The neural basis of choice behavior has been intensely studied with laboratory tasks in which a subject sees a stimulus and makes a corresponding motor response, but the issue of timing has been hard to tackle: How much time is necessary to make the perceptual judgment versus executing the motor report? When and how does a subject commit to a particular choice, and what neural mechanisms determine that? A major limitation has been that reaction times (RTs) are affected by sensory and motor factors (e.g., task difficulty, urgency, expectation) that can be covertly traded. Recently, we designed a task that overcomes these problems and allows us to construct a new curve that unambiguously reveals how a subject’s perceptual judgment unfolds in time. Specifically, the slope of this “tachometric” curve depends on the perceptual difficulty of the task and the perceptual capacity of the subject, but not on motor execution. This technique shows that monkeys can make accurate color discriminations in less than 30 ms. More importantly, it provides a novel metric for correlating the time courses of psychophysical and neuronal responses, opening up a new avenue for investigating choice behaviors in a wide variety of experimental conditions.

A driver notices a traffic light change and must quickly decide whether to step on the brake or the gas pedal; the time needed to respond will depend at least on two factors, the subject’s perceptual speed (how fast he can tell apart green from red) and his motor speed (how soon can his foot start moving once the appropriate action is selected). Measuring these separate contributions is tricky because the experimental quantity that is directly observable, the RT, includes both, and often depends on additional task contingencies; in humans, for instance, RTs can change dramatically simply by specifying whether response speed or choice accuracy is more important.14 Thus, although choice behavior has been thoroughly studied both in psychophysical and neurophysiological experiments,5-9 our neurobiological understanding of fast choices and their timing10-12 has been severely limited by such covert processes.

In a recent study,13 we reported a new task design that overcomes these problems and allows us to isolate the perceptual component of a choice with minimal contamination from motor or other, non-sensory processes. The key idea is to compel the subject to make a response first, before presenting the relevant sensory information (a green and a red spot in this experiment; Fig. 1A). In this way, the sensory cue informs a choice process that is already in progress. Although this may seem counterintuitive, it is not unlike sports such as baseball, cricket, tennis or squash, in which a player must start his/her motion early to overcome inertia, and the ensuing judgment about the ball’s trajectory must be made extremely rapidly.14-16

The experimentally controlled parameter in this compelled-saccade task is the time gap between the instruction to make a...
The crucial interval occurs afterward. We call it the effective processing time (ePT), and corresponds to the time when the cue is actually visible (Fig. 1 and caption). Performance in the task is best understood at two extremes. At very short or negative processing times (i.e., long gaps) the cue information does not become available, so the subject simply makes a guess to one of the two yellow spots. In contrast, at long processing times (i.e., short gaps) the cue is revealed early, so the subject has ample time to see the red and green spots and make a correct, informed choice. Thus, performance should change systematically as a function of ePT, going from chance (50% correct) to nearly perfect (100% correct) discrimination. This is indeed what happened (Fig. 1B). We called the resulting curve the tachometric curve because it directly indicates how much cue-exposure time is needed to achieve a particular success level—thus revealing the subject’s perceptual discrimination speed.

If the slope of the tachometric curve truly characterizes the perceptual capacity of a subject, then two things should occur. First, the slope should change if the perceptual difficulty of the task changes (e.g., by altering the chromatic contrast of the red and green spots). We have not verified this yet, but experiments are planned. The second prediction is the converse: if perceptual difficulty remains constant, there should be no change in the slope even if other aspects of the task, such as mean RT and motor execution, do change. To test this, we manipulated the rewards associated with correct responses to the two sides so that the subjects would develop a strong preference for one of them.17 In this biased condition, choices to one side were much more frequent, less accurate, and had significantly shorter RTs than choices to the other side; however, the corresponding tachometric curves had identical slopes, as predicted.13 This, we believe, is because the perceptual discrimination remained constant.

As in other choice tasks,4,11,18-21 a simple phenomenological model provided important intuition and mechanistic insight (Fig. 1C). In the model, each trial is a race between two developing motor plans, such that the first one to reach a threshold choice (go signal) and the sensory cue, but the crucial interval occurs afterward. We call it the effective processing time (ePT), and corresponds to the time when the cue is actually visible (Fig. 1 and caption). Performance in the task is best understood at two extremes. At very short or negative processing times (i.e., long gaps) the cue information does not become available, so the subject simply makes a guess to one of the two yellow spots. In contrast, at long processing times (i.e., short gaps) the cue is revealed early, so the subject has ample time to see the red and green spots and make a correct, informed choice. Thus, performance should change systematically as a function of ePT, going from chance (50% correct) to nearly perfect (100% correct) discrimination. This is indeed what happened (Fig. 1B). We called the resulting curve the tachometric curve because it directly indicates how much cue-exposure time is needed to achieve a particular success level—thus revealing the subject’s perceptual discrimination speed.

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As in other choice tasks,4,11,18-21 a simple phenomenological model provided important intuition and mechanistic insight (Fig. 1C). In the model, each trial is a race between two developing motor plans, such that the first one to reach a threshold
is executed. Following the go signal, both plans start building up with random rates—this corresponds to the subject’s initial guess—but then, once the gap period has elapsed, the cue information accelerates the plan toward the target side and decelerates the plan toward the distractor side. This model produced both guesses (Fig. 1B, top) and informed choices (Fig. 1B, bottom) in a way that mimicked in great detail the psychophysical performance of the subjects, including their RT distributions at specific gaps, which had complicated shapes. Furthermore, it agreed extremely well with the responses of single neurons recorded during task performance from the frontal eye field, a cortical area that participates in the generation of eye movements, the activity of these cells accelerated and decelerated as predicted by the model.

What is the significance of these results? First, the compelled-response design can be easily adapted to the discrimination of visual features other than color, such as orientation, shape or motion, or of auditory features, such as sound location or sound frequency, for instance. Hence, it will be possible to characterize perceptual processing capacity under diverse conditions. Second, neuronal activity recorded across such experiments should provide substantial insight about the circuit dynamics underlying rapid choices. That is, what neuronal properties determine whether a neuronal circuit processes sensory information more quickly or more slowly? In particular, interpreting neuronal activity as perceptual, motor or both, is an extremely challenging problem, and the tachometric curve sets a temporal benchmark that permits such dissociation. And third, if extended to humans, this approach has potential consequences for characterizing and improving everyday activities. What makes one fighter pilot perform better than others, the speed with which he identifies incoming targets or his motor coordination? Or, what goes wrong when a baseball player goes through a slump, does he fail to judge the ball’s trajectory correctly, or are his muscles responding more slowly than usual? Notably, abnormal RTs are commonly used as diagnostic indicators of various mental disorders, but their utility is limited because they do not distinguish abnormalities in sensory versus motor processing. Such distinction could help to identify the neural substrates of a disease and its degree of progression, and perhaps to adopt more effective remedial strategies.

In conclusion, a deceivingly simple conceptual advance in task design allows us to study the timing of fast choices with high resolution. And so, many new research directions are now open for exploration.

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