Supporting Information

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This section provides details concerning the apparatus, the training protocol, and the monitoring of animal performance.

Apparatus for Rats

The main chamber of the apparatus (Fig. 1) was illuminated by dark red LEDs and by ambient lighting whose intensity could be modulated according to the stage of training. Two video systems monitored the rat's actions. First, mounted 40 cm above the apparatus floor, a webcam (HD Webcam C310; Logitech) collected images of the entire apparatus at 30 frames per s. Second, mounted above the stimulus delivery port, a high-speed video camera (CamRecord 450; Optronis) equipped with a macro zoom (LMZ45T3 18–108 mm lens; Kowa Company) collected images of the snout, whiskers, and stimulus plate at 500 frames per s.

The chamber contained left and right reward spouts mounted on 8-cm-high pedestals. Each spout housed a custom-made infrared LED-based contact sensor. An AVR32 board (National Instruments) acquired all sensor signals and controlled the liquid syringe pump (NE-500 programmable OEM; New Era Pump Systems) for reward delivery. Three audio speakers were positioned just outside the walls of the apparatus. The central one, located at the back of the apparatus, delivered the go cue. The two lateral speakers were positioned near the two reward spouts to present a "reward delivery cue" as a reinforcer of the release of juice.

Exclusion of Nontactile Signals

We took numerous steps to be certain that rats used tactile rather than acoustic signals to judge the stimuli. We recorded sounds (LAN-XI type 3052; Bruel and Kjaer) during playback of the complete vibration library and examined the frequency spectrum (Fig. S4). The highest acoustic frequencies generated by the motor were below 500 Hz so that albino rats, which possess the higher-frequency hearing characteristic of mammals (1–3), would be expected to be insensitive to such sounds.

As a further test, in numerous sessions with well-trained rats we detached the motor from the plate assembly. Auditory cues remained but with no accompanying whisker motion; the performance of rats dropped to the chance level (Fig. S5). As a final control, we left the motor attached to the plate but removed the adhesive surface from the plate so that the whiskers slipped along it and no longer followed the motor. Again, auditory cues remained but with reduced whisker motion, and performance dropped to about 60%. The behavioral tests were limited to strings of about 10–20 trials because the absence of whisker stimulation might confuse the rats. In no case did we clip off the whiskers as a test because this would lead to general disorientation and would not be a specific test of whisker use in the task.

Apparatus for Humans

Human subjects viewed a computer monitor and wore headphones that presented acoustic noise and eliminated ambient sounds. They rested their left arm on a firm cushion and placed the left index finger in contact with the tip of a probe driven by a motor (Fig. 2D). To start a trial, the subject pressed the keyboard up arrow with the right hand. This triggered presentation of the base and comparison stimuli. After a poststimulus delay, a blue panel illuminated on the monitor, and the subject pressed the left or right arrow on the keyboard, signifying selection of the base or comparison stimulus, respectively.

In pilot experiments the stimulus scale used for rats was perceived by humans as intense; this is because stimulus energy was delivered directly to the skin at a normal angle (unlike the case in rats where stimuli were tangential to the skin surface and the interposed whisker shaft absorbed much energy). For this reason, we imposed an upper bound of SD equal to 270 mm/s.

Training of Rats

Good performance of the working memory and acuity task was the outcome of a seven-stage training routine. Typical duration of training was 2–3 mo but varied according to the experiment's intended data set and individual differences in rate of learning.

Stage 1: Handling. For half an hour each day, the investigator held and petted the rat and fed it by hand. This stage lasted for 10 d. After every session of handling and, later, after training sessions in the apparatus, the subject was placed in a large enriched play arena (Imac, Tezze di Arzignano, Italy) with other rats. From this stage onward, a water restriction schedule was implemented, whereby the rat collected rewards in the apparatus and was given ad libitum access to water for 1 h after each session.

Stage 2: Training to Nose Poke and to Collect Rewards. The goal of stage 2 was for the rat to explore the apparatus and to learn that three zones were crucial to obtaining rewards: the nose poke in the stimulus delivery port and the left and right spouts (Fig. 1). Specifically, the aim was to teach the rat a simple sequence of actions and events: (*i*) position snout in nose poke, (*ii*) attend the go cue, and (*iii*) withdraw and move toward the baited reward spout.

The arena was provided with visible ambient lighting. To start the first session, the rat was placed in the apparatus and allowed about 1/2 h of free exploration. Both spouts released a reward (pear juice diluted in water 1:3) whenever the rat licked them. Simultaneously with the reward, a speaker placed just outside the chamber emitted a train of five clicks.

Later in the first session, the investigator began to draw the rat into the nose poke in the stimulus delivery port by offering it, just external to the hole, a handheld dropper containing diluted juice. The whisker stimulation plate was present but immobile. The entry of the rat's snout into the nose poke was detected by an optic sensor; this event immediately triggered a 200-ms 5-KHz acoustic go cue. The go cue signaled the enabling of one reward spout. At the conclusion of the go cue, a click train was initiated at the speaker lateral to one of the reward spouts. Because this click train had the same pitch as the reward delivery cue and its purpose was to draw the rat toward the baited spout, we refer to it as the "reward target cue." Once triggered, the reward target cue remained active until the rat reached the designated spout. As the rat licked for a reward of 0.1 mL of diluted pear juice, the reward delivery cue was emitted. The rat quickly learned to place its snout in the nose poke to trigger the go cue and the reward target cue; at this point it was no longer necessary for the investigator to manually guide it with the dropper.

A blue LED positioned within the stimulus delivery port served as an additional cue to draw the rat's attention to the nose poke and then to give the rat feedback on correct positioning. In this and all successive stages, the LED was illuminated until the rat entered the nose poke and was turned off when the rat interrupted the nose poke LED sensor. As soon as the rat collected the reward, the LED was again illuminated, signaling that the rat may return to the nose poke to start the next trial.

Stage 2 lasted for two to three sessions and was terminated when the rat showed at least 100 repetitions per session of a stereotyped behavior consisting of nose poke entry followed by withdrawal to either the left or right spout to retrieve a reward.

Stage 3: Training to Wait for the Go Cue. In stage 2, entry into the nose poke immediately triggered the go cue. In stage 3, we introduced a delay before initiation of the go cue, with the objective of prolonging the period spent in the stimulus delivery port. In addition to the nose poke sensor, high-speed video of the stimulus delivery port was now acquired, and a custom algorithm was operated online to measure head movement. The rat needed to occupy the nose poke and maintain head movement below a userset threshold for a specified waiting period. If the rat left the nose poke before the go cue sounded (early withdrawal), no reward was made available. Provided that early withdrawal did not occur, the go cue was followed by the reward target cue at either the left or right speaker (chosen randomly for that trial), and the corresponding spout was baited.

In the first session the waiting period was just 10–100 ms. In the next sessions, according to the rat's ability to remain immobile, the maximum period was gradually increased while maintaining trials with shorter periods (e.g., interspersed waiting periods of 100, 200, 300, and 400 ms). Finally, waiting periods of up to 5 s were presented. In parallel with the increase in the waiting period, the threshold for an acceptable level of head movement was steadily reduced.

The arena lighting level was reduced so that by the end of stage 3, the rat worked at full speed under dim red light. Like in stage 2, the whisker stimulation plate remained immobile. This stage lasted for two to three sessions, with 200–400 trials per session, and terminated when the rat registered an early withdrawal on fewer than 10% of the 5-s delay trials.

Stage 4: Introduction of Tactile Stimuli. The goal of stage 4 was for the rat to learn to receive whisker stimuli and to become aware of the relationship between stimulus features and the reward location. Now, when the rat entered the nose poke, the go cue was not sounded until completion of two sequential whisker vibrations, denoted base and comparison (Fig. 2*B*). As before, no reward was made available if the rat left the nose poke before the go cue sounded. After the go cue, the reward target cue was sounded adjacent to the baited spout. The side of the reward depended on a rule associated with the velocity distributions, σ_{base} and $\sigma_{\text{comparison}}$, of the two whisker vibrations. For instance, the rule for one subject might be as follows: when $\sigma_{\text{base}} > \sigma_{\text{comparison}}$, the reward is at the left spout, and when $\sigma_{\text{base}} < \sigma_{\text{comparison}}$, the reward is at the right spout. The rule was assigned randomly to each rat and was fixed for the remainder of the study.

In this stage, the difference between σ_{base} and $\sigma_{\text{comparison}}$ [as quantified by the SD index (SDI)] was 0.4. The range of velocity SDs was 128–300 mm/s. Other task parameters were varied. Stimulus duration was varied from 50 to 500 ms. The interstimulus delay also was varied, in 100-ms steps, from 200 ms to 3 s. Stimulus parameters and other experimental variables are given in Table S1. The objective of such variations was for the rat to learn that stimulus features, as well as the time course of the trial, were changeable. The rat's acceptance of trial-to-trial unpredictability was crucial for the later implementation of the stimulus generalization matrix (SGM).

In this stage, the rat did not receive the reward at the side deemed incorrect on that trial; however, when its first choice was wrong, it was allowed to continue to the opposite (correct) spout, where the reward was dispensed. By this error remediation protocol, the rat began to uncover the relationship between stimulus features and reward location. Although we did not score the performance of the rats, there was evidence that they began to attend to the vibratory whisker stimulation: by examining video recordings of the whiskers, we found that by the end of stage 4 the rat began to hold its whiskers immobile on the vibrating plate, presumably to optimize the collection of signals. Whisker position in one trial is illustrated in Movie S2.

This stage lasted for 10-20 sessions, with 200-300 trials per session, and terminated when the rat registered an early with-drawal on fewer than 10% of trials.

Stage 5: Implementation of the Stimulus Comparison Rule. This stage differed from the preceding one in the following ways. First, the reward target cue was omitted. This means that the rat could identify the correct reward spout only through the tactile stimulus comparison rule rather than by following the acoustic signal. The reward delivery cue was still used to reinforce correct choices. Second, error remediation was no longer allowed. If the rat's first choice was incorrect, it could not find a reward by checking the opposite (correct) spout. This increased the error cost. Third, an error led to a 5-s timeout. During the timeout, the blue LED above the stimulus delivery port remained off, and the rat could not initiate a new trial. The timeout further increased the error cost.

As the rat gained competence, the SDI was decreased progressively from an absolute value of 0.4 to 0.35 (Table S1).

In this stage we quantified accuracy according to the rat's first choice on each trial. It is important to note that because the number of stimulus pairs in this stage was limited, rats may start to use alternative strategies to do the task, rather than the intended comparison rule (*Stimulus Generalization Matrix* in *Results*). To avoid that, the next stage of training was introduced as soon as performance rose above chance.

Stage 6: Tolerance to Variation in Parameters. In this stage the stimulus comparison rule (stages 4–5) was stabilized through the execution of many hundreds of trials. Beyond that, the goal of stage 6 was for the rat to continue to learn that stimulus features, as well as the time course of the trial, were changeable. Rodents are known to have a tendency to form stereotyped, inflexible patterns (1). Stage 6 was crucial in maintaining the rat's elasticity and thus minimizing its likelihood of developing superstitious timing routines. Moreover, the rat's learned tolerance to variation allowed us to run future test sessions with all experiment parameters randomized from trial to trial. Among the varied parameters were the σ value of the vibrations, vibration durations, and interstimulus interval (Table S1).

By varying the σ value of the vibrations, we required the rat to generalize the stimulus comparison rule. Stimulus pairs were selected pseudorandomly across trials. The purpose of generalizing the rule was described in *Stimulus Generalization Matrix*.

Our long-term goal is to exploit this behavioral task to study the neuronal basis of tactile sensation, working memory, decision making, and action selection. To accomplish these aims, it is necessary that the structure of each trial allows the cognitive operations to be at least partially separated in time. At the conclusion of the comparison stimulus, all possible sensory data have been collected. We inserted a poststimulus delay between the comparison stimulus and the go cue (Fig. 2B) to allow us to examine the motor program of the rat following the integration and comparison of sensory signals. To be certain that the rat attends to both stimuli and the go cue before acting, we made stimulus duration and poststimulus delay variable.

Fig. S1 illustrates the timing of the rat's withdrawal in one session. Each trial is represented by one point. The x axis plots the poststimulus delay, defined as the time from the end of the comparison stimulus until the onset of the go cue (see Fig. 2*B* for time line). The y axis plots the sum of the poststimulus delay and the withdrawal latency, where latency is defined as the time from the go cue onset until the instant in which the rat's snout left the nose poke sensor. Aside from a small number of early withdrawals, all trials lie about 200–400 ms above the diagonal line. From these data, we draw two conclusions. First, the rat attended

the conclusion of the comparison vibration, independently of the duration of the two vibrations and the delay between them; otherwise, many early withdrawals would have occurred. Second, the time of withdrawal was bound to the time of the go cue. If the time of withdrawal were bound to the conclusion of the comparison stimulus rather than the go cue, the points would have been distributed in the horizontal, not diagonal, direction.

When performance was above 80% averaged across all conditions for three consecutive sessions, the rat was ready for the next stage. This usually required 10–15 sessions.

Stage 7: Finalization of the Vibration Comparison Task. In stage 7, the rat was presented with new combinations of stimulus pairs until it reached the final form of the SGM, which was composed of 10–14 stimulus pairs; this SGM configuration is illustrated in Fig. 3*A*. Stage 7 usually required 20–30 sessions. When performance was above 80% in the basic SGM for three consecutive sessions, the rat proceeded to the testing stage, with findings described in *Results*. Fig. S2 shows the improvement of performance in four rats across stages 6 and 7.

Analysis of Learning in Delayed Comparison. To chart rats' learning, we carried out an analysis to weigh the contributions of σ_{base} and $\sigma_{\text{comparison}}$ to the animal's choice, as follows. From the data originating in a single training session, for each [σ_{base} , $\sigma_{\text{comparison}}$] stimulus pair, we fit the animal's choice with a logistic regression using a generalized linear model. This model posits a linear combination of $\sigma_{\text{comparison}}$ and σ_{base} which is mapped nonlinearly onto the animal choice (i.e., percent of trials in which the subject judged $\sigma_{\text{base}} > \sigma_{\text{comparison}}$) through a link function as follows:



where w_1 is the σ_{base} regressor, w_2 is the $\sigma_{\text{comparison}}$ regressor, and c is the baseline regressor that captures the overall (stimulusindependent) bias of the subject in calling $\sigma_{\text{base}} > \sigma_{\text{comparison}}$ (for instance, a bias against turning right, the side associated with the judgment $\sigma_{\text{base}} > \sigma_{\text{comparison}}$).

The coefficients w_1 , w_2 , and c were derived to most closely reproduce the observed performance in that session by an iteratively reweighted least squares algorithm. The w_1 and w_2 regressors quantify the strength of the relationship between σ_{base} and $\sigma_{\text{comparison}}$, respectively, and the animal's choice. If the regressors are plotted in Cartesian coordinates, the critical issue becomes the direction of the vectors formed by w_1 and w_2 . An ideal performer—one who precisely encodes the base stimulus, holds it in the memory, precisely encodes the comparison stimulus, and then accurately judges the difference between σ_{base} and $\sigma_{\text{comparison}}$ —would yield $w_1 = -w_2$, corresponding to the dashed line.

Data from four rats are illustrated in Fig. S2. Any possible bias *c* is independent of stimulus weighting and would not affect angle. Each vector of form (w_1, w_2) derives from one training session. Sessions from stage 6 are plotted in red; sessions from stage 7 are plotted in blue. It is evident that from stage 6 to stage 7 the vectors became more closely aligned to the dashed line, indicating that rats learned to give nearly equal weight to the values of σ_{base} and $\sigma_{\text{comparison}}$. To quantify the changes in vector direction, we carried out a circular version of the Watson–Williams test on the distribution of angles. For rats 2, 3, and 4, there was from stage 6 to stage 7 a significant shift (P < 0.002) of vector direction toward the angle $w_1 = -w_2$. For rat 1, the single-session vectors (w_1, w_2) by stage 6 were already distributed, on average, symmetrically around $w_1 = -w_2$. In this rat, the evolution from stage 6 to stage 7 consisted of a significant decrease in angular

dispersion, indicating that the rat became more consistent in attributing equal weight to σ_{base} and $\sigma_{comparison}$.

Psychometric Curves. In the tactile acuity protocol (Fig. 5), we computed the proportion of trials in which subjects reported $\sigma_{comparison} > \sigma_{base}$. We fit the data with a four-parameter logistic function using the maximum likelihood method in MATLAB, as follows:

Percent judged
$$\sigma_{\text{comparison}} > \sigma_{\text{base}} = \frac{\text{Min} - \text{Max}}{1 + \left(\frac{\text{SDI}}{\text{IF}}\right)^{\text{Slopefactor}}} + \text{Max},$$

where the four parameters are as follows: Min is the lower asymptote determined by the number of alternative choices (two in our task), Max is the upper asymptote, IF is the inflection point along the SDI axis, and Slopefactor is the maximum slope of the curve. The slope is calculated by taking the derivative of the curve and setting SDI = IF:

Slope = Slopefactor
$$\frac{(Max - Min)}{4IF}$$
.

Statistical Test for Delayed Comparison Performance. A given value of $\sigma_{comparison}$ could be preceded by either a smaller or a larger value of σ_{base} . For these two cases, the rat correctly judged $\sigma_{\text{comparison}} > \sigma_{\text{base}}$ or $\sigma_{\text{comparison}} < \sigma_{\text{base}}$, respectively, on some percent of trials. In Fig. 6A, the frequency of the choice $\sigma_{comparison} > \sigma_{base}$ is plotted in the boxes. Gray shading links trials with one value of $\sigma_{comparison}$ preceded by one of two values of $\sigma_{\text{hase.}}$ If performance were perfect, values on the left side would be 100, and those on the right would be 0. The difference between the frequency of these two choices, averaged across animals, is given on the right edge of the gray bars (values are 61, 51, 39, 39, and 22). If rats attended to $\sigma_{comparison}$ but ignored σ_{base} , the difference values would be close to 0. To test the significance of the observed values, for each rat and each fixed $\sigma_{comparison}$ value, we computed the choice difference for 500 trials selected pseudorandomly from that rat's data set and then repeated the resampling 1,000 times. This generated a new bootstrap distribution of differences. Next we compared this resampled difference distribution to a difference distribution obtained after randomly shuffling the σ_{base} and $\sigma_{comparison}$ labels on each trial. The shuffled distribution simulated the expected choices of rats if those choices were not determined by comparing σ values. The distance between the mean of the resampled difference (obtained from real observations) and the mean of the simulated, shuffled distribution, divided by the SD of the distributions, gave a Z-score. On the right side of Fig. 6A, the Z scores are aligned by $\sigma_{\text{comparison}}$ value, with each rat plotted as a point. Conventionally, Z scores > 2 are considered significant (dashed line), and in this analysis, Z scores were found to be much higher. Thus, for most $\sigma_{comparison}$ values, the effect on rats' actions of σ_{base} exceeded 10 SDs and was thus strongly significant. The statistical procedure was repeated on data from human subjects in Fig. 6B.

Similarly, a given value of σ_{base} could be followed by either a larger or smaller value of $\sigma_{comparison}$. For these two cases, the rat correctly judged $\sigma_{comparison} > \sigma_{base}$ or $\sigma_{comparison} < \sigma_{base}$, respectively, on some percent of trials. In Fig. S3A, the frequency of the choice $\sigma_{comparison} > \sigma_{base}$ is plotted in the boxes. Gray shading links trials with one value of σ_{base} followed by two values of $\sigma_{comparison}$. If performance were perfect, values at the bottom end of each gray bar would be 0, and those at the upper end would be 100. The difference between the frequency of these two choices, averaged across animals, is given at the top of the gray bars (values are 45, 49, 56, 67, and 52). If rats attended to σ_{base} but ignored $\sigma_{\text{comparison}}$, the difference values would be close to 0. The significance test was equivalent to that applied in Fig. 6. At the top of Fig. S3A, the Z-scores are aligned by the σ_{base} value,

with each rat plotted as a point. For most σ_{base} values, the effect on rats' actions of $\sigma_{\text{comparison}}$ exceeded 10 SDs and was thus strongly significant. The statistical procedure was repeated on data from human subjects in Fig. S3*B*.

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Fig. S1. Withdrawal from nose poke is triggered by the go cue. Data from one session are illustrated. The *x* axis plots the poststimulus delay, defined as the time from the end of the comparison stimulus until the onset of the go cue. The *y* axis plots the sum of the poststimulus delay and the withdrawal latency, where latency is defined as the time from the go cue onset until the instant in which the rat leaves the nose poke sensor. The plot shows that the time of withdrawal was bound to the time of the go cue.



Fig. S2. Rats learned to perceive and compare the two stimuli. The analysis method is described in *SI Text*. Here data from four rats are illustrated. Any possible bias *c* is independent of stimulus weighting and is not illustrated in this analysis. Each vector of form (w_1, w_2) derives from one training session. Sessions from stage 6 are plotted in red; sessions from stage 7 are plotted in blue. It is evident that from stage 6 to stage 7 the vectors became more closely aligned to the dashed line, indicating that rats learned to give nearly equal weight to the values of σ_{base} and $\sigma_{\text{comparison}}$. To quantify the changes in vector direction, we carried out a circular version of the Watson–Williams test on the distribution of angles. For rats 2, 3, and 4, there was from stage 6 to stage 7 a significant shift (P < 0.002) of vector direction toward the angle $w_1 = -w_2$. For rat 1, the single-session vectors (w_1, w_2) by stage 6 were already distributed, on average, symmetrically around $w_1 = -w_2$. In this rat, the evolution from stage 6 to stage 7 consisted of a significant decrease in angular dispersion, indicating that the rat became more consistent in attributing equal weight to σ_{base} and $\sigma_{\text{comparison}}$.



Fig. S3. Statistical analysis of effect of $\sigma_{comparison}$. (*A*) Values in the boxes give the percent of trials in which rats judged $\sigma_{comparison} > \sigma_{base}$. The difference between paired boxes in a gray band represents the dependence of choice on whether σ_{base} was followed by smaller or larger $\sigma_{comparison}$. The statistical significance of the choice for all single rats is given as a Z-score at the top. (*B*) Same analysis carried out on data from humans.



Fig. S4. Sound cues were below rats' acoustic sensitivity. Recordings in the apparatus (gray plot) show that the vibratory stimuli emitted sound in a frequency range that is not perceived by rats. The plots in the higher-frequency range indicate the sensitivity of albino rats, adapted from (2). This analysis is consistent with behavioral evidence that performance dropped to chance level when whiskers were not moved by the plate.



Fig. S5. Task execution depended on motion of the plate. We tested whether rats could use the acoustic cues associated with actuation of the motor without actual movement of the whiskers. To do so, with well-trained rats we divided four sessions into three blocks: (*i*) pretest, trials executed before detaching the motor from the plate; (*ii*) test, trials executed with the rod/plate assembly still present in the stimulus delivery port but detached from the motor; and (*iii*) posttest, trials executed after reattaching the rod/plate assembly to the motor. With the rod/plate assembly detached, the sound of the motor remained. Each block consisted of approximately 20 trials. Mean performance per block is illustrated, and it is evident that accuracy dropped to chance level when the rod/ plate assembly was detached. From this we conclude that rats could not achieve good performance using acoustic cues.

Parameter	Stage 4: introduction of tactile stimuli	Stage 5: implementation of the stimulus comparison rule	Stage 6: tolerance to variation in parameters
Prestimulus delay, ms	300	300	200–500
Base stimulus duration, ms	50–500	50–500	50-600
Comparison stimulus duration, ms	50–500	50–500	50–600
Interstimulus delay, ms	200–3,000	2,000–3,000	500–5,000
Poststimulus delay, ms	100	300	300–800
Velocity SD, mm/s	128–300	50–300	23–420
Reward target cue	Yes	No	No
Error remediation allowed	Yes	No	No
5-s time-out after error	No	Yes	Yes
SDI	-0.4-0.4	-0.35-0.35	-0.35-0.35



Movie S1. Performance of the tactile working memory task. A well-trained rat is shown on a single trial. The rat places its snout in the nose poke and, after a prestimulus delay, receives two vibrations, separated by a delay. On presentation of the go cue the rat turns to the left reward spout. Visible lighting was used to augment video quality; however, normally, the behavior was carried out in the dark. Acoustic noise signals originating in the motor were readily perceived by human observers but not by the rats.

Movie S1



Movie S2. Motor and whisker motion are tracked across one trial. High-speed video reveals the transmission of motor motion to the whiskers. At the outset, the plate and the whisker of interest are indicated as green bars. Both bars are tracked throughout the duration of the trial by custom-made tracking programs. The whisker closely follows the plate during both the base stimulus (blue trace) and comparison stimulus (red trace). Self-generated whisking was suppressed.

Movie S2