Temporal Information Can Influence Spatial Localization

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Maij F, Brenner E, Smeets JB. Temporal information can influence spatial localization. *J Neurophysiol* 102: 490–495, 2009. First published May 13, 2009; doi:10.1152/jn.91253.2008. To localize objects relative to ourselves, we need to combine various sensory and motor signals. When these signals change abruptly, as information about eye orientation does during saccades, small differences in latency between the signals could introduce localization errors. We examine whether independent temporal information can influence such errors. We asked participants to follow a randomly jumping dot with their eyes and to point at flashes that occurred near the time they made saccades. Such flashes are mislocalized. We presented a tone at different times relative to the flash. We found that the flash was mislocalized as if it had occurred closer in time to the tone. This demonstrates that temporal information is taken into consideration when combining sensory information streams for localization.

INTRODUCTION

We combine information from different modalities to make sense of the world. These information sources do not necessarily have the same neuronal latencies. The latencies can differ by tens of milliseconds (Schmolesky et al. 1998). Yet signals that belong together must somehow be related to the same event. It might be that all the different latencies are known and are all taken into account. However, it has been shown that we tolerate artificial differences in timing of $\leq$100 ms between signals, probably because we know we are uncertain about the timing (Munhall et al. 1996; van Mierlo et al. 2007).

Tolerating differences in latency will yield errors if the signals are changing fast as is the case during a saccade. It has been shown that under some conditions flashes presented $\leq$100 ms before or after a saccade are mislocalized (Matin and Pearce 1965; reviewed by Schlag and Schlag-Rey 2002). If this misjudgment is (partly) due to errors in judging time of the flash relative to the eye movement, we should be able to manipulate the errors by changing the judged moment of the flash. To do so, we make use of the expected effect of a tone on the flash. Tones cannot be neglected when judging the number of flashes (Shams et al. 2002). Furthermore, it has been shown that a tone can alter the perceived time of a visual stimulus (Morein-Zamir et al. 2003; Vroomen et al. 2004). We anticipated that people would be unable to neglect a tone presented near the time of a flash when they are required to localize the flash. If the tone and flash are perceived as being one event, we expect the time of that event to be a weighted average of the times of two components (Ernst and Bülthoff 2004). Therefore we predict that a tone will influence the

(mis)localization of a flash presented near the time of a saccade: presenting a tone just before a flash will have the same effect as presenting the flash earlier (at the same retinal position), and presenting a tone just after the flash will have the same effect as presenting the flash later. This prediction will be quantified with the help of two experiments on explicit temporal judgments and will be tested experimentally in an experiment involving peri-saccadic mislocalization.

METHODS

The two temporal judgment experiments will be discussed in the model prediction section. Here we describe the main peri-saccadic mislocalization experiments.

Design and participants

We conducted the experiment in five parts in a normally illuminated room (~500 lux measured on the table just in front of the participant). The parts only differed in the timing of the tone. Eleven colleagues volunteered to participate in the experiment (including 1 of the authors). There were four participants in parts 1 and 3 and three in the other three parts. Some participants took part in more than one part of the experiment. Only the author was aware of the specific conditions. All participants had normal or corrected-to-normal vision and normal hearing. The research in this study was approved by the ethics committee of the Faculty of Human Movement Sciences.

Experimental setup

Visual stimuli were presented on a touch screen (EloTouch CRT 19", 1,024 × 768 pixels, 36 × 27 cm, 85 Hz) using the Psychophysics Toolbox in MATLAB (Brainard 1997). The visual stimuli were viewed from a distance of 60 cm. Eye movements were registered using an Eyelink II (SR Research, Mississauga, Ontario, Canada) at a sample frequency of 500 Hz using the Eyelink toolbox (Cornelissen et al. 2002). Participants were asked to follow a 0.5° diameter jumping white dot (108 cd/m²) with their eyes. The dot was presented at a new position every 400 ms (Fig. 1). It jumped in steps of 7.6° across a gray screen (100 cd/m²). Each jump displaced the dot randomly in one of eight radial directions: horizontal, vertical, and diagonal, but never choosing a direction that would bring the dot within 115 pixels (4°) of the edge of the screen.

After a series of three, four, or five steps (determined at random with equal probabilities), the white dot was removed from the screen. One frame later, a 0.5° diameter black dot (7 cd/m²) was flashed (on 1 frame, which means that it was actually on the screen for <1 ms). It was flashed at 2/3 or 4/3 of the 7.6° displacement between the last two positions of the white dot. The flash was thus always 2.5° visual angle from the saccade target. After the flash the screen remained empty (gray) until the participant touched it to indicate where they had perceived the flash. Beside the visual stimuli, we presented a tone [75 dB (A) at the position of the participant; multiple sine-waves with an amplitude that steadily declined to 0 in 25 ms] at different moments with respect to the flash. The tone was generated by two loudspeakers that were placed on top of the monitor.
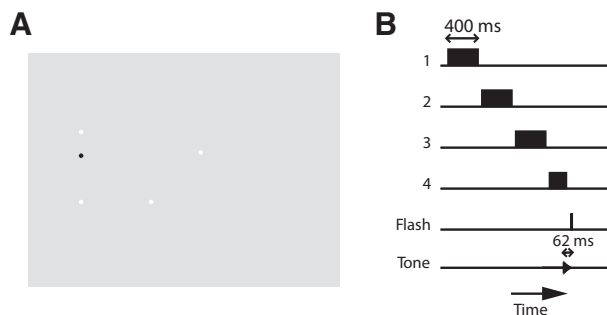
FIG. 1. Schematic spatial (*A*) and temporal (*B*) overview of a single example trial. The white dot started near the center of the screen and jumped consecutively in a diagonal, leftward, and upward direction. The black dot flashed at 2/3 of the white dot's last displacement. The flash appeared ~1 saccadic reaction time after the last white dot appeared on the screen. On this trial a tone was presented 62 ms before the flash.

Calibration

To synchronize the eye movement recordings with the images, we measured the moment of the flash with a photo diode and used the signal from the photo diode to drive an IRED that blinded one of the Eyelink cameras. This was done in a separate session and provided the information that we needed to correct for delays between presenting the flash and measuring eye movements. The delay between tone onset and flash was determined using an oscilloscope connected to the above-mentioned photo diode as well as to the audio output. Tone onset was considered as the time of the tone.

Before each session the participant was asked to calibrate the touch screen using a standard nine-point calibration provided by EloTouch. Next, the recording of eye movements was calibrated using the standard nine-point calibration procedure of the Eyelink II.

Procedure

Because the mislocalization of the flash only occurs around the moment of the saccade, we wanted to present as many as possible flashes at about that time. We used the saccadic reaction times on previous trials to predict the saccade onset. Dafoe et al. (2007) showed that the saccadic reaction time depends on the saccade direction, so we considered the direction in our predictions. We used the average saccadic reaction time on the five previous trials in which the saccades were in the same direction as that of the trial in question for the prediction. We used Dafoe et al.'s (2007) average reaction times for each direction at the beginning of each session. At the predicted saccadic reaction time, the black dot was flashed on the screen for one frame at either 2/3 or 4/3 of the last displacement of the white dot. If the predicted reaction time was shorter than the interval between the tone and the flash, the tone was presented immediately after the saccadic target appeared and the flash was delayed accordingly.

The participants were asked to touch the screen at the location at which they saw the black flash. If no new white dots appeared and the participant had not seen a black flash (for instance because he or she blinked), the participant indicated having missed the target by touching the screen in one of the corners. In total there were 480 trials in each session. Participants performed three or four sessions within each part of the experiment (see Table 1).

Data analysis

We used the gaze position data of the right eye to determine the characteristics of the saccades, and the first location at which the finger touched the screen as the perceived position. For an eye movement to be considered to be a saccade, its tangential velocity had to exceed 35°/s for at least two consecutive samples (4 ms). We

discarded trials in which the touched location differed by >200 pixels (7° visual angle) from the actual location of the flash (usually because the participant touched one of the corners, but sometimes they accidentally touched the wrong part of the screen; for instance accidentally touching the screen with other parts of the hand instead of the planned index finger). We also discarded trials if the direction of the last saccade deviated by >22.5° from the direction of the last displacement of the white dot, irrespective of saccade amplitude.

We only analyzed the mislocalization in the direction of the saccade: the component of the vector between the touched location and the true location of the flash in the direction of the last displacement of the dot. We plotted these signed errors as a function of the different moments of the flash relative to saccade onset (for individual trials). To draw a smooth curve through these data (for each condition; i.e., each interval between tone onset and flash), we averaged the errors for each participant and condition with a (moving) Gaussian window ($\sigma = 5$ ms). The smooth curve was drawn as long as there were at least five data points within 2σ of the peak of the Gaussian. We will refer to this curve as the mislocalization curve. We ignored the whole condition for a participant if there was no data for >5 ms at any time between 50 ms before and 50 ms after saccade onset because this period is critical for judging the timing of the mislocalization.

To determine whether the pattern of localization errors is shifted in time between the different conditions (which only differed in the timing of the tone), we looked for the shift that would produce the best, single mislocalization curve for each participant in each part of the experiment (Fig. 2). We determined the time shifts between the conditions that minimize the median squared difference (considering both flashes at 2/3 and 4/3 of the last displacement of the white dot) between a single mislocalization curve (for each flash location) and all the data points for that participant in that part of the experiment (see Supplementary material[1] for a detailed mathematical description of this method).

This method for finding the temporal shift only yields differences between conditions. To align the different parts, and to relate all values to a condition with no tone (while not all parts included a no-tone condition), we combined the above-mentioned differences in three steps. We first aligned the data points of the different participants within each part by minimizing the total between-participant variability across conditions: the average value across conditions was set to the same arbitrary value for all participants. We then aligned the temporal shifts between parts (without shifting the relative positions within each part) on the basis of the overall average values of the common conditions. Finally, the average value of the no-tone condition was considered to be the origin (i.e., 0; see Supplementary material for a detailed mathematical description of the method).

Model prediction

We used a model based on the following reasoning to predict the temporal shift that a tone will induce in the mislocalization pattern. If

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[1] The online version of this article contains supplemental data.

TABLE 1. *Some experimental details*

Part	Number of Participants	Number of Sessions	Condition
1	4	3*	−62, 42
2	3	4	−62, −4, 42, no tone
3	4	4	−202, −152, −98, −62, −4
4	3	3	−62, 42, 143
5	3	4	−62, −46, −26, −4

The conditions are characterized by how long after the flash the tone was presented (in ms). *one participant performed 4 sessions.
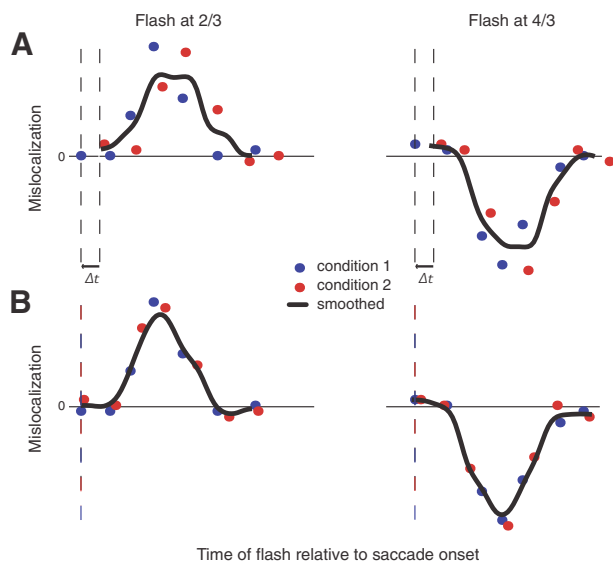
FIG. 2. Schematic illustration of how the temporal shift of the mislocalization patterns [Δ(t)] was determined. *A*: hypothetical data with a clear shift in time between the mislocalization in the 2 conditions (both with a flash at 2/3 and 4/3 of the last displacement of the white dot). The black curve is the smoothed average of all data points. *B*: the data points of condition 2 have been shifted in time to find the best fit [the value of Δ(t) that minimizes the median squared deviation of the points from the black curves for both flash locations].

there is some uncertainty about the timing of the flash, and a tone is presented near the moment of the flash, the participant may judge the flash and the tone to have resulted from the same event. If the interval between the flash and the tone is long, they will be considered to arise from separate events. We describe the probability of considering the flash and the tone to have occurred simultaneously by a normal distribution with parameters that will be estimated later (thick line in Fig. 3*A*). If the tone and flash are perceived to originate from the same event, the moment of the flash can best be judged from a weighted average of the timing of the two signals. Such weighted averaging will cause a shift in the judged moment of the flash toward the time of the tone (Fig. 3*B*).

Our prediction for the influence of the timing of the tone on the timing of the mislocalization of the flash [Δ(t)] is the product of the probability of considering the flash and tone to have occurred simultaneously and the influence that the tone has when they are considered to occur simultaneously

$$\Delta(t) = wt \cdot ce^{\frac{-(t-b)^2}{2\sigma^2}} \qquad (1)$$

where t is the time difference between the flash and the tone, w is the weight given to the tone when determining the time of the combined event from the estimates of the timing of the flash and tone (slope in Fig. 3*B*), b is the offset between the flash and the tone for which the two are most likely to be considered synchronous, σ is the width of the distribution of times for which flash and tone are considered to arise from the same origin, and c is the peak likelihood of considering the tone and flash to be simultaneous (Fig. 3*A*). Figure 3*C* shows our prediction for the temporal shift of the mislocalization curves (the product of *A* and *B*).

To estimate reasonable values for this interpretation (and thus to be able to draw curves in Fig. 3), we performed two temporal judgment experiments. Both were performed after the main experiment. To determine the moment of simultaneity, we showed 14 participants the same displays as in the main experiment and instructed them to follow the white dots in the same manner, but rather than asking them to localize the flash we asked them to report whether or not the tone and the flash occurred simultaneously. The participants touched the screen in one of

the two lower corners to indicate whether the flash and tone occurred simultaneously or not. We fit a normal distribution to each participants' data by using psignifit version 2.5.6 (see http://bootstrap-software.org/psignifit/), a software package that implements the maximum-likelihood method described by Wichmann and Hill (2001). The median values of the parameters of these fits were an amplitude (c) of 0.82, an uncertainty (σ) of 82 ms and a peak when the tone is presented 31 ms before the flash ($b = -31$; Fig. 3*A*).

To determine the weight given to the tone in the perception of the time of the flash (slope of Fig. 3*B*), we showed 14 participants a sequence of three black flashes (same specifications as in the main experiment) at the screen center. The third flash was 1,200 ms after the first, whereas the second was between 400 and 800 ms after the first (steps of 50 ms). The participants were asked to judge whether the first or the second interval was longer by pressing the lower left or right corner of the touch screen. The second flash was accompanied by
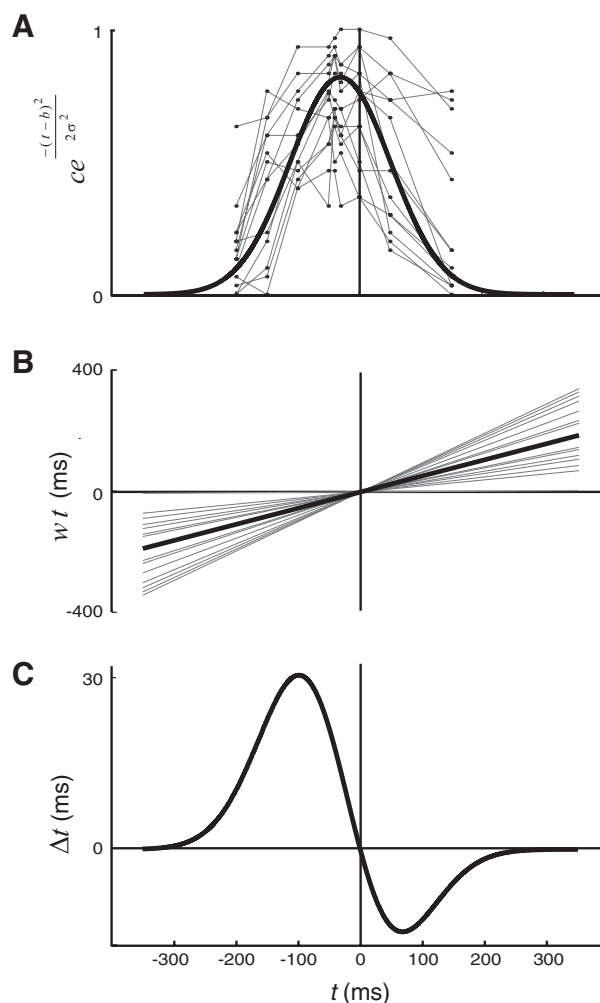

FIG. 3. Model predicting the temporal shift of the mislocalization pattern as a result of presenting a tone at various times. *A*: probability of the flash and tone being considered to arise from the same event. The thick curve is based on the median values from fits of normal distributions to 14 participants' simultaneity judgments (dots connected by thin lines). *B*: the influence of the tone on the judged time of the flash if the 2 are considered to arise from the same event is a weighted average of the time of the flash and the tone. The thin lines are individual participants' data and the thick line is the median value based on 14 participants' interval judgments. *C*: predicted temporal shift as function of the time (t) of the tone relative to the flash: product of the values in *A* and *B*. Because interpreting the retinal stimulation by the flash as if it had occurred later means that the eye orientation signal will influence earlier flashes, the sign is inverted.

a tone that was presented either 46 ms before or 42 ms after the flash. We fit each participant's data for each interval between tone and flash with a psychometric function to estimate the points of subjective equality. Again psychometric functions were fit using psignifit. The difference between the points of subjective equality for the two intervals between tone and flash gives us a measure of the influence of the tone (for each participant). By dividing the median difference between the points of subjective equality by the difference between the times of the tones (-46 ms and 42 ms), after correcting for the likelihood of considering the tone to arise from the same events (on the basis of the values from the simultaneity judgment experiment at those times), we estimated that the median weight (*w*) given to the tone was 0.53 (Fig. 3*B*).

RESULTS

Eye movements

We obtained useful localization judgments from 21,227 trials. This is $70 \pm 10\%$ (mean $\pm$ SD across participants) of the ~30,000 trials. For 22% of the trials, the judgments were ignored because there was no detectable saccade near the moment of the flash (including trials in which the participant blinked). In a further 3% of the trials, the deviation of the direction of the saccade differed too much ($>22.5°$) from the expected saccade direction. Another 1% of the trials was discarded because the screen was touched >200 pixels ($7°$) from the actual location of the flash. Ninety percent of these missed flashes had been presented at 4/3 of the last displacement of the white dot. This occurred as frequently when the tone was presented before as when it was presented after the flash. The last 4% of the total number of trials was discarded because we removed the whole condition for a participant if there was >5 ms of data missing in the critical period for judging the timing of the mislocalization (between 50 ms before and 50 ms after the saccade onset). This was so for the trials of three of the four participants when we presented a tone 202 ms before the flash in part 3.

Earlier research showed that saccadic reaction times depend on the radial direction (Dafoe et al. 2007). We found similar results (Fig. 4*A*). Presenting the tone before the flash means that on average it was presented before the saccade, because on average the flash was presented at the time of the saccade. We found no evidence that presenting a tone before the flash decreases the saccadic reaction time (illustrated for part 2 in Fig. 4*B*; see Table S1 of the Supplementary material for the
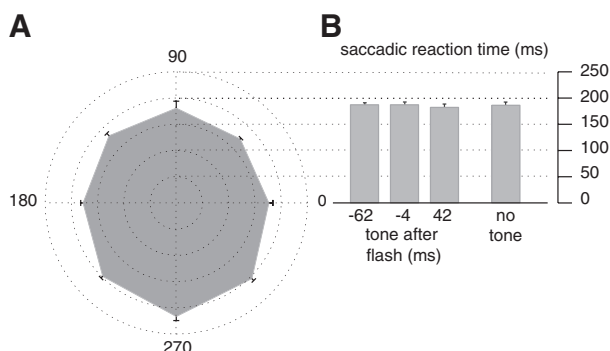

FIG. 4. Saccadic reaction times in part 2. *A*: times for target jumps in different directions with standard errors across participants. Reaction times were largest for downward saccades. *B*: reaction times for different moments of (or absence of) the tone. The axis on the right applies to both *A* and *B*.
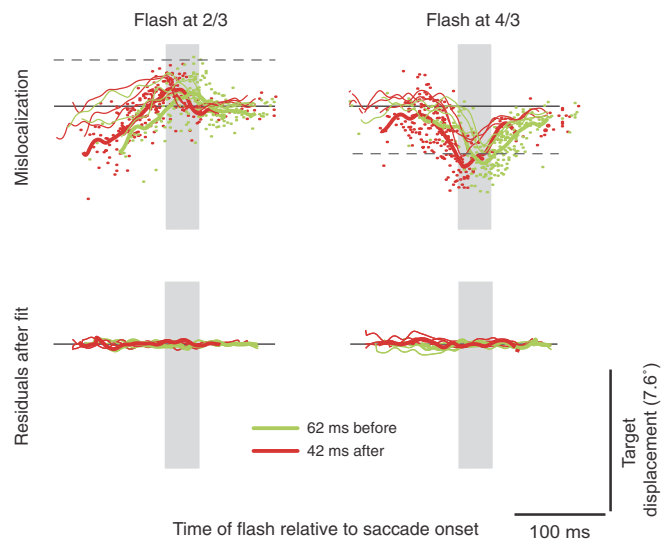

FIG. 5. Pattern of mislocalization in part 1. Data for targets flashed at 2/3 (*left*) and 4/3 (*right*) of the last displacement of the white dot. The gray bar indicates the average duration of the saccade (aligned at onset). *Top*: green and red dots show one participants' errors for individual flashes when the tone was presented 62 ms before the flash and 42 ms after the flash, respectively. The thick lines are smoothed averages of the dots of the same color. Curves for the other participants (thin lines) are shown without the raw data. The horizontal continuous line indicates the position of the flash (no mislocalization). The dashed line indicates the position of the saccade target. *Bottom*: mislocalization that cannot be accounted for by shifting a single mislocalization curve in time [to obtain $\Delta(t)$]. The curves show the difference between the mislocalization curves of the *top panel* and shifted best-fitting single average curves for each participant.

other parts) Also for various other saccade parameters we found no dependency on the condition (see Table S1 of the Supplementary material).

Mislocalization

From Fig. 5, *top,* we can see that participants make systematic errors when targets are presented near the time of saccade onset (the left edge of the gray bar) and that the timing of these errors depends on when the tone was presented. The mislocalization curve is shifted to the right in the condition in which the tone was presented 62 ms before the flash (green) compared with when it was presented 42 ms after the flash (red). A rightward shift indicates that flashes presented at a certain time were perceived as if they were presented earlier. This is consistent with participants perceiving the flash at an earlier moment if it was *preceded* by a tone than if it was *followed* by a tone.

To see whether the differences between the conditions were really pure time shifts, we calculated the residual variability with respect to that single mislocalization curve for each condition. These residuals were then smoothed with a (moving) Gaussian window ($\sigma = 5$ ms). The fact that the curves in Fig. 5, *bottom,* are flat and similar for both conditions shows that shifting the data in time captures most of the variability between the conditions.

In Fig. 6 we show the mislocalization curves (before any time shifts) for each condition of the other parts (see Table 1). We noticed that some participants showed peculiar patterns of mislocalization. For example the participant in part 2 whose
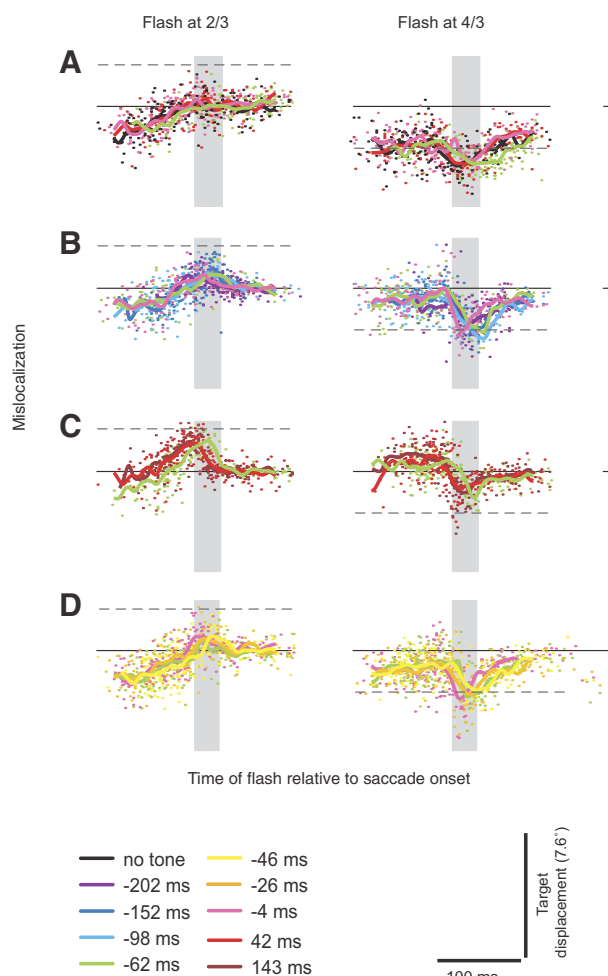
FIG. 6. Mislocalization curves in part 2 (A), part 3 (B), part 4 (C), and part 5 (D). Data of a different participant are presented for each part. See Fig. 5 for other details.

data are shown in Fig. 6A shows an overall systematic error that is independent of the timing for flashes presented at 4/3 of the last displacement of the white dot. Dassonville et al. (1992) attributed similar results to misjudged retinal eccentricity (evidence for misjudged eccentricity can be found in studies such as Müsseler et al. 1999). Importantly, in our study, participants that showed unusual patterns of mislocalization showed a similar temporal shift as the others, so such participants' behavior need not be considered separately. One other aspect that is worth mentioning is that the mislocalization was similar for the eight radial directions that we used (not shown), which is in line with earlier reports (Honda 1991). There is no overall bias toward mislocalizing targets in a specific direction in space, such as the location of the loudspeakers (also not shown).

Temporal shift

The data in Fig. 6 are typical examples, showing only one participant per part. The best-fitting shift values for each participant in each condition are shown in Fig. 7. How the data of the different participants and parts are aligned is explained in the data analysis section of METHODS (and in the Supplemen-

tary material). The temporal shift was ~20 ms when the tone was presented 62 ms before the flash and ~5 ms when the tone was presented 42 ms after the flash. The dashed line in Fig. 7 shows the model prediction with the parameters from the two temporal judgment experiments. This prediction overestimates the effect of the tone.

The solid line in Fig. 7 shows a fit of our model (*Eq. 1*) to the data (solid line in Fig. 7). The following parameters fit our data best: $c \cdot w = 0.28$, $b = -51$ ms and $\sigma = 65$ ms. Based on the value of c from the simultaneity judgments of 0.82, the weight *w* given to the tone is ~0.34. A χ^2-test (Press et al. 1992) indicates, that the data do not deviate significantly from this model [$\chi^2(54) = 62.22$, $P > 0.05$]. A similar test indicates that we can reject a model whereby the tone has no effect [$\chi^2(57) = 303.78$, $P < 0.001$; i.e., the data do deviate significantly from 0]. The data are also significantly different from the model prediction with the parameters from the two temporal judgment experiments [$\chi^2(54) = 149.10$, $P < 0.001$].

DISCUSSION

In this study, we examined whether the presence of an irrelevant tone near the time of a flash influences the location at which the flash is perceived. We presented the tone at different moments with respect to the flash and found a temporal shift of the mislocalization as a result of doing so. This temporal shift was largest when the tone was presented 40–100 ms before the flash, and negligible when the tone was presented >150 ms after the flash or >200 ms before the flash. When it had an effect, presenting a tone influenced the perceived location of the flash in the way that presenting the flash nearer to the time of the tone would have done. We interpret this as evidence that the tone changes the perceived time of the flash. Note that this happened although participants were not instructed to pay attention to the tone, so we can consider the tone to be task irrelevant. In this respect our study differs from a study by Binda et al. (2007) where tones were presented at different positions and the position of the tone was relevant for the task.
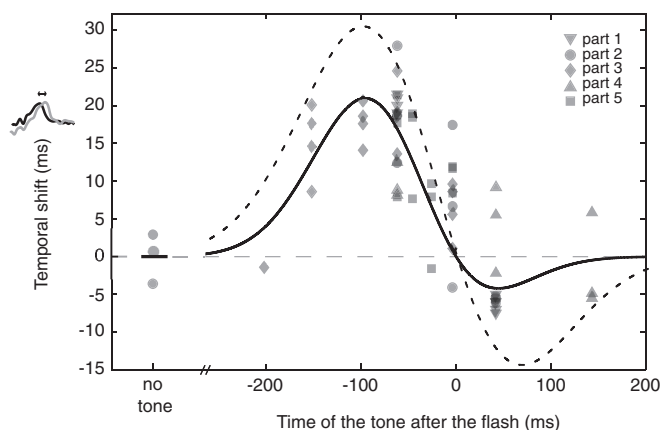

FIG. 7. Temporal shift of the mislocalization curve as a function of the interval between tone onset and flash. Each symbol represents the best shift for 1 participant in 1 condition of a part of the experiment (considering both flashes at 2/3 and 4/3 of the last displacement of the white dot). Different symbols represent different parts. The dashed line represents the model of *Eq. 1* with parameter values that were predicted from the 2 temporal judgment experiments (reproduced from Fig. 3C). The solid line represents the best fit of *Eq. 1* to the data.

We presented the flash at two different locations: at 2/3 and 4/3 of the distance between the last displacements of the white dot. Having different locations revealed that the mislocalization was mainly in the direction of the saccade target. Some other studies have reported such compression of the locations of flashed targets (Ross et al. 1997), whereas others did not find such compression (Dassonville et al. 1992). This compression is still not fully understood. The compression is not found when the experiment is performed in the dark (Dassonville et al. 1992), the critical issue being whether there are visual references after the saccade (Lappe et al. 2000; Morrone et al. 2005a), but even studies performed in a dimly lit room do not always show this compression (Brenner et al. 2005). The compression has been related to saccadic speed because it is negligible for saccades that are <5° (Ostendorf et al. 2007) or to changing receptive field size and location (Hamker et al. 2008). Compression has also been related to temporal uncertainty (Brenner et al. 2006). Our results support the latter interpretation by showing that there is indeed uncertainty about the time of the flash. We here show that the compression does not only occur for isolated saccades made repeatedly to the same position (e.g., Lappe et al. 2000; Morrone et al. 2005b) but also during continuous scanning behavior with frequent saccades in unpredictable directions.

Our main results are nicely summarized by *Eq. 1*. When we compare the estimates of w, b, and σ from the two temporal judgment experiments described in the model section ($w \cdot c = 0.43$, $b = -31$ ms, $\sigma = 82$ ms) with the results of the fit to the main experiment ($w \cdot c = 0.28$, $b = -51$ ms, $\sigma = 65$ ms), we find that the values are similar but not identical. We are not concerned by these differences because the variability of the temporal judgment tasks across participants is large (thin lines in Fig. 3). Moreover, it has been shown that the precise values of parameters for temporal precision depend strongly on the methods used (Vatakis et al. 2008), and our two temporal judgment tasks are not completely comparable to the main experiment. For instance, in the main experiment, we did not instruct the participants to pay attention to the tone, whereas in the simultaneity judgment task (which was therefore performed later), we obviously did. Similarly, in the main experiment, the flashes were presented at unpredictable locations on the screen, whereas in the experiment in which a sequence of three flashes was presented, the flashes were always presented at the center of the screen. Moreover, in the main experiment, the participant was making saccades to follow the randomly moving dot, whereas in the three-flash experiment, the participant was probably fixating the screen center.

To conclude, we show that introducing an irrelevant tone at different moments with respect to the time of a flash shifts the pattern of mislocalization of flashes presented near the time of saccades. We show that a model based on weighted averaging of the judged times of the flash and the tone, and that considers the probability of the two being perceived as arising from one event, provides a good description of the data. We therefore conclude that temporal information is taken into consideration when combining spatial information from different sensory streams for localization.

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