Comparing neuronal and behavioral thresholds for spiral motion discrimination

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As we move, the projection of moving objects on our retinas generates an array of velocity vectors known as optic flow. One class of optic flow is spiral motion, defined by the angle between a local vector direction and the direction of the steepest increase in local speed. By discriminating among such angles, an organism could discern between different flow patterns and effectively interact with the environment. In primates, spiral-selective neurons in medial superior temporal area are thought to provide the substrate for this ability. We found that these cells show higher discrimination thresholds than found behaviorally in humans, suggesting that when discriminating spiral motions the brain integrates information across many of these neurons to achieve its high perceptual performance. ***NeuroReport***

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Introduction

When we move through the environment, a spatial pattern of velocity vectors, commonly known as optic flow, is projected onto our retinas [1]. One family of optic flow patterns, the spirals, can be described by a single parameter: the angle between the local motion direction and the direction of the steepest increase in local speed [2]. This angle, or spiral direction, is 0° in an expanding spiral, 180° in a contracting spiral, and 90 and 270° in clockwise and counterclockwise rotating spirals, respectively.

Earlier studies in primates have found neurons in the dorsal division of the medial superior temporal area that are tuned for spiral direction [2,3], in a similar manner as middle temporal neurons are tuned for the direction of linear motion [4]. These neurons may play an important role in optic flow perception [5]. They can encode expanding and contracting spirals with similar accuracy as the animals [6]. It is, however, unclear whether this ability is restricted to coarse differences between these spiral types (Fig. 1), or it also generalizes to fine discrimination between spiral directions.

In humans, imaging studies have isolated a region adjacent to the middle temporal area that is selectively activated by spirals [7–9], and where lesions produce deficits in complex motion perception [10]. It is reasonable to assume that this region is the human homologue to the medial superior temporal area in macaques, and that in both primate species spiral-selective neurons within the region have similar physiological properties. On the basis of this assumption, we asked the question of how the ability of humans to discriminate spirals compares with the one of medial superior temporal neurons in the monkey.

Methods

Human participants

Seven healthy human males (age 28–40 years), with normal or corrected to normal vision participated in the experiments, conducted at York University (Toronto, Canada) and preapproved by the University Institutional Ethics Review Board. All participants were trained in the task for two to three sessions before the experiments.

Apparatus and task

Participants sat in front of a 22″ CRT computer monitor (LaCie Inc., Oregon, USA), using a chin rest at a viewing distance of 57 cm. Stimuli were generated using an Apple Power PC and custom made software.

We measured spiral direction discrimination thresholds near the cardinal directions in spiral motion space (i.e. rotation, expansion, and contraction) in seven human participants using the method of constant stimuli. In one set of trials, the standard stimulus was an expanding spiral (0°), and the test stimuli were expanding spirals with clockwise or counterclockwise rotation components (350, 352, 354, 356, 358, 2, 4, 6, 8, 10°). In a second set

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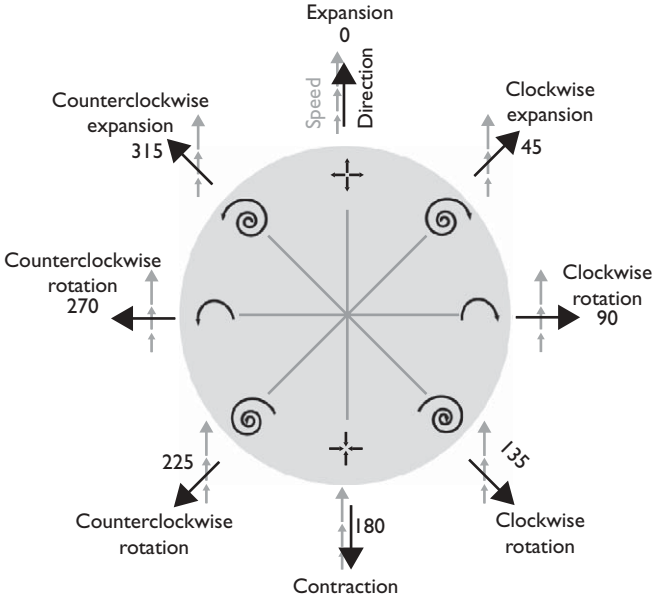
Fig. 1



Spiral space is a coordinate system that interprets expansion (0°), contraction (180°), and rotations (clockwise: 90°, counterclockwise: 270°) as cardinal directions with in and outward spiraling movement patterns placed in between.

of trials, a contracting stimulus served as the standard (180°), and the test stimuli were contracting stimuli with clockwise or counterclockwise rotation components (170, 172, 174, 176, 178, 182, 184, 186, 188, 190°). Participants reported whether the stimulus moved clockwise or counterclockwise.

In a third set of trials, clockwise or counterclockwise rotating stimuli served as standard. The test stimuli were (a) clockwise rotating spiral stimuli with different amounts of expansion or contraction (80, 82, 84, 86, 88, 92, 94, 96, 98, 100°) for the clockwise standard stimulus (90°), and (b) counterclockwise rotating stimuli with different amounts of expansion and contraction (260, 262, 264, 266, 268, 272, 274, 276, 278, 280°) for the counterclockwise standard stimulus (270°). Participants reported whether the stimulus contracted or expanded.

Trials started when the participants foveated the fixation point and pressed the space bar on a computer keyboard. This initiated the appearance of a random dot pattern for 500 ms to the right of the fixation point. In trials with expanding/contracting patterns, participants pressed the '3' (clockwise), or '1' (counterclockwise) key. In trials with rotating patterns, participants pressed '3' (expansion) or '1' (contraction). The experiment was run in two blocks of 240 trials, one block of expanding/contracting trials and the other of rotating trials. After two to three training sessions, each participant performed six blocks (three of each type) in a randomized order. We instructed participants to fixate and monitored eye movements using a video camera. A session was excluded from the analysis if the experimenter detected that a participant broke fixation in at least 10% of trials by visually inspecting the video recordings. As our participants were trained in the task, no session met this criterion.

Stimuli

Stimuli were black random dots on a white background, moving coherently behind a circular aperture (diameter: 10.2°), and centered 7.6° to the right of a central fixation point. The dot density was 5 dots/deg^2, the monitor resolution was 33 pixels/degree, and the monitor refresh rate was 75 Hz. The dot size was 3×3 pixels. The dot speed formed a linear gradient with zero at the center and 6.9°/s at the edge.

Data analysis

We computed a psychometric function for each participant and block type by fitting equation 1 to the proportion of times $P(s)$ that the participants reported: (a) the stimulus rotating clockwise, for contracting/expanding spirals with rotating components, and (b) the stimulus expanding, for rotating spirals with expanding/contracting components. Data from blocks of the same spiral type were pooled.

$$P(s) = \frac{1}{1+e^{-(a1+a2\times s)}} \quad (1)$$

The discrimination threshold was the distance (in degrees) between the point of subjective equality [spiral direction at which $P(s) = 0.5$] and the point where $P(s) = 0.25$, s is the spiral angle and a1 and a2 the function parameters.

Single cell recordings

Participant

We recorded the responses of spiral-selective neurons to moving random dot patterns, in the dorsal subdivision of the medial superior temporal area in the superior temporal sulcus of one rhesus monkey (4-year-old, 6.5 kg male *Macaca mulatta*) while the animal performed a detection task. Before the recordings and the final training, a head holder and recording chamber were implanted under general anesthesia (see Ref. [11] for more details). Recordings were conducted at the University of Tuebingen, Germany. All the procedures were in agreement with the German local and national rules and regulations, and were approved by the Regierungspraesidium Tuebingen.

Apparatus and task

The experimental procedures have been described in more detail elsewhere [11]. Stimuli were white random dots on a dark background (luminance: 55 cd/m^2, background luminance: 0.1 cd/m^2), with dot size and density similar

to the ones used in the human experiments. The dots' average speed was optimized to match the preferred speed of the neurons. The pattern eccentricity varied from 5 to 12° from the fixation point, and the pattern size was approximately equal to that eccentricity. Most neurons had preferred speeds between 4 and 16°/s. We adjusted the speeds of the dots at the aperture's border depending on that preferred speed. To successfully complete a trial, the animal had to maintain fixation within 0.5° from the fixation spot.

A trial consisted of the following sequence of events: (a) a fixation spot and a static random dot pattern appeared inside the cell's receptive field, (b) the monkey fixated the spot and pressed a lever, (c) 200 ms later the pattern began to move, (d) the animal was rewarded with a drop of juice for releasing the lever in response to a transient speed change in the dots (200 ms duration) occurring between 200 and 2000 ms after motion onset. We recorded the responses to eight different spiral directions (0, 45, 90, 135, 180, 225, 270, and 315°).

Data analysis

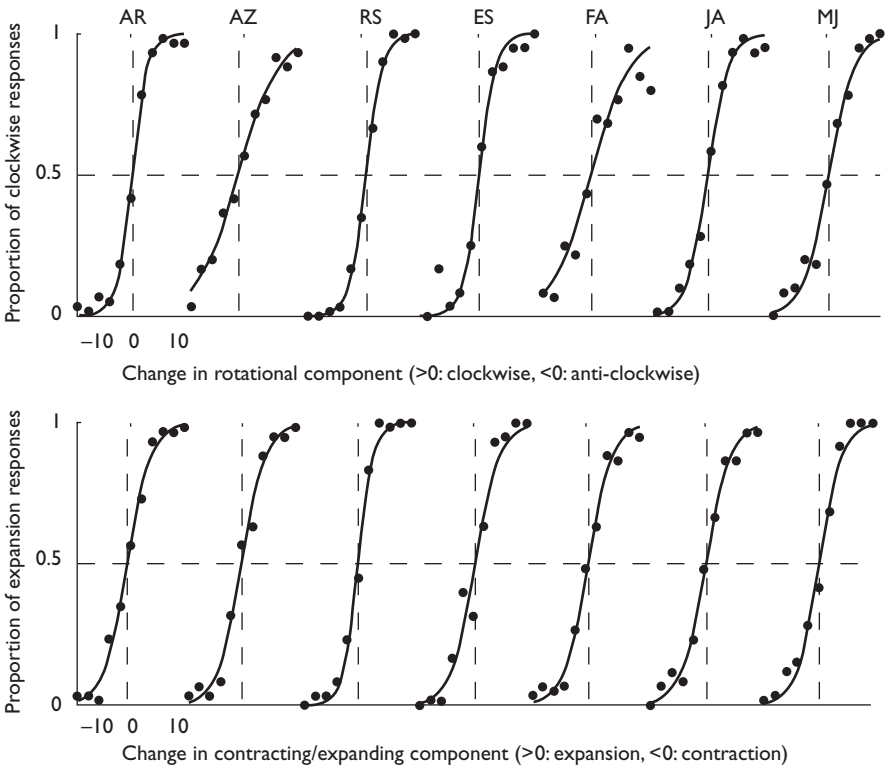
We determined the spiral tuning of each cell ($n = 26$) by fitting the mean responses in correctly performed trials averaged over the time period from 300–800 ms after stimulus onset with a Gaussian function (Equation 2). We only included neurons in which we recorded at least one correctly performed trial per direction. A cell was considered spiral-selective if the fit provided by the function yielded a correlation coefficient ≥ 0.9, and if responses to spirals were better fit than responses to random dot patterns moving in 8 different directions of linear motion. Usually, spiral-selective neurons had large receptive fields that extended into the hemifield ipsilateral to the recording site [12].

$$\text{Response} = r_{\min} + r_{\max} * e^{-0.5 \cdot \left[\frac{(direction - center)}{sigma}\right]^2} \qquad (2)$$

$r_{\min}$ represents the cells response to the antipreferred spiral direction, $r_{\max}$ the difference between $r_{\min}$ and the response to the preferred direction (sensitivity), center represents the preferred direction, and sigma the standard deviation of the Gaussian (selectivity) [2,4,12].

Using the fit parameters, we simulated responses to 600 trials of each one of 46 different spiral directions (spaced every 4°). We assumed that the response variance of a spiral-selective neuron follows a Fano factor of 1.0 (i.e. variance = mean firing rate), as a frequently reported property of cortical neurons [13].

Fig. 2



Averaged psychometric functions (upper row, clockwise/counterclockwise rotation; lower row, expansion/contraction) for human participants. The abscissa represents the amount of variation in the spiral direction and the ordinate the proportion of a given response type. The lines represent the fits through the data. All fits yield correlation coefficients (r) larger than 0.9.

From the responses we computed neurometric functions for seven different response levels around the flanks of the tuning curves [4], within the range of 0.7*maximal response and 1.3*minimal response. For each level, we calculated the probability that more than a given number of spikes would be elicited for each stimulus. These data were fitted with Equation (3) resulting in the criterion level neurometric function. The discrimination threshold for each function was considered as the distance in degrees of spiral direction between the 0.5 and 0.25 probability values.

$$P = \gamma - (\gamma - \partial) * \ e^{-1\left(\frac{d}{\alpha}\right)^{\beta}} \qquad (3)$$

d is the spiral angle, α the direction at which a criterion probability is reached, β is the parameter governing the slope of the function, ∂ is the asymptotic value of P (when $d = 0$), and γ is the probability of reaching criterion for the least preferred direction. These functions are similar to the psychometric functions in that they describe the cell's ability to encode spiral direction [4].

Results

Human measurements

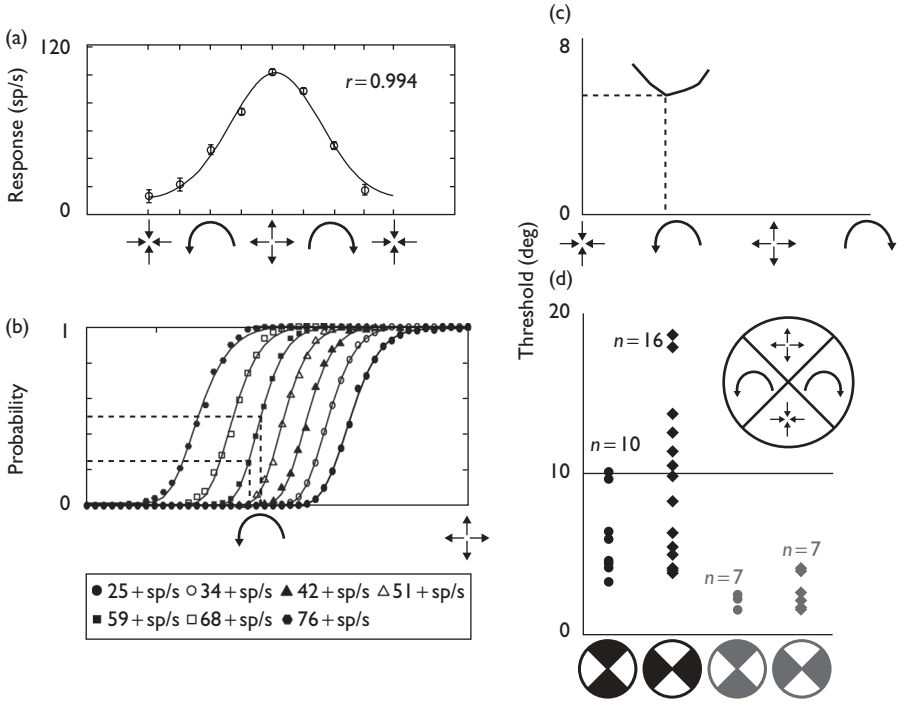
We measured spiral discrimination thresholds in seven human participants (Fig. 2). For changes in the rotational component, the lowest discrimination threshold was 1.58° (AR), and the largest 4.1° (AZ). For changes in the expanding–contracting components, the lowest threshold was 1.54° (RS) and the largest was 2.49° (JA). There was a trend for thresholds for the expansion/contraction components to be lower (mean = 2.55 for rotation and mean = 2.29 for expansion/contraction), but it was not statistically significant ($P > 0.8$, Wilcoxon signed-rank test for paired data).

Neurometric analysis

For the 26 neurons included in our analysis, a Gaussian function provided an excellent fit to the data (Fig. 3a). The distribution of tuning curve parameters across neurons was comparable with previous studies of spiral selectivity in the medial superior temporal area (see Supplemental Digital Content 1, *http://links.lww.com/WNR/A16* and Ref. [2]), suggesting that we sampled a representative set of neurons.

For each neuron we computed a neurometric function and threshold values for the different criterion levels as a function of spiral type (Fig. 3b). The curve is U-shaped; its minimum (5.7°) represents the neuron's best discrimination threshold, that is, the smallest change in spiral direction that the neuron could reliably discriminate.

Fig. 3



(a) Tuning curve of a medial superior temporal neuron to spiral motion. The abscissa represents spiral direction and the ordinate the response (spikes/s). Error bars represent standard errors. (b) Neurometric functions (symbols), and (c) thresholds. (d) Minimum threshold (ordinate) of each neuron (black), and for each participant (gray). For the cells, the data are grouped according to the preferred direction of the neuron in spiral space (symbols in abscissa). For the human participants, the data were divided according to the discrimination task.

We grouped the neurometric thresholds according to the neurons preferred spiral directions (Fig. 3c, abscissa). Six neurons preferred spiral directions within 45° from pure expansion (0°) and four directions within 45° from pure contraction (180°). From the remaining 16 cells, six preferred directions within 45° from clockwise (90°) and 10 preferred directions within 45° from counterclockwise (270°) rotation. We pooled thresholds of neurons selective for expansion/contraction and for the rotation components and compared the values between these two groups. Although we observed a trend for expansion/contraction thresholds to be lower than for rotation, the trend was not statistically significant ($P = 0.07$, Wilcoxon rank-sum test).

In general, when participant thresholds were grouped into the same categories, they show lower thresholds than the correspondent group of neurons ($P < 0.001$, Wilcoxon rank-sum test for both comparisons) (Fig. 3c).

Discussion

Different from previous behavioral studies in humans using spiral stimuli [14–16], our estimation of spiral discrimination thresholds did not show a significant perceptual bias toward a particular spiral type. These studies, however, used different tasks [14,15] or more eccentric stimuli [16], making a direct comparison with our data difficult. Nevertheless, we found a nonsignificant trend for neurons selective for expansion/contraction to have lower thresholds than neurons selective for rotation (Fig. 3).

The neurometric thresholds in our study were significantly larger than human behavioral thresholds. This result apparently disagrees with a previous report of medial superior temporal neurons having sensitivities equal or superior to monkey's thresholds for expanding and contracting spirals [6]. However, in that study the authors used a task in which animals performed a coarse discrimination between expanding and contracting stimuli embedded in noise. In contrast, our task required a fine discrimination judgment, and we used 100% coherence random dot patterns. Given their tuning properties, the neurons in our study should be highly capable of discriminating spiral directions 180° apart. Previous studies in the medial superior and middle temporal area of monkeys have reported similar results as ours [17–19].

A plausible explanation for our results is that in our study the stimulus feature (spiral angle) was not behaviorally relevant to the animal, as it performed a fixation task, leading to underestimation of the neurons sensitivity and selectivity [12,20–22]. We, however, estimated that the tuning curve height (sensitivity) would need to increase by at least 400%, or the width (selectivity) decrease by 55% for the mean threshold value across units to reach the average human threshold. These effects are disproportionally larger than the ones reported in previous studies, making this explanation unlikely.

A recent study examined the ability of single neurons in monkey middle temporal area to discriminate linear motion direction [23] using a coarse discrimination task and similar response integration times as us (500 ms). They concluded that at such short integration times (but not at longer times) neurometric thresholds were higher than behavioral thresholds [23,24]. This suggests that the integration time used in the neurometric analysis plays a role in computing neuronal thresholds.

Finally, several studies in monkeys have shown that medial superior temporal neurons receive inputs from different sources, such as vestibular and eye movements signals [18,25]. Under conditions in which the information from those sources becomes available, the performance of some of these neurons correlates better with behavior [18]. Thus, it may be that medial superior temporal units perform best when integrating signals from multiple sources.

Conclusion

Our results show that neurometric spiral direction-discrimination thresholds of primate medial superior temporal neurons are significantly higher than behavioral thresholds. This suggests that the computations underlying this discrimination are either conducted by these units using population codes [13], and/or by other neurons located in different brain areas with higher selectivity and/or sensitivity for spirals.

Acknowledgements

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