$ and DV, and determined its significance using a randomization test (see Methods).

d, Model-based analysis. We applied a linear regression between the $\gamma$ of the task-related electrodes (black traces) and the corresponding value of the modeled DV (red trace). This provided a set of weights that enabled us to predict the modeled DV from the $\gamma$. We calculated the mean value of the regressed $\gamma$ over a 100 ms window preceding movement onset for each trial ($y$), computed the correlation between $y$ and DV, and determined its significance using a randomization test (see Methods).
Figure S4. Model-based analysis. Same as Fig. 4b with the broadband gamma signals circularly shuffled (see Methods, ns p > 0.05).

Figure S5. Decision-related signals in the peripheral nervous system. a, Electromyographic (EMG) activity of the hand pressing the button (mean ± s.e.m., z-scored, n = 13) as a function of time. b, Horizontal eye gaze (mean ± s.e.m., z-scored, n = 13) as a function of time. In each session, the EMG and eye gaze signal was normalized by subtracting the trial-averaged signal for saccade and button press choice, respectively. On each trial, the amplitude of eye gaze was taken as the maximal value within the period from 200 ms preceding to 200 ms following saccade onset. The EMG amplitude was taken as the averaged value within the period from 50 ms preceding to 50 ms following a button press.
Figure S6. Proportion of electrodes within individual Brodmann area over all electrodes. a, Effector-independent task-related (Fig. 3a) and DV-modulated (Fig. 5a) electrodes. b, Saccade (red) and button press (blue) effector-specific task-related (Fig. 3b) and DV-modulated (Fig. 5b) electrodes. c, The proportion of electrodes located within individual Brodmann area over all electrodes. Subject S8 provided access also to deep brain targets. Electrodes from all 13 sessions (8 subjects) are included. The numbers above each bar indicate the number of sessions (numerator) and number of subjects (denominator).