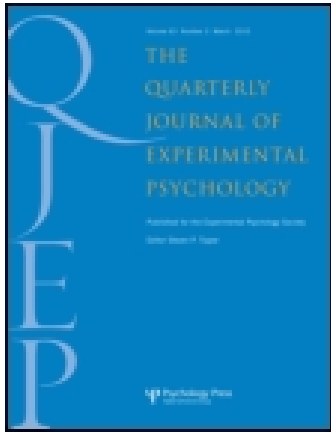


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Publisher: Routledge

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The Quarterly Journal of Experimental Psychology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/pqje20>

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Accepted author version posted online: 08 Jul 2013. Published online: 17 Jul 2013.

To cite this article: Alexis D. J. Makin, Rebecca Lawson, Marco Bertamini & Jayne Pickering (2014) Auditory clicks distort perceived velocity but only when the system has to rely on extraretinal signals, *The Quarterly Journal of Experimental Psychology*, 67:3, 455-473, DOI: [10.1080/17470218.2013.816751](https://doi.org/10.1080/17470218.2013.816751)

To link to this article: <http://dx.doi.org/10.1080/17470218.2013.816751>

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Auditory clicks distort perceived velocity but only when the system has to rely on extraretinal signals

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Previous work has found that repetitive auditory stimulation (click trains) increases the subjective velocity of subsequently presented moving stimuli. We ask whether the effect of click trains is stronger for retinal velocity signals (produced when the target moves across the retina) or for extraretinal velocity signals (produced during smooth pursuit eye movements, when target motion across the retina is limited). In Experiment 1, participants viewed leftward or rightward moving single dot targets, travelling at speeds from 7.5 to 17.5 deg/s. They estimated velocity at the end of each trial. Prior presentation of auditory click trains increased estimated velocity, but only in the pursuit condition, where estimates were based on extraretinal velocity signals. Experiment 2 generalized this result to vertical motion. Experiment 3 found that the effect of clicks during pursuit disappeared when participants tracked across a visually textured background that provided strong local motion cues. Together these results suggest that auditory click trains selectively affect extraretinal velocity signals. This novel finding suggests that the cross-modal integration required for auditory click trains to influence subjective velocity operates at later stages of processing.

Keywords: Velocity; Smooth pursuit; Eye movements; Click trains; Multimodal integration.

Many studies have explored the effect of repetitive auditory stimulation (also known as click trains) on subsequent perceptual and cognitive processing (Droit-Volet, 2010; Jones, Allely, & Wearden, 2011; Penton-Voak, Edwards, Percival, & Wearden, 1996; Treisman, Faulkner, Naish, & Brogan, 1990). It has been repeatedly shown that clicks trains elongate the subjective duration of a subsequent visual or auditory event. This has been demonstrated with a number of procedures, for example with verbal estimation or temporal reproduction (Penton-Voak et al., 1996), bisection or comparison (Wearden, Philpott, & Win, 1999).

The effect of clicks on perceived duration is multiplicative—that is, the clicks add a constant proportion to subjective duration, so that the slope of the relationship between actual duration and estimated duration is steeper after clicks than silence (Penton-Voak et al., 1996, and see Wearden, Edwards, Fakhri, & Percival, 1998, for elucidation of the theoretical significance of *slope effects* in cognitive timing). Recently it has been shown that click trains increase the amount of cognitive processing within a given duration. For example, after clicks, a greater number of items can be encoded in a brief presentation, or mental arithmetic operations

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A Leverhulme Trust Early Career Fellowship sponsored Alexis Makin. An Experimental Psychology Society Student Bursary sponsored Jayne Pickering, who collected data during summer 2012.

This article was originally published with errors. This version has been corrected. Please see corrigendum (<http://dx.doi.org/10.1080/17470218.2013.837266>).

can be completed more quickly (Jones et al., 2011). Although nobody knows exactly how auditory click trains elongate subjective duration, the phenomenon is robust and well established.

In a recent study, Makin, Poliakoff, Dillon, et al. (2012) reported that clicks also increase subjective velocity. In one experiment, participants heard clicks, silence, or white noise through headphones and then observed a sinusoidal black-and-white grating that drifted rightwards. At the end of each trial, they estimated the velocity of the moving grating. Mean velocity estimates were greater after clicks than after either silence or white noise. In the current work, we test *which* velocity signals in the human brain are altered by prior presentation of auditory click trains.

This is an interesting question because researchers do not yet understand the multimodal connections that mediate the effect of auditory clicks on subsequent processing. One possibility is that the effect is produced by changes in early visual regions, V1 to V5. It is now well known that even primary visual cortex responds to auditory stimuli, and that the traditional model of early, encapsulated unimodal regions is outdated (e.g., Ghazanfar & Schroeder, 2006; Romei, Murray, Cappe, & Thut, 2009). Alternatively, clicks could selectively alter representations in higher level areas, traditionally referred to as “association cortex”, whilst leaving more peripheral visual processing untouched. This is perhaps more likely, given that the clicks can alter representations several seconds after offset. In contrast, most work on low-level multisensory interactions has demonstrated facilitation when stimuli are presented almost concurrently and when other precise constraints are met (Bolognini, Senna, Maravita, Pascual-Leone, & Merabet, 2010).

Retinal versus extraretinal velocity signals

Various velocity signals are involved in eye movement control, and velocity processing has been extensively studied (for reviews see Barnes, 2008; Leigh & Zee, 2006; Lisberger, 2010; Thier & Ilg, 2005). Target motion across the retina produces *retinal velocity signals*. In the absence of

fixation instructions, retinal velocity signals trigger a smooth pursuit reflex, where a smooth pursuit eye movement is executed to cancel the retinal velocity. The smooth pursuit reflex is a negative feedback loop that minimizes retinal velocity signals. However, accurate smooth pursuit can be maintained for long periods, and the maintenance phase of pursuit is not controlled by the smooth pursuit reflex alone but is also under the guidance of top-down, *extraretinal velocity signals* (Barnes & Asselman, 1991). The existence of extraretinal control is demonstrated by the fact that people can pursue targets that predictably accelerate and decelerate, with the eye *anticipating* changes in target velocity (Bennett, de Xivry, Barnes, & Lefevre, 2007). Pursuit can also continue under conditions of retinal stabilization, where feedback from an eye tracker is used to prevent all retinal motion (Barnes, Goodbody, & Collins, 1995). Furthermore, anticipatory smooth pursuit eye movements, scaled according to expected target velocity, occur before motion onset (Barnes, Grealy, & Collins, 1997; Poliakoff, Collins & Barnes, 2005). These phenomena would not be possible without extraretinal velocity signals supplementing the negative feedback loop.

Extraretinal velocity signals arise from several sources. Efference copy of the motor command to the eyes and ocular proprioception from the eye muscles provides information about current pursuit velocity. This information may be used for top-down guidance of further pursuit, or for making judgements about target velocity (Churchland, Chou, & Lisberger, 2003). Stored velocity representations can be retained in short-term memory for many seconds after target motion ends (Chakraborti, Barnes, & Collins, 2002; Magnussen & Greenlee, 1992; Makin & Poliakoff, 2011), and these stored velocity signals can also be used for subsequent top-down control of pursuit (Barnes & Collins, 2008) or to make other judgements (Makin, Poliakoff, Ackerley, & El-Deredy, 2012).

In summary, there is a fundamental difference between retinal velocity signals, which are produced when the target moves across the retina, and extraretinal velocity signals, which are available even when retinal motion is cancelled by smooth

pursuit. It is likely that neurons in V1, V3a, and MT (middle temporal) area code retinal motion signals during fixation (Born & Bradley, 2005; McKeefry, Burton, Vakrou, Barrett, & Morland, 2008), while neurons in MST (medial superior temporal) area and the frontal eye fields (FEFs) code extraretinal motion signals during pursuit (Ferrera & Barborica, 2010; Ilg, 2008). Makin, Poliakoff, Dillon, et al. (2012) did not measure eye movements, so it is unknown whether auditory click trains distorted retinal or extraretinal velocity signals. This question was addressed in the present studies.

Current work

The effect of clicks has been shown for time (Penton-Voak et al., 1996), velocity (Makin, Poliakoff, Dillon, et al., 2012), and other dynamic presentations (Droit-Volet, 2010). However, the mechanism by which clicks alter subsequent perceptual judgements is unknown (Jones et al., 2011). Given this, it is instructive to seek potentially

illuminating constraints on the phenomena. The distinction between retinal and extraretinal velocity signals is remarkably well specified, and dissociable neural mechanisms have been clearly defined, allowing a unique opportunity to clarify the nature of the click effect. We may ask whether the effect is ubiquitous, common to all perceptual judgements about dynamic stimuli, or is mediated by specific connections between the auditory cortex and other specific sensorimotor regions. A selective effect of clicks on retinal or extraretinal velocity signals would support the latter hypothesis.

EXPERIMENT 1

Figure 1 shows the trial structure of Experiment 1. Participants observed single dot-targets that moved leftwards or rightwards at speeds ranging from 7.5 to 17.5 deg/s. Motion was preceded by 5 s of 4-Hz auditory clicks, or a single-click-bounded silent interval of the same duration. After each trial, participants estimated target

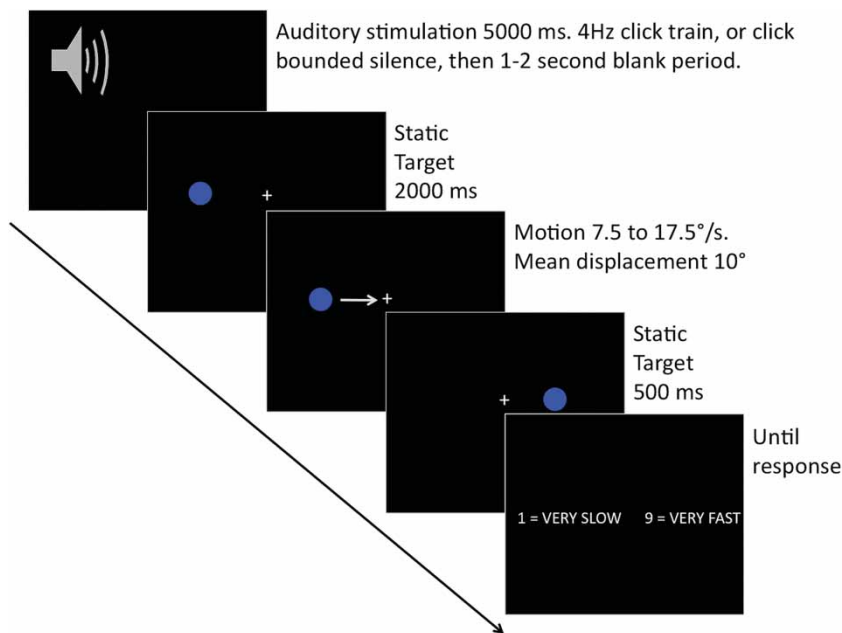


Figure 1. Trial structure of Experiment 1. The central fixation cross was only present on the fixation trials and served as a cue, indicating trial type. To view a colour version of this figure, please see the online issue of the Journal.

velocity by entering numbers from 1 to 9 using the computer keyboard. Velocity estimates were taken in both fixation and pursuit conditions. Velocity estimates must be based on retinal motion signals during fixation and based on extraretinal motion signals during pursuit. If auditory clicks selectively alter retinal or extraretinal velocity signals, there should only be an effect of clicks in the fixation or in the pursuit conditions, respectively.

Method

Participants

A total of 24 participants (aged 18 to 36 years, 9 male, 1 left-handed) were involved. They had normal or corrected-to-normal vision and received either £10 compensation or course credit as compensation. The study was carried out with local ethics committee approval and was conducted in accordance with the 2008 Declaration of Helsinki.

Apparatus

Stimuli were presented on a 34 × 25.5-cm LCD monitor, with a refresh rate of 75 Hz. Head position was stabilized 57 cm from the monitor with a chin rest. Stimuli were generated and controlled with open-source Psychopy software (Peirce, 2007). Eye position was monitored with an ASL 6000 desk-mounted, infrared eye tracker, sampling at 120 Hz.

Design

There were 144 trials in total. Nine different speeds were presented (7.5 to 17.5 deg/s in 1.25 deg/s increments), with four additional factors (leftward vs. rightward motion, fixation vs. pursuit instructions, clicks vs. silence, and time controlled vs. displacement controlled). These factors were fully counterbalanced. Trials were presented in a different, randomized order for every participant.

Procedure

After participants were informed about the experiment, the eye tracker was calibrated using a nine-point array. Participants then viewed four demonstration trials showing the slowest and fastest velocities that would be presented. They

were warned that trials would be preceded by clicks or a click-bounded silence, but were told that these sounds merely “warned them that the next trial was about to start”. After the demonstration trials, a 24-trial practice block further familiarized participants with the different velocities used in the experiment. After practice, the eye tracker was recalibrated, and the experiment began.

The structure of a single trial is shown in Figure 1. First participants listened to 5 s of 4-Hz auditory clicks (20 individual clicks) or a click-bounded silence of the same duration. The single clicks at the beginning and end of the silent interval meant that participants were still warned that the trial was about to start. These characteristics were chosen for consistency with Makin, Poliakoff, Dillon, et al., 2012, who first reported an effect of clicks on subjective velocity. There was then a blank period, randomized between 1 and 2 s. After this the visual target was static in its starting position for 2 s, either to the left or to the right of the midline. On fixation trials a fixation cross was presented in the middle of the screen. On pursuit trials there was no cross. During this 2-s static-target period, participants prepared to follow the oculomotor instructions by either fixating on the central fixation cross, or fixating the peripheral target in readiness for pursuit across the midline. The target then moved leftwards or rightwards at speeds ranging from 7.5 to 17.5 deg/s. The target remained static for 500 ms in its final position before a response screen was presented, which prompted participants to enter a number from 1 to 9, where 1 was the slowest possible speed and 9 the fastest. The experiment was broken into four blocks of 48 trials, and the eye tracker was recalibrated between blocks if necessary.

It is impossible to vary velocity without covarying either distance covered by the target or the duration of the trial. In half the trials, all targets travelled for 10° of visual angle (5° either side of the midline), so slower targets were presented for longer than faster targets (571 ms minimum, 1333 ms maximum). On the remaining trials, trial duration was fixed at 800 ms; the slowest targets covered 6°, and the fastest covered 14°. These displacement control and time control

trials were interleaved, and all trials were presented in random order, so participants could not easily perceive the systematic relationships between velocity, distance, and trial duration.

Analysis

Eye tracking. Data from the eye tracker were used to ensure that the oculomotor instructions were obeyed on the majority of trials. On fixation trials, participants were considered to have violated fixation instructions if eye position changed by more than 4° over the course of the trial. Eye velocity was calculated for the middle 50% of each trial, and this central portion was smoothed with a 100-ms moving-average window. If eye velocity was greater than 100 deg/s during this period, the pursuit instructions were considered to have been violated, as this is likely to reflect a saccade rather than pursuit. Finally, if the eye tracker lost signal during the central portion, perhaps due to the participant blinking, the trial was also flagged (note that this is a conservative criterion, because sometimes the eye tracker lost signal for reasons unrelated to the participant's behaviour). According to these criteria, oculomotor instructions were obeyed on 96% of all trials across all participants (best participant 100%, worst participant 88%). The minority of problematic trials were not included in any

further analysis. We acknowledge that these criteria are somewhat arbitrary. The proportion of included trials after employing different criteria is shown in Table 1, which gives a sense of the prevalence of different kinds of ocular artefact in our data.

Horizontal eye velocity and angular position data are shown in Figures 2A and 2B, respectively. During fixation, eye velocity was low, and the distance covered by the eye was minimal. During pursuit, eye velocity increased with target velocity, and distance covered was similar to the actual distance covered by the target. The patterns in Figure 2A were confirmed with a three-factor repeated measures analysis of variance (ANOVA), eye instruction (fixation, pursuit) \times direction (leftwards, rightwards) \times speed (7.5 to 17.5 deg/s). Importantly, there was a significant three-way interaction between eye instruction, direction, and speed, $F(4.45, 102.25) = 244.45$, $MSE = 4.40$, $p < .001$, $\eta_p^2 = .914$. Data in Figure 2B for distance covered were analysed in the same way, but with control type (time control, displacement control) included instead of direction. There was a three-way interaction between eye instruction, control type, and speed, $F(8, 184) = 166.68$, $MSE = 0.25$, $p < .001$, $\eta_p^2 = .879$. We do not report other main effects and interactions from these ANOVAs for the sake of brevity, but the three-way interactions confirm that

Table 1. Proportion of trials remaining after different oculomotor exclusion criteria

Experiment	Fixation window on fixation trials (deg)	Maximum eye velocity allowed (deg/s)	Amount of trial analysed (%)	Proportion of trials included
Experiment 1	4	100	50	.962
	4	40	100	.882
	2	40	100	.851
	1	40	100	.611
Experiment 2	4	100	50	.917
	4	40	100	.760
	2	40	100	.703
	1	40	100	.407
Experiment 3	4	100	50	.957
	4	40	100	.883
	2	40	100	.829
	1	40	100	.558

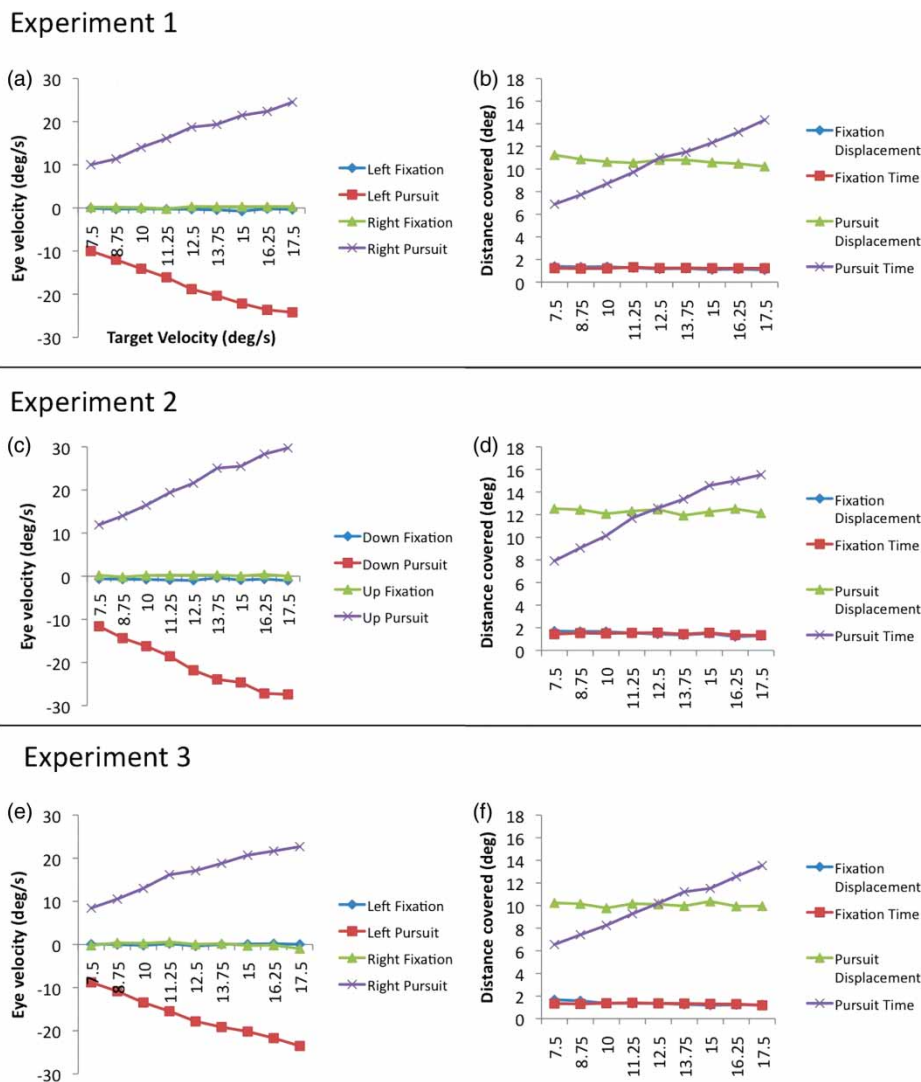


Figure 2. Eye movements in Experiments 1, 2, and 3. (A) Eye velocity as a function of target velocity in the leftwards, rightwards, fixation, and pursuit conditions of Experiment 1. (B) Total distance covered by the eye as a function of target velocity in the time control, displacement control, fixation, and pursuit conditions of Experiment 1. Panels C and D show the equivalent data from Experiment 2, while Panels E and F show the data from Experiment 3. To view a colour version of this figure, please see the online issue of the Journal.

participants fixated and pursued the targets according to their instructions in all the included trials.

Velocity estimates. Trials were excluded if oculomotor instructions were violated (see criteria above). For each participant, we then recalculated velocity estimates (1 slowest, 9 fastest) as a deviation from

that participant’s mean estimate across all trials (average 3.23–6.35). This normalizing procedure accounted for individual differences in the use of the response scale. Normalized velocity estimates were then explored with repeated measures ANOVAs. The Greenhouse–Geisser correction factor was applied when the assumption of

sphericity was violated. The majority of analysed variables were normally distributed, with only a few violations of the normality assumption according to the Shapiro–Wilk test (6/70). We used an alpha level of $<.05$, and we report all significant effects and the proportion of variance they explain (η_p^2).

Results

Figure 3A shows three effects. First, subjective velocity increased with actual velocity. Second, subjective velocity was higher in the fixation trials than in the pursuit trials. Third, and most interestingly, subjective velocity was higher after clicks than

after silence, but only in the pursuit condition. This interaction is clearer in Figure 3B, where the same data are collapsed across velocity.

These patterns were confirmed with a three-factor repeated measures ANOVA, 2 (eye instruction: fixation, pursuit) \times 2 (auditory stimulation: clicks, silence) \times 9 (velocity: 7.5 to 17.5 deg/s). There was a significant main effect of velocity, because estimated velocity increased with target velocity, $F(3.13, 71.93) = 258.57$, $MSE = 3.92$, $p < .001$, $\eta_p^2 = .918$. Participants estimated the motion as faster in the fixation than in the pursuit condition, $F(1, 23) = 32.37$, $MSE = 3.32$, $p < .001$, $\eta_p^2 = .585$. There was also a main effect of auditory stimulation, with higher estimates after

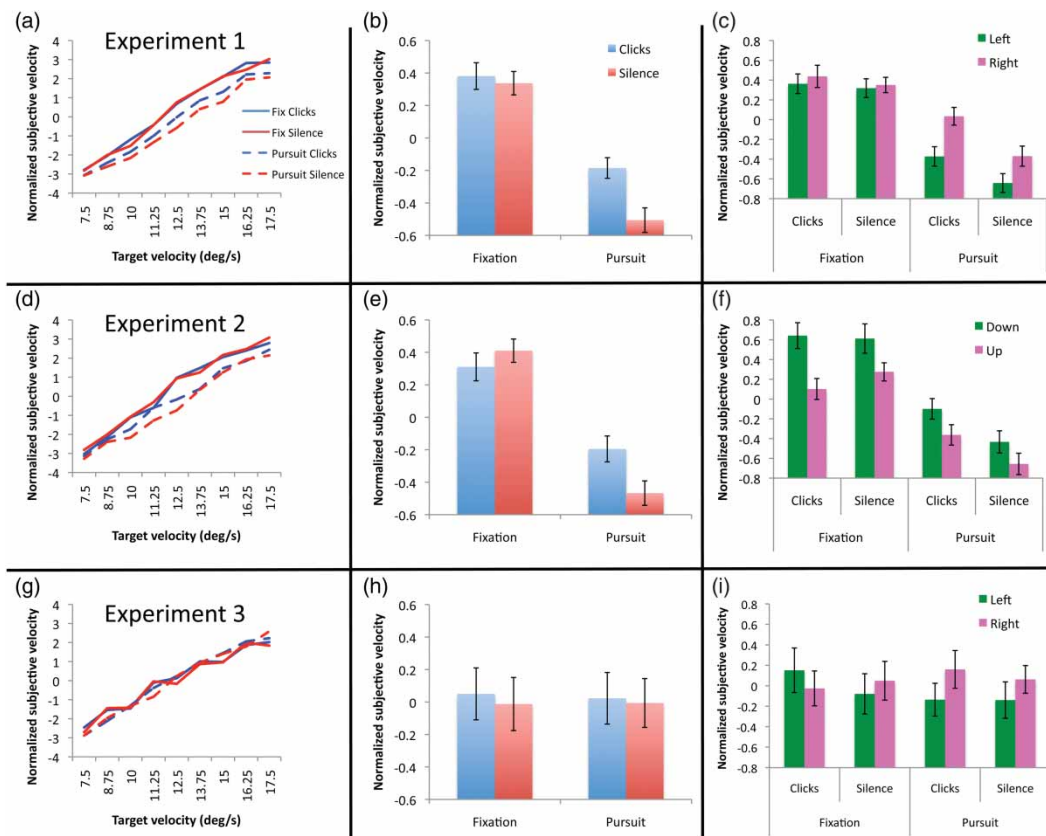


Figure 3. Velocity estimates from Experiments 1 (top row), 2 (middle row), and 3 (bottom row). Left column: Normalized velocity estimates as a function of target velocity, eye instruction, and auditory stimulation. Middle column: Normalized velocity estimates as a function of eye instruction and auditory stimulation. Right column: Normalized velocity as a function of eye instruction, auditory stimulation, and direction. Error bars = ± 1 SEM. To view a colour version of this figure, please see the online issue of the Journal.

clicks than after silence, $F(1, 23) = 10.01$, $MSE = 0.72$, $p = .004$, $\eta_p^2 = .303$. The most important effect was an eye instruction \times auditory stimulation interaction, $F(1, 23) = 7.95$, $MSE = 0.52$, $p = .010$, $\eta_p^2 = .257$. This was because clicks increased velocity estimates in the pursuit condition, $t(23) = 4.13$, $p < .001$, but not in the fixation condition, $t(23) < 1$, *ns*. There was also an eye instruction \times velocity interaction, $F(8, 184) = 2.61$, $MSE = 0.59$, $p = .010$, $\eta_p^2 = .102$, because the difference between fixation and pursuit trials was more pronounced at some velocities than others. There was no auditory stimulation \times velocity interaction, $F(1, 184) < 1$, *ns*, or three-way interaction between all factors, $F(1, 184) < 1$, *ns*.

As mentioned above, it is impossible to vary velocity without introducing spatial or temporal confounds. Either all trials are presented for the same duration (time control trials), and faster targets travel a greater distance, or all targets travel the same distance (displacement control trials), and faster targets are presented for a shorter duration. We interleaved both time and displacement control trials in Experiment 1 and assessed the impact of this manipulation on performance with a control type \times velocity ANOVA. There was no main effect of control type, $F(1, 23) < 1$, *ns*, or control type \times velocity interaction, $F(5.41, 124.35) = 1.505$, $MSE = 0.42$, $p = .188$, indicating that velocity estimation was comparable across both conditions. Next we tested whether the theoretically important eye instruction \times auditory stimulation interaction was selectively driven by judgements from the time control or displacement control trials. Velocity estimates were entered into a three-factor repeated measures ANOVA, 2 (eye instruction: fixation, pursuit) \times 2 (auditory stimulation: clicks, silence) \times 2 (control type: time, displacement). Importantly, there were no effects or interactions involving the factor control type, largest $F(1, 23) = 1.502$, $MSE = 0.08$, $p = .233$. Other effects involving eye instruction and auditory stimulation are essentially as reported above, so are not repeated here.

Figure 3C shows normalized velocity estimates as a function of eye instruction (fixation, pursuit), auditory stimulation (clicks, silence), and direction

(left, right). This pattern was analysed with three-factor ANOVA. We only report effects involving the factor direction (again, the others are essentially described above). The main effect of direction did not reach significance, $F(1, 23) = 4.03$, $MSE = 0.46$, $p = .057$; however, there was an eye instruction \times direction interaction, $F(1, 23) = 8.74$, $MSE = 0.11$, $p = .007$, $\eta_p^2 = .275$, because participants estimated rightward motion as faster than leftward motion in the pursuit trials, $t(23) = 3.07$, $p = .005$, while there was no effect of direction in the fixation trials, $t(23) < 1$, *ns*. Finally, there was no auditory stimulation \times direction interaction, $F(1, 23) < 1$, *ns*, or three-way interaction between all factors, $F(1, 23) < 1$, *ns*.

Discussion

The most important result of Experiment 1 was that in the pursuit condition, where velocity estimates were probably based on extraretinal velocity signals, there was a strong effect of clicks. However, in the fixation condition, where velocity estimates had to be based on retinal velocity signals, there was no effect of clicks. This result is consistent with the claim that auditory click trains alter extraretinal but not retinal velocity signals.

Two other known effects were replicated in Experiment 1. First, motion was judged faster in the fixation trials than in the pursuit trials, even though the range of actual velocities was identical. This is the Aubert–Fleischl illusion (Freeman, Champion, & Warren, 2010), and its presence supports our assumption that different signals were used to guide responses in the fixation and pursuit trials. Second, in the pursuit trials, rightward motion was judged faster than leftward motion, which has also been reported before (Leigh & Zee, 2006).

EXPERIMENT 2

The term “extraretinal velocity signals” covers a range of different mechanisms. One possibility is that subcortical oculomotor nuclei project back to area MST via the thalamus, as well as to the motor neurons that control the eye muscles

(Thier & Ilg, 2005). It is known that horizontal and vertical smooth pursuit are controlled by different muscles that are, in turn, controlled by different motor nuclei in the brain stem (Leigh & Zee, 2006). It is thus possible that the effect of clicks during pursuit would be specific to horizontal motion. To investigate this, Experiment 2 replicated Experiment 1 except the target moved upwards or downwards rather than left or right.

Method

A new group of 24 participants were tested (aged 16 to 61 years; 10 male, 1 left-handed). The procedure was identical to that of Experiment 1 except that the target moved vertically. Violations of oculomotor instructions were defined as before. On average, participants obeyed oculomotor instructions on 92% of the trials (best participant 99%, worst 78%). Eye movement data from the valid trials are shown in Figures 2C and 2D. The patterns are comparable to those in Experiment 1, and, again, these patterns were confirmed with three-factor repeated measures ANOVAs. For eye velocity, there was significant three-way interaction between eye instruction, direction, and speed, $F(3.83, 87.98) = 87.76$, $MSE = 20.38$, $p < .001$, $\eta_p^2 = .792$. For distance covered, there was a three-way interaction between eye instruction, control type, and direction, $F(4.27, 98.12) = 45.48$, $MSE = 1.74$, $p < .001$, $\eta_p^2 = .664$. Participant mean velocity estimates ranged from 4.01 to 6.57. Normalized velocity estimates were obtained as described above. Again few of the analysed variables violated the normality assumption (3/70).

Results

Results were similar to those of Experiment 1 (Figures 3D–3F). Velocity estimates increased with target velocity, $F(3.17, 72.96) = 339.59$, $MSE = 2.88$, $p < .001$, $\eta_p^2 = .937$ (Figure 3D) and were greater in the fixation than in the pursuit condition, $F(1, 23) = 27.65$, $MSE = 3.74$, $p < .001$, $\eta_p^2 = .546$. Unlike Experiment 1, the main effect of auditory stimulation was not significant, $F(1, 23) = 1.97$, $MSE = 0.82$, $p = .174$, but the same, theoretically important eye instruction \times auditory

stimulation interaction was replicated, $F(1, 23) = 11.31$, $MSE = 0.66$, $p = .003$, $\eta_p^2 = .330$. This interaction is shown most clearly in Figure 3E, where data are collapsed across velocity. As with Experiment 1, participants judged motion as faster after clicks than after silence in the pursuit trials, $t(23) = 3.37$, $p = .003$, but not in the fixation trials, $t(23) = -1.18$, $p = .251$. There was also a significant interaction between eye instruction and velocity, $F(5.05, 116.18) = 4.68$, $MSE = 1.08$, $p = .001$, $\eta_p^2 = .169$. There was no auditory stimulation \times velocity interaction, $F(1, 184) < 1$, *ns*, or three-way interaction between all factors, $F(5.68, 130.54) = 1.385$, $MSE = 0.69$, $p = .228$.

As with Experiment 1, we explored velocity judgements in the time and displacement control trials conditions. Velocity estimates were equally accurate in both conditions: There was no main effect of control type, $F(1, 23) < 1$, *ns*, or Control Type \times Velocity interaction, $F(8, 184) < 1$, *ns*. Next, velocity estimates were entered into a three-factor repeated measures ANOVA, 2 (eye instruction: fixation, pursuit) \times 2 (auditory stimulation: clicks, silence) \times 2 (control type: time, displacement). Importantly, there were no effects or interactions involving the factor control type, largest $F(1, 23) = 2.175$, $MSE = 0.15$, $p = .154$.

Figure 3F shows normalized velocity estimates as a function of eye instruction (fixation, pursuit), auditory stimulation (clicks, silence), and direction (up, down). There was a main effect of direction, because participants estimated downward motion as faster than upward motion, $F(1, 23) = 12.56$, $MSE = 0.44$, $p = .002$, $\eta_p^2 = .353$. Unlike Experiment 1, the effect of direction was not specific to the pursuit condition, and thus there was no eye instruction \times direction interaction, $F(1, 23) = 1.47$, $MSE = 0.312$, $p = .238$. There were no interactions between auditory stimulation and direction, $F(1, 23) = 1.123$, $MSE = 0.16$, $p = .300$, or between eye instruction, auditory stimulation, and direction, $F(1, 23) < 1$, *ns*.

Discussion

As with Experiment 1, prior presentation of auditory click trains increased the apparent velocity of

subsequent visual motion, but only under pursuit conditions. This replication confirms and extends the results of Experiment 1. Figure 3D suggests that the selective effect of auditory stimulation in the pursuit condition disappears with higher velocities, but the relevant statistical comparisons were not significant—for example, the eye instruction \times auditory stimulation interaction was not further modulated by velocity, so we do not overinterpret this apparent effect.

Two other known findings were replicated. First, the Aubert–Fleischl effect was found, with greater velocity estimates during fixation than during pursuit. Second, downward motion was judged faster than upward motion in all conditions. This effect could be related to “cognitive gravity” and may result from experience with real-life object movements where falling objects tend to accelerate (Zago & Lacquaniti, 2005).

EXPERIMENT 3

In the first two experiments, participants tracked dot targets across a uniform black background. However, real-world pursuit targets typically move across a visually textured background. Here, the opponent motion of the background provides retinal velocity information, which may be used to estimate target velocity (Leigh & Zee, 2006). The relative weighting of extraretinal and retinal velocity signals during pursuit across textured background is probably variable and experience dependent, with different velocity signals graded according to their reliability (Freeman et al., 2010). For example, if there are additional moving objects in the background, or the background scenery is very unevenly distributed or low contrast, then background motion would not provide reliable information about target velocity, and these unhelpful signals could be discounted. Alternatively, if the background is static and

regularly textured, then people may use this reliable velocity information and ignore extraretinal signals.

In Experiment 3, we explored the effect of auditory clicks during horizontal pursuit of a dot across a vertically oriented one cycle-per-degree sine wave grating (Figure 4). The pursuit condition of Experiment 3 was identical to that of Experiment 1, except for the striped background. This stimulus was designed so that opponent motion of the background during pursuit was a salient and highly reliable indicator of target velocity.

A fixation condition was also tested in which the dot-target remained static in the centre of the screen, and the striped background moved (Figure 4).¹ The design of the fixation condition in Experiment 3 differed from the template of Experiments 1 and 2, where the target moved across the retina in the fixation condition. The new fixation condition in Experiment 3 had two key advantages over any alternative design. First, it confirmed that the fixation condition results in Experiments 1 and 2 were not due to specific stimulus characteristics. We noted that a moving dot would activate fewer elementary motion detectors than a large sine-wave grating, and it could be that retinal motion would be altered by clicks when it reaches some unknown threshold, contradicting our conclusions. Second, we wanted to make retinal motion signals as similar as possible in the fixation and pursuit trials. We designed Experiment 3 so that if fixation and pursuit were perfect, retinal motion signals resulting from the background moving during fixation would be identical to the opponent motion signals arising from the background during pursuit. Because of this, a selective effect of clicks during pursuit could only be attributed to the use of extraretinal velocity signals, and not due to greater level of retinal motion stimulation. If we had presented a fixation condition more similar to that of Experiments 1 and 2, where the dot moved, the results of Experiment 3 would necessarily have been inconclusive.

¹ In all experiments the room was dimly lit, but was not in perfect darkness. Participants could easily see the edge of the screen and the wall behind. This could have provided opponent motion signals in the visual periphery during pursuit. However, in the pursuit trials of Experiment 3, the static background would produce much stronger retinal opponent motion signals in the foveal region and across the whole visual field.

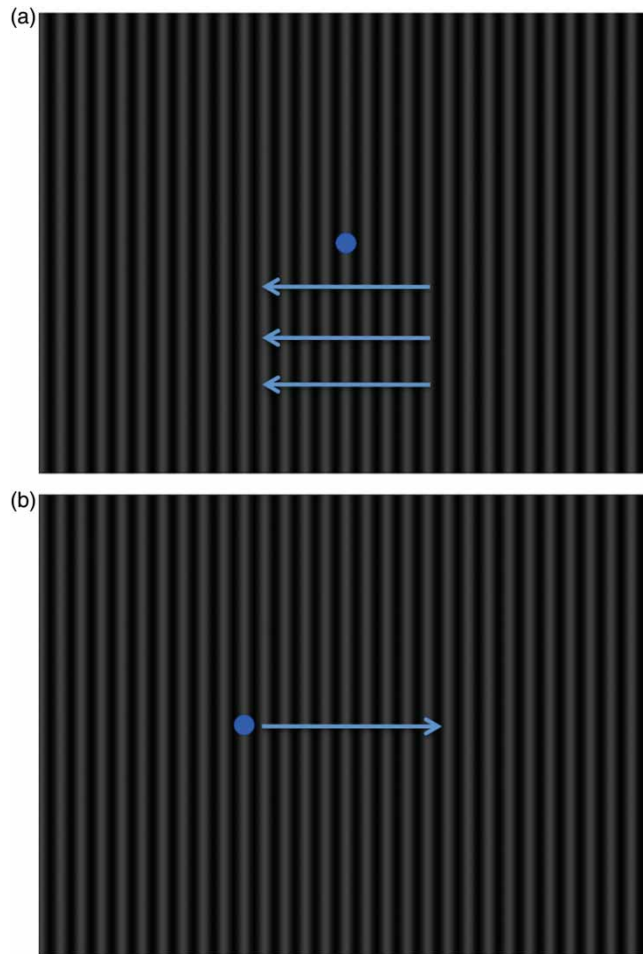


Figure 4. Stimuli in Experiment 3. (A) On fixation trials, participants fixated while the background moved. (B) On pursuit trials, participants tracked the target across a vertically oriented 1 cycle-per-degree sine wave grating background. Assuming perfect tracking and fixation, retinal motion signals should be identical in both conditions. To view a colour version of this figure, please see the online issue of the Journal.

To summarize: Based on the results of Experiments 1 and 2 we predicted that clicks would have no effect on velocity estimates in the fixation condition, where estimates are based on retinal velocity information. There were two possibilities for the pursuit condition. First, participants could base their velocity estimates on the reliable opponent motion signals. This should result in *no effect* of clicks, as in the fixation condition. Second, participants could base their judgements on extraretinal velocity signals (despite the

availability of reliable background-motion signals), and clicks would increase subjective velocity, as in Experiments 1 and 2.

Method

Another 24 participants were tested (aged 17 to 61 years, 7 male, 1 left-handed). The procedure was similar to that of Experiment 1, except a one cycle-per-degree sine wave grating was presented behind the blue target. The background covered

the entire screen, and the bars were vertically orientated. On pursuit trials, the background was static, and the target moved horizontally, exactly as in Experiment 1. On fixation trials, the target remained static in the centre of the screen, and the background moved horizontally over the same distances and at the same speeds as the dot moved in Experiment 1 (Figure 4).

Eye position data were processed in the same way as in Experiment 1. Oculomotor instructions were obeyed on 96% of the trials (best participant 100%, worst participant 80%). Eye movement metrics from this experiment are shown in Figures 2E and 2F and were again analysed with a three-factor ANOVA. There were significant three-way interactions between eye instruction, direction, and speed, $F(4.06, 93.36) = 144.67$, $MSE = 8.65$, $p < .001$, $\eta_p^2 = .863$, for eye velocity, and between eye instruction, control type, and direction, $F(4.73, 108.87) = 60.09$, $MSE = 0.90$, $p < .001$, $\eta_p^2 = .723$, for distance covered. Participants' mean velocity estimates ranged from 3.46 to 7.34. Velocity estimates were normalized as above, and few of the variables analysed deviated significantly from the normality assumption (6/70).

Results

In Figure 3G it can be seen that while participants were highly sensitive to target velocity, there was no eye instruction \times auditory stimulation interaction of the type found in Experiments 1 and 2.

These patterns were explored with a three-factor repeated measures ANOVA. There was a main effect of velocity, $F(3.62, 83.26) = 224.05$, $MSE = 2.76$, $p < .001$, $\eta_p^2 = .907$, but not of eye instruction, $F(1, 23) < 1$, *ns*, or auditory stimulation, $F(1, 23) < 1$, *ns*. Crucially, unlike previous experiments, there was no eye instruction \times auditory stimulation interaction, $F(1, 23) < 1$, *ns* (Figure 3H). There was, however, an interaction between eye instruction and velocity, $F(3.64, 83.78) = 3.34$, $MSE = 2.37$, $p = .017$, $\eta_p^2 = .127$. There was no auditory stimulation \times velocity interaction, $F(1, 184) < 1$, *ns*, or three-way interaction between all factors, $F(1, 184) = 1.544$, $MSE = 0.44$, $p = .145$.

In Experiments 1 and 2, there were no effects involving the factor control type (whether trials were controlled so as to have fixed duration or fixed displacement). Conversely, in Experiment 3, control type had some influence on velocity estimates. Again, we first explored velocity estimates as a function of control type and velocity. There was a main effect of control type, $F(1, 23) = 7.06$, $MSE = 0.29$, $p = .014$, $\eta_p^2 = .235$, because of slightly higher velocity estimates in the time control trials than in the displacement control trials. There was also a control type \times velocity interaction, $F(8, 184) = 2.388$, $MSE = 0.35$, $p = .018$, $\eta_p^2 = .094$. However, this was not systematic (the effect of control type was only apparent at 8.25, 11.25, and 13.25 deg/s). Performance was very strong in both conditions: main effect of velocity in displacement control condition, $F(3.79, 87.23) = 162.20$, $MSE = 0.93$, $p < .001$, $\eta_p^2 = .876$; in time control, $F(4.85, 111.43) = 134.89$, $MSE = 0.86$, $p < .001$, $\eta_p^2 = .854$. This confirms that participants could easily do the task in both cases, despite some subtle differences. Next, velocity estimates were entered into a three-factor repeated measures ANOVA, 2 (eye instruction: fixation, pursuit) \times 2 (auditory stimulation: clicks, silence) \times 2 (control type: time, displacement). There were no interactions involving control type, largest $F(1, 23) = 2.255$, $MSE = 0.26$, $p = .147$.

As with Experiments 1 and 2, we analysed velocity estimates as a function of eye instruction, auditory stimulation, and direction (Figure 3I). In Experiment 3, this analysis revealed no effects or interactions, largest $F(1, 23) = 2.93$, $MSE = 0.16$, $p = .101$.

Discussion

Experiment 3 found no effect of auditory click trains on estimated velocity when participants pursued the target across a static, textured background. Here, participants could have based their velocity estimates on the opponent motion of the background, or the extraretinal velocity signals produced by pursuit execution. There are two reasons to believe that their velocity judgements were

based on retinal motion signals in the pursuit condition. First, in Experiments 1 and 2, targets were judged faster during fixation than during pursuit, but this Aubert–Fleischl illusion was absent in Experiment 3, suggesting that the same velocity signals were used in all trials. Second, the opponent motion of the salient static background during pursuit provided reliable retinal information about target velocity, and people are likely to weigh their use of different velocity signals based on reliability (Freeman et al., 2010). In Experiment 3, the opponent motion present during pursuit trials was identical to the background motion present during the interleaved fixation trials. This consistency across the two trial types could have encouraged participants to use retinal velocity signals in all trials.

Given that retinal velocity signals were probably used to guide all velocity estimates, and there was no effect of clicks in any condition, Experiment 3 provides further evidence that auditory click trains only distort extraretinal, not retinal, velocity signals. Future work could manipulate the reliability of opponent motion signals from the background during pursuit. We predict that uneven or low-contrast backgrounds that result in unreliable opponent motion signals would encourage people to base their judgements on extraretinal velocity signals, and that the effect of clicks would return.

It may appear that Experiment 3 was a failure to replicate Makin, Poliakoff, Dillon, et al. (2012); however, that is not the case. In Makin, Poliakoff, Dillon, et al. (2012) participants probably tracked the individual bars of the sine-wave grating as it drifted rightwards within a static window, and they used extraretinal velocity signals resulting from this pursuit eye movement to guide velocity estimation. This differs from both the fixation and the pursuit conditions of Experiment 3, where the grating moved across the retina and provided retinal motion signals.

The fact that there was no effect of clicks during fixation in Experiment 3 is also instructive because the stimulus contained a lot of motion energy, with the whole screen covered by a large drifting grating.

We thus conclude that the absence of click effects in the fixation conditions of Experiments 1 and 2 cannot be attributed to insufficient retinal stimulation.

Combined analysis and checks

We performed several additional analyses on the combined data from the three experiments. Our discussion focuses on the eye instruction \times auditory stimulation interactions in Experiments 1 and 2 and the absence of an equivalent interaction in Experiment 3 (Figures 3B, 3E, and 3H), so it is necessary to establish that the pattern in Experiment 3 differed from that of the first two experiments statistically (see Nieuwenhuis, Forstmann, & Wagenmakers, 2011, for a discussion of this issue in cognitive neuroscience). We thus conducted a mixed ANOVA, with eye instruction and auditory stimulation as within-subjects factors and experiment as a between-subjects factor. There was an eye instruction \times auditory stimulation interaction, $F(1, 69) = 13.19$, $MSE = 0.06$, $p = .001$, $\eta_p^2 = .161$, and, importantly, this was modulated by the between-subjects factor of experiment, $F(2, 69) = 4.70$, $MSE = 0.06$, $p = .012$, $\eta_p^2 = .120$. We broke this down further by comparing each pair of experiments. For Experiments 1 and 2, there was a strong eye instruction \times auditory stimulation interaction, $F(1, 46) = 19.24$, $MSE = 0.07$, $p < .001$, $\eta_p^2 = .295$, which was not modulated by experiment, $F(1, 46) < 1$, *ns*. Conversely, this eye instruction \times auditory stimulation interaction was further modulated by experiment when comparing Experiments 1 and 3, $F(1, 46) = 5.86$, $MSE = 0.05$, $p = .019$, $\eta_p^2 = .113$, and Experiments 2 and 3, $F(1, 46) = 8.63$, $MSE = 0.06$, $p = .005$, $\eta_p^2 = .158$. Crucially, these analyses show that the interaction effects in Experiments 1 and 2 were significantly different from the null effect in Experiment 3.

In the cognitive timing literature, it is common to analyse the slope of the relationship between subjective duration and actual duration under different conditions. The existence of slope effects

is instructive because it is indicative of an internal process with a variable rate, such as the pacemaker component in pacemaker-accumulator clock models (e.g., Wearden et al., 1998). Here, we focused on the pursuit conditions and analysed estimated velocity versus actual velocity slope values after clicks or silence. There was no effect of auditory stimulation in Experiment 1 (clicks = .72, silence = .70), $t(23) = 1.21$, $p = .238$, Experiment 2 (clicks = .70, silence = .72), $t(23) < 1$, *ns*. This suggests that when clicks do increase subjective velocity, they do not do so by a *constant proportion* (e.g., 10% of actual velocity), but rather by a *constant value*. From our data, it seems that click trains add approximately 0.4 deg/s to subjective velocity in the pursuit conditions of Experiments 1 and 2, irrespective of actual velocity. Of course, a different response protocol would be able to provide a more precise estimate of effect size.

There are two other things worth noting about the data. First, all the main patterns were still significant when we included all the trials, rather than removing those in which oculomotor instructions were violated. Second, we reanalysed the velocity estimates when more stringent oculomotor exclusion criteria were applied. Table 1 shows the proportion of trials included with the original criteria, when the whole trial was analysed, when maximum eye velocity was set at 40 rather than 100 deg/s, and when the fixation window was set at 1 or 2 deg rather than 4 deg. More stringent criteria resulted in a greater loss of data points and with 1-deg fixation window, too many trials were excluded for valid analysis. We therefore reexamined the combined data from Experiments 1 and 2 when trials were excluded with the second most stringent criteria (whole trial, 40 deg/s max eye velocity, 2 deg fixation window). There was still a strong eye instruction \times auditory stimulation interaction, $F(1, 46) = 7.95$, $MSE = 0.11$, $p = .007$, $\eta_p^2 = .147$, because velocity estimates were significantly higher after clicks than after silence in the pursuit condition, $t(47) = 4.85$, $p < .001$, but not in the fixation condition, $t(47) < 1$, *ns*. Thus the most important result from this work was reliable when both more and less stringent exclusion criteria were applied.

GENERAL DISCUSSION

Previous work has found that prior presentation of auditory click trains increases subjective velocity (Makin, Poliakoff, Dillon, et al., 2012). The present results extend this finding to provide a more specific account, suggesting that auditory click trains only increase velocity estimates when judgements are based on extraretinal velocity signals. In Experiments 1 and 2, participants either fixated while a single dot-target moved across the retina, or pursued the target with their eyes. Click trains had no effect in fixation conditions where judgements were based on retinal velocity signals. However, click trains increased subjective velocity in the pursuit conditions where extraretinal velocity information was readily available, and retinal velocity signals were limited.

In Experiment 3, a large and salient visually textured background was presented behind the dot target. During pursuit, this static background produced retinal velocity signals that were probably used to guide velocity judgements. There was no effect of clicks in Experiment 3, consistent with the conclusion that clicks only alter judgements that are based on extraretinal velocity information.

Alternative explanations

The results of all our experiments are consistent with the parsimonious claim that clicks selectively alter extraretinal velocity signals. However, some alternative explanations require consideration.

It is possible that *any* manipulation that increases prestimulus alertness would alter subsequent perceptual judgements, but this is unlikely to explain the effect of clicks in this experiment for the following reasons. The “silence” in the silence trials was click-bounded, with a single click at the beginning and end of the silent period, and the target always appeared in the starting position for two seconds before motion began. This design meant that participants were equally prepared for the upcoming motion in clicks and silence trials. Furthermore, Makin, Poliakoff, Dillon, et al. (2012) compared clicks, silence, and white noise

and found that white noise did not increase subjective velocity, even though it was louder than the clicks and presented for the same duration. Thus it seems unlikely that the effect of clicks on subjective velocity is due to increased prestimulus alertness.

In our experiments, participants compared a given velocity signal with an internal representation of the range of velocities seen throughout the experiment. Clicks could *speed up* the apparent velocity of the current trial or *slow down* the remembered velocity of previous trials. We cannot conclusively distinguish between these explanations. However, if clicks alter remembered rather than perceived velocity, they must alter the remembered velocity on pursuit trials only. Perhaps participants form two representations—average velocity on fixation trials, and average velocity on pursuit trials—and use these different internal standards depending on whether current trial required fixation or pursuit. Future experiments could manipulate the range of velocities presented under pursuit and fixation conditions to explore this.

Another possibility is that clicks do not alter sensory or motor velocity signals at all, but simply bias responses. Makin, Poliakoff, Dillon, et al. (2012) explored one type of response bias by reversing the scale, so that participants entered smaller numbers for faster motion and larger numbers for slower motion. Clicks still increased velocity estimates although participants now entered lower numbers after clicks than after silence or white noise. This suggests that the effect of clicks cannot simply be attributed to a bias to use the higher end of the response scale. The selective effect of clicks during pursuit also militates against any general explanation based on response bias, because such a bias would apply to fixation and pursuit conditions equally.

Given that $\text{speed} = \text{distance}/\text{time}$, a final possibility is that auditory clicks could alter velocity estimates *indirectly*, by distorting spatial or temporal representations. Of course it is well known that clicks increase subjective duration (e.g., Jones et al., 2011; Penton-Voak et al., 1996; Treisman et al., 1990), so one might expect them to reduce subjective velocity (if it takes more time to get from a to b, the

target must be moving slower). However, this is the opposite of the obtained results, so this is not viable.

The observed increase in subjective velocity *could* theoretically be explained by an increase in perceived distance (if the target covered a greater distance in the given duration, it must be moving faster). However, we think this account is also unlikely: Makin, Poliakoff, Dillon, et al. (2012) found the same effect with drifting gratings, which do not have a clear start and end position. Furthermore, in the current work, the distance covered by the target was predictable before motion onset, and Droit-Volet (2010) found no effect of clicks on the perceived length of a single line. More generally, we note that velocity computation does not arise from this kind of post hoc cognitive comparison of separate duration and distance information, whether it is based on retinal or extraretinal signals (Barnes, 2008; Burr & Thompson, 2011). Finally, any explanation involving spatial distortion would have to account for the fact that clicks only increased subjective velocity in the pursuit condition. We think our results are most easily explained by a direct effect of clicks on extraretinal velocity signals.

Possible mechanisms

The mechanisms by which auditory click trains alter subsequent perceptual judgements are unknown. It has been suggested that clicks create arousal and that this affects other cognitive processes (e.g., Wearden et al., 1999), but solid evidence for any account remains elusive (Jones et al., 2011). In this section, we consider various perceptual judgements and how they could be “touched” by auditory clicks.

When considering the results of this study alone, many researchers have noticed the intriguing resemblance and overlap between auditory click trains, which have a certain temporal frequency, and models of visual velocity coding, which consider neurons tuned to combinations of spatial and temporal frequency (Burr & Thompson, 2011; McKeefry, Burton, & Vakrou, 2007). This link could be explored by systematically varying

the temporal frequency of auditory click trains and the spatial or temporal frequencies of moving gratings. However, we predict the influence of clicks to be unrelated to the spatiotemporal characteristics of moving gratings, because these factors alter retinal velocity signals, and we have established that click trains do not interfere with velocity processing at this level.²

Moreover, a satisfactory explanation of the click train effect must consider the full range and judgments that are influenced by clicks, not just velocity. For example, Droit-Volet (2010) reported that click trains increase the estimated combined length of several sequentially flashed lines or the estimated sum of sequentially presented numbers, as well as subjective duration. There was no effect of clicks on estimated magnitude of equivalent static presentations. The putative effects of click trains on temporal filters cannot explain these effects, only effects on velocity.

Perhaps we should look to more general models of perceptual estimation for instruction. Many experiments have shown interference between different subjective magnitude judgements, even when the dimensions are objectively independent (Walsh, 2003). For example, people sometimes judge heavier objects to have been presented for longer durations. These findings have led to the proposal that the brain has a common magnitude estimation system, where “more” on one dimension is interpreted as “more” on all dimensions (Lu, Mo, & Hodges, 2011). Click trains may interact with this system, resulting in higher magnitude estimates across a range of perceptual qualities. However, there is nothing in common magnitude literature that predicts the specificity of the click effect: For example, why should clicks alter judgements based on extraretinal but not retinal velocity signals, or dynamic but not static presentations?

So, can we say anything positive about how auditory click trains alter a subset of perceptual judgements? Perhaps the most promising line of

enquiry involves the functional significance of brain oscillations (Jones et al., 2011). According to the inhibition-timing model, synchronization of low-frequency neural oscillations is a form of neural inhibition (Klimesch, Sauseng, & Hanslmayr, 2007). Prestimulus click trains could drive low-frequency neural oscillations across multimodal networks, inhibiting irrelevant processing before motion onset (Hanslmayr et al., 2005). Rebound from this click-driven inhibition could increase subjective velocity. If so, our findings imply that auditory click trains do not produce driven alpha rhythms in the more peripheral brain regions that code retinal velocity, such as areas V1, V3a, and MT, but only in higher sensory-motor areas, like MST and the FEFs. Recording neural oscillations during the prestimulus click trains could test this prediction.

Future work

We have considered the sensory and motor transformations involved in smooth pursuit and seen that auditory clicks selectively distort representations on the *motor side* of the continuum. Perhaps this conclusion is not specific to eye movements? It is now well understood that action planning is a fundamental part of mental simulation, imagery, and cognition (e.g., Poliakoff, Galpin, Dick, & Tipper, 2009; Rizzolatti, Riggio, & Sheliga, 1994; Schubotz, 2007). We tentatively suggest that repetitive stimulation might distort all mental activity that involves motor or premotor networks. For example, in a manual analogue of the current work, one could contrast tactile velocity signals, where a textured stimulus moves across the skin, with haptic velocity signals, where participants track the same stimulus with their hand. We predict that haptic, but not tactile, velocity signals will be affected by prior presentation of click trains. It has also been suggested that at least

² We cannot make any predictions regarding different click train frequencies based on the current data, but Penton-Voak et al. (1996) found no difference between 5- and 25-Hz click train frequencies on subjective duration, so it is possible that the frequency of clicks will have no effect on subjective velocity. Nevertheless, there are reported cases where click train frequency was consequential, for example Wearden et al. (1999) reported that 25-Hz clicks had greater effect than 5-Hz clicks, so this remains an open question.

some forms of mental object rotation involve covert motor activity (e.g., Dalecki, Hoffmann, & Bock, 2012), and thus click trains might affect completion time for these tasks. Finally, in order to get a complete multimodal picture, it would be possible to use other kinds of repetitive stimuli, perhaps visual flicker or tactile vibration, instead of auditory click trains.

CONCLUSIONS

This work demonstrates that auditory click trains presented before motion onset selectively distort extraretinal velocity signals. This could be because higher level neural regions coding extraretinal velocity signals have greater multimodal connectivity. Areas that are traditionally considered unimodal, such as primary visual cortex, are now known to respond to multisensory inputs (e.g., Ghazanfar & Schroeder, 2006). However, our data point to audio-visual interactions at a higher level, where extraretinal velocity signals are coded, perhaps area MST (Their & Ilg, 2005). We also note that there was a relatively long and variable lag between the last click and the onset of motion (between 3 and 4 s). This contrasts with the high temporal precision required for audio-visual facilitation in V1 and V2 (e.g., Bolognini et al., 2010; Romei et al., 2009).

For over 20 years, the effect of auditory click trains on subsequent perceptual judgements has been empirically documented, but not fully explained. The effect of clicks is interesting because it may provide evidence about neural architecture, indicating which brain regions are susceptible to cross-modal inputs, and also the functional significance of oscillations at different frequencies. Although a satisfactory explanation for the click effect remains elusive, this work narrows the search, showing that click trains alter some velocity representations but not others.

Original manuscript received 23 January 2013

Accepted revision received 30 April 2013

First published online 18 July 2013

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