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A low-frequency oscillatory neural signal in humans encodes a developing decision variable

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ABSTRACT

We often make decisions based on sensory evidence that is accumulated over a period of time. How the evidence for such decisions is represented in the brain and how such a neural representation is used to guide a subsequent action are questions of considerable interest to decision sciences. The neural correlates of developing perceptual decisions have been thoroughly investigated in the oculomotor system of macaques who communicated their decisions using an eye movement. It has been found that the evidence informing a decision to make an eye movement is in part accumulated within the same oculomotor circuits that signal the upcoming eye movement. Recent evidence suggests that the somatomotor system may exhibit an analogous property for choices made using a hand movement. To investigate this possibility, we engaged humans in a decision task in which they integrated discrete quanta of sensory information over a period of time and signaled their decision using a hand movement or an eye movement. The discrete form of the sensory evidence allowed us to infer the decision variable on which subjects base their decision on each trial and to assess the neural processes related to each quantum of the incoming decision evidence. We found that a low-frequency electrophysiological signal recorded over centroparietal regions strongly encodes the decision variable inferred in this task, and that it does so specifically for hand movement choices. The signal ramps up with a rate that is proportional to the decision variable, remains graded by the decision variable throughout the delay period, reaches a common peak shortly before a hand movement, and falls off shortly after the hand movement. Furthermore, the signal encodes the polarity of each evidence quantum, with a short latency, and retains the response level over time. Thus, this neural signal shows properties of evidence accumulation. These findings suggest that the decision-related effects observed in the oculomotor system of the monkey during eye movement choices may share the same basic properties with the decision-related effects in the somatomotor system of humans during hand movement choices.

Introduction

We often make important decisions based on sensory evidence accrued over a time period. For instance, a driver often needs to change lanes. To do so, she must carefully assess the position and speed of the neighboring vehicles. Once she has obtained enough evidence that it is safe to change lanes, she moves the steering wheel.

Pioneering work in the oculomotor system of the monkey has shed light on the neural signals that underly the fine-grained accumulation of sensory evidence and on the signals that underly the generation of the subsequent motor command. This work has revealed that neurons in oculomotor structures including the parietal eye fields (Roitman and Shadlen, 2002; Shadlen and Newsome, 1996), the frontal eye-fields (Gold and Shadlen, 2000), and the superior colliculus (Horwitz and Newsome, 1999) reflect the cumulated amount of evidence ("decision variable") on which monkeys base their decision to make an eye movement. This neural effect is observed already during the presentation of the stimulus while evidence is being accumulated. Furthermore, this work has demonstrated that the evidence for a decision to make an eye movement is represented within the same oculomotor circuits that give rise to the subsequent eye movement (Gold and Shadlen, 2000; Hanks et al., 2006).

The work in the macaque oculomotor system has laid the grounds for neurally informed theories of choice behavior (Gold and Shadlen, 2007; Ratcliff and McKoon, 2008). However, that work also raises the question whether the neural findings obtained in the macaque oculomotor systems generalize to other systems. There is some evidence

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that this may be the case. In particular, recordings in monkeys have demonstrated that activity in sensorimotor regions is modulated by certain parameters of a stimulus in vibrotactile decision tasks in which a response is mediated using a hand movement (Haegens et al., 2011; Hernández et al., 2010). Furthermore, a study in humans (Donner et al., 2009) found that in a motion detection task, the centroparietal cortex shows a gradually building low-frequency signal that indicates a person's upcoming choice of which hand to use to press a button. The gradual signal buildup reported in that study is reminiscent of the signal buildup observed in the oculomotor system during an animal's plan to make a saccade into the neuronal response field (Shadlen and Newsome, 1996). As in the oculomotor system, this signal may be modulated by a decision variable (DV) on which subjects base their decision to make a given movement, and this modulation may be observed already during the presentation of the stimulus while the evidence is being accumulated. Although this possibility has been proposed (Donner et al., 2009), it has not been directly tested.

There is some evidence in recent human literature that cortical signals may be modulated by a DV (O'Connell et al., 2012; Wyart et al., 2012). The study of Wyart et al. (2012) in part shows a modulation of a low frequency cortical signal by an accumulated DV. However, this signal is modulated by the accumulated DV only shortly prior to a movement and not during the time when the evidence is being accumulated. The study of O'Connell et al. (2012) demonstrates a modulation of cortical potentials by a DV already during the accumulation period. These cortical potentials nonetheless differ from the low-frequency neural signal confined to centroparietal regions (Donner et al., 2009).

To test whether or not the centroparietal low-frequency neural signal (Donner et al., 2009) is modulated by a decision variable informing the decision to make a hand movement, we engaged humans in a perceptual decision task while recording electroencephalographic (EEG) activity. We designed a task in which the evidence for a decision is delivered to subjects in discrete quanta, through click sounds presented to the right ear and to the left ear over a brief period of time. This discrete design enables the computation of the decision variable on which a subject bases her decision on each trial, as well as the investigation of the behavior of the neural signal in regard to each quantum of the decision evidence. We found that the signal is strongly graded by the decision variable on which subjects base their decision to make a hand movement. The signal further exhibits properties of accumulation of the individual quanta of evidence.

Materials and methods

Subjects

Ten right-handed human subjects participated in the study. The subjects comprised 6 males and 4 females, aged 21 to 58. All subjects were healthy, had a normal hearing capacity, and gave informed consent through a protocol reviewed and approved by the Wadsworth Center Institutional Review Board.

Task

Subjects sat in a comfortable chair 60 cm in front of a flat-screen monitor. They wore a 16-channel EEG cap (see the Electrophysiological recordings section). Subjects wore headphones (MDR-V600, Sony) which presented a stereo auditory stimulus (see the Auditory stimulus section). The right arm rested comfortably on a pillow that was placed on a fixed table. The subjects' right hand was steadily holding a joystick (ATK 3, Logitech); subjects were ready to simultaneously press the front and top buttons of the joystick using their right index finger and the right thumb, respectively. Gaze position of each eye was measured using an eye tracker (Tobii T60, Tobii Technology) that was integrated into the flat-screen monitor. Acquisition of EEG signals, eye gaze parameters, joystick button press parameters, as well as control of the experimental design were accomplished with the BCI2000 system (Schalk and Mellinger, 2010; Schalk et al., 2004).

Each trial (see Fig. 1A) started with the presentation of a red fixation cross, 2 visual degrees in size. Subjects had to fixate at the center of the cross, and keep the eye gaze within a radius of 2 visual degrees. An absence of eye gaze within the fixation radius for more than 150 ms was considered as a break of fixation. After acquiring fixation, two icons appeared, 15° to the right and 15° to the left of the fixation cross. The right icon was a sketch of a joystick with highlighted top and front red buttons. The left icon was a sketch of the eye. At the same time, subjects were presented with a stereo auditory stimulus (click sounds, see the Auditory stimulus section), 1.0 s in duration. Subjects had to determine whether they heard more clicks in the right ear or more clicks in the left ear. The stimulus was followed by a variable delay interval, 0.3–1.3 s in duration. After the delay, the fixation cross shrank to 1° in diameter and changed its color to green. This event cued the subjects to make a movement (choice). If subjects heard more clicks in the right ear than in the left ear, they simultaneously pressed the front and the top button of the joystick using the right index finger and the right thumb, respectively. We opted for the two-finger response, as it may engage movement planning circuitry more prominently compared to if we had only used the response of a single finger response. In the analyses, movement onset was taken as the time of the earlier button press (in Figs. 2C bottom and 9, the button press is detected if either button is pressed). On the other hand, if subjects heard more clicks in the left ear than in the right ear, they made an eye movement to the left icon. If subjects broke fixation or pressed any button before the go cue, or if they failed to indicate a response within 1200 ms after the go cue, the trial was aborted and excluded from the analyses. A trial was also aborted if subjects responded with both movements. The type of error was indicated to the subjects in red, large-font text (TOO EARLY, TOO LATE, MOVED BOTH). A successful choice was communicated to the subject by shrinking the icon corresponding to the chosen movement (the eye icon or the joystick icon) from 2° in size to 1° in size. After subjects re-acquired fixation and released all buttons, they were given feedback, 0.6 s in duration, 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). 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.

Auditory stimulus

The auditory stimulus presented to each ear consisted of a train of brief (0.2 ms) click sounds drawn from a homogeneous Poisson process. Each train lasted 1.0 s. The stereo stimulus was composed such that the sum of clicks presented to the left ear (C_l) plus the sum of clicks presented to the right ear (C_r) summed to a fixed number $C_l + C_r = \Omega$, $\Omega \in \{25,32,39,46\}$. The value of Ω was drawn randomly on each trial. We imposed the Ω randomization to ensure that subject had to pay attention to the click sounds in both ears. Stimulus presentation was also subject to the constraint that two consecutive clicks had to be separated by at least 5 ms. Furthermore, during early tests of the paradigm, subjects often claimed that they were biased toward the ear that presented either the first or the last click. To avoid such possible bias, the first and the last clicks in each stimulus occurred in both ears simultaneously, at time 0.0 s and 1.0 s, respectively. Thus, each ear heard at least 2 clicks, and at most $\Omega - 2$ clicks. We generated ten random versions of all the 130 possible combinations of C_l and C_r, and loaded the corresponding files into the memory of the BCI2000 system prior to the start of each experiment.

Behavioral model

We inferred the variable on which subjects base their decision ("decision variable") using a behavioral model. The model takes the number of clicks presented to the right ear C_r and to the left ear C_l in