Report

Temporal Dynamics of Auditory and Visual Bistability Reveal Common Principles of Perceptual Organization

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Summary

When dealing with natural scenes, sensory systems have to process an often messy and ambiguous flow of information. A stable perceptual organization nevertheless has to be achieved in order to guide behavior. The neural mechanisms involved can be highlighted by intrinsically ambiguous situations. In such cases, bistable perception occurs: distinct interpretations of the unchanging stimulus alternate spontaneously in the mind of the observer [1]. Bistable stimuli have been used extensively for more than two centuries to study visual perception [2]. Here we demonstrate that bistable perception also occurs in the auditory modality. We compared the temporal dynamics of percept alternations observed during auditory streaming [3, 4] with those observed for visual plaids [5, 6] and the susceptibilities of both modalities to volitional control. Strong similarities indicate that auditory and visual alternations share common principles of perceptual bistability. The absence of correlation across modalities for subject-specific biases, however, suggests that these common principles are implemented at least partly independently across sensory modalities. We propose that visual and auditory perceptual organization could rely on distributed but functionally similar neural competition mechanisms aimed at resolving sensory ambiguities.

Results and Discussion

The study of bistable perception has generated a sustained interest in visual neuroscience, as it decouples the conscious perception of the observer from the characteristics of the physical stimulation: the same stimulus evokes different percepts. This provides a powerful method to probe the neural bases of perception, because changes in neural responses that correlate with subjective percepts cannot be traced to changes in the stimulation [7]. Bistability has been described with a wide range of stimuli: ambiguous figures [8], binocular rivalry [2, 9], and moving plaids [5], to cite a few. Some theoretical accounts of bistability are based on sensory fatigue, adaptation, or inhibition of peripheral neural channels and are thus specific to the type of bistability studied [10–12]. Others posit a central switching mechanism [1, 13]. Neural correlates have been exhibited for both types of models [1, 8, 9, 14].

In spite of the value that bistable perception presents for the study of perceptual organization, it has been described systematically only in the visual modality. There are reports of alternating perceptual interpretations of an unchanging auditory stimulation, such as in the verbal transformation effect where the repetition of a same word can produce different meanings [15], or for auditory grouping [4]. It is unclear, however, what similarities or differences exist between such phenomena and visual bistability. The present study of bistable perception in two sensory modalities aims to investigate whether the rules governing the alternation of perceptual states are general principles of brain function or specific to the visual system.

We chose a simple auditory scene to study "auditory bistability." We used a stimulus where high-frequency tone A alternates with low-frequency tone B in repeated ABA... patterns. Listeners report hearing the sequence either as one stream (ABA-ABA) or as two streams (A-A-A-A and -B—B-). This streaming stimulus has become a canonic paradigm to study auditory scene analysis behaviorally [3, 4] or, recently, to address the neural basis of auditory scene analysis [16–20]. Three of these studies took advantage of spontaneous percept alternations to look for corresponding changes in neural activity [17–19]. It seems timely to assess the commonalities of this phenomenon with visual bistability, which has been the subject of intense investigation.

Moving plaids were chosen as visual stimuli. When a network of crossing lines is seen moving through a circular aperture, it can be perceived either as a single plaid moving in a given direction or as two gratings sliding in opposite directions on top of each other [5, 6]. Plaids are typical illustrations of visual bistability, with similar characteristics to binocular rivalry [5, 21, 22] but displaying less indeterminate percepts (blending or piecemeal rivalry). Moreover, there is a formal correspondence between the visual and auditory stimuli chosen in terms of organization of the sensory scene: a decision has to be made whether to group the scene into one stream/one plaid, or to split the scene between two streams/two gratings. We will refer to these situations as grouped or split percepts. Examples of auditory and visual stimuli are provided as Supplemental Data available with this article online.

Leopold and Logothetis [1] established three characteristics of perceptual alternations observed in all instances of visual bistability: exclusivity, randomness,

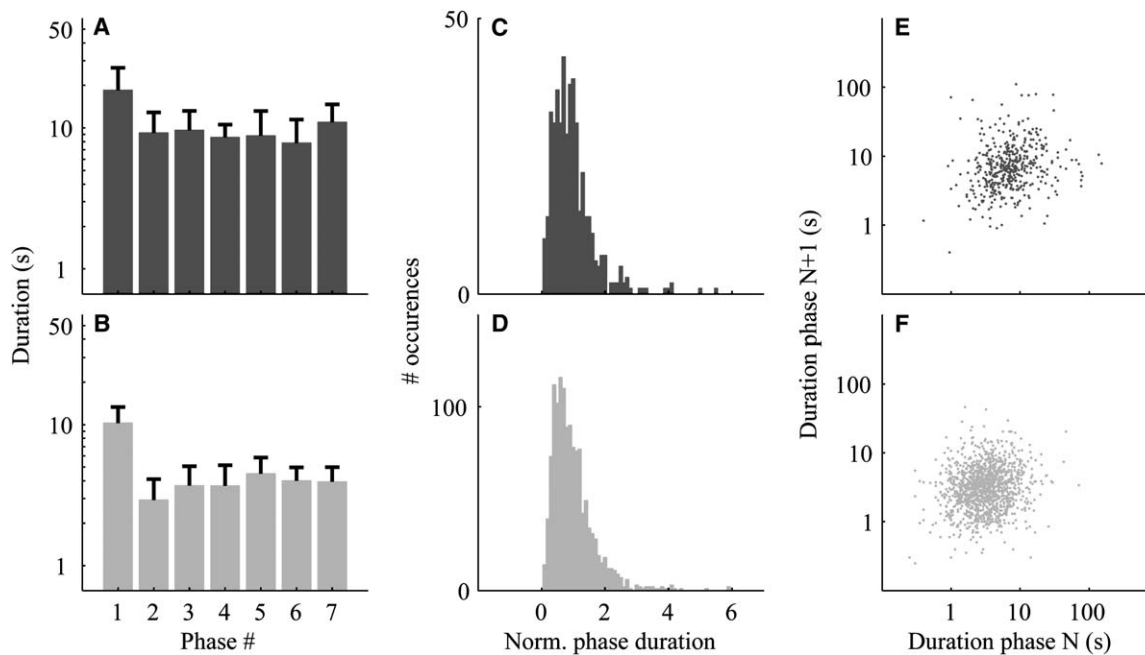*Correspondence: daniel.pressnitzer@ens.fr

Figure 1. Temporal Dynamics for Auditory and Visual Bistability

(A and B) The durations of the first seven successive phases are presented for both the auditory modality ([A], dark gray) and the visual modality ([B], light gray). Durations were first transformed to a log scale, then averaged across all participants that experienced seven or more successive phases (audition n = 20, vision n = 23). The error bars represent 95% confidence intervals around the mean estimated by 1.96 standard error. The log-scale is converted back to seconds for display purposes. The first percept is significantly longer that subsequent ones. There is no long-term trend in the duration of phases after the first one.

(C and D) The histograms of durations of grouped and split phases are presented, compiled for all participants (n = 23) and percept types (grouped and split). All durations were normalized by the average phase duration in each given run. The first phase was excluded from the analysis because it lasted longer than subsequent ones. There is no significant difference between the distributions for the two modalities (Kolmogorov-Smirnov test, p = 0.1).

(E and F) The duration of a percept is shown as a function of the duration of the previous percept, for all participants (n = 23). These are the same data that constitute the histograms of (C) and (D), but in raw format without any normalization. The duration of a phase does not influence the duration of the next phase, for both modalities. All data in this figure from the neutral task.

and inevitability. Exclusivity means that perceptual interpretations are mutually exclusive. Randomness characterizes the statistical distribution of the time spent in each percept. Inevitability indicates that observers have only limited volitional control on perceptual alternations. We now show that these criteria are met for both auditory and visual ambiguous stimuli, with similar characteristics in their temporal dynamics.

Exclusivity

23 participants listened to ABA… sequences or observed moving plaids for 4 min intervals. They were instructed to report continuously their conscious perception (grouped, split, or indeterminate). All participants reported spontaneous alternations during prolonged exposure to either type of stimuli. In the auditory case, the time spent in the grouped or split percepts was equally divided on average across the population of participants. This proportion is expected to depend on the parameters chosen for the ABA… stimulus [3]. Importantly, very little time was spent in an "indeterminate" perceptual state: less than 3% of total presentation time, even though this was the default response when stimulus presentation began. Mean and standard deviation for the percentage of time spent were: grouped, 51.4 (21.2); split, 45.8 (20.4); indeterminate, 2.8 (3.5). Results were similar in the visual modality: grouped,

50.1 (14.6); split, 48.5 (15.1); indeterminate, 1.3 (2.0). Both modalities thus display the basic feature of bistability, the spontaneous alternation between mutually exclusive percepts.

Randomness

A hallmark of visual bistability is that the durations of alternating percepts, or phases, follow a random law that can be fitted with a gamma or lognormal distribution [5, 23, 24]. A lognormal distribution suggests the multiplication of a large number of independent random processes [24], whereas a gamma distribution results from the combination of a small number of consecutive Poisson processes [25]. Although observed for a variety of phenomena, lognormal or gamma distributions are not observed when subjects are asked to press buttons randomly [26].

The average durations for successive phases are shown in Figures 1A and 1B. For both the auditory and visual modalities, the first phase had a longer duration than subsequent phases. This is consistent with previous results obtained in the visual modality [5]. With the first phase excluded, the switching rate was constant over observation time with no long-term trends (see also Supplemental Data). There is a tendency for auditory phases to last longer than visual ones, which might be due to the specific stimulus parameters used here.
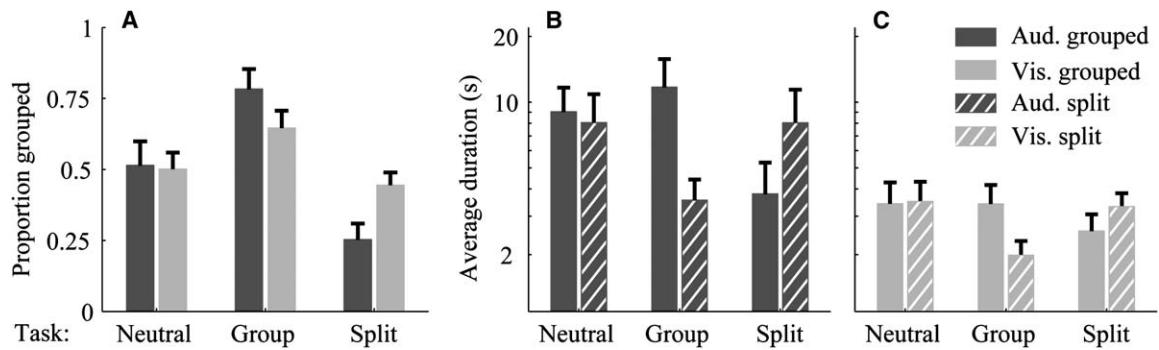
Figure 2. Effect of Volitional Control on Auditory and Visual Bistability

(A) The proportion of time spent in the grouped percept is shown as a function of the task (neutral, group, split) and modality of presentation (auditory in dark gray, visual in light gray). Mean and 95% confidence intervals across participants. Data for all participants (n = 23). Each participant performed each task once. In the neutral task, the grouped percept was experienced for about 50% of the time on average, for both modalities. Participants could influence the amount of time spent in a given perceptual state according to their intention. The effect is observed in both modalities with a stronger magnitude in the auditory modality (group minus split difference 53% versus 20%).

(B and C) The time spent in grouped (solid lines) and split (dashed lines) percept is shown as a function of the task, for each modality. Durations were converted to a log-scale, with the corresponding values shown in seconds for display purposes. Mean and 95% confidence intervals across participants. In both modalities and for both volitional tasks, intention translated into a shortening of the duration of the unwanted percept but caused no increase in the duration of the target percept.

The distribution of phase durations for the auditory and visual modality are illustrated in Figures 1C and 1D. Analyses of phase distribution require that the switching rate be stable over time, so the first percept was excluded. Phases were normalized by the average phase duration over a given trial to limit the influence of interindividual differences, as proposed for visual bistability [21, 27]. The normalized phase distributions are skewed toward longer durations, a characteristic of gamma or lognormal distributions. Distinguishing between the two is beyond the scope of the present paper, where only potential similarities between auditory and visual distributions are of interest. An analysis of variance (Experimental Procedures) showed that both distributions were not statistically different from lognormal. A Kolmogorov-Smirnov test further indicated that the auditory distribution was not significantly different from the visual distribution. The temporal dynamics of both phenomena thus display a strong similarity.

Scatterplots of the duration of a given phase as a function of the duration of the previous phase are shown in Figures 1E and 1F. These panels display all available data points and illustrate the large variability observed among phase durations when no normalization is applied. No correlation exists between successive durations, consistent with what is observed for binocular rivalry [23] (statistical analyses as described in Supplemental Data).

Inevitability

Volitional control can bias the perception of some visual bistable stimuli [28–31]. The amount of volitional control that can be exerted has been proposed as an indication of the neural level where competition between percepts occurs, with large control reflecting higher-level processes [8]. We investigated the effect of observer intention on the reported percepts for auditory streaming and visual plaids. On successive runs, participants were instructed to try to maintain a given perceptual interpretation throughout stimulus presentation. For both

modalities, volitional control had a significant effect (Figure 2A). When subjects tried to group, the proportion of grouped percepts increased as compared to the neutral task. The opposite was true when they tried to split. The effect of volitional control was stronger for the auditory modality than for the visual modality. Bistable perception is, however, inevitable in the two modalities, as alternations persist even in the presence of intention.

Volitional control had a specific effect on the duration of each percept type (Figures 2B and 2C). In the neutral task, no difference was found between the grouped and split durations. When subjects tried to group, the mean duration of the grouped phases did not actually increase—rather, the mean duration of the split phases was reduced. This pattern of result is identical for the two intentions and the two modalities: volitional control shortens the unwanted phases but does not increase the duration of the target phases. This systematic and somewhat counterintuitive effect argues against unspecific demand characteristic biases, where observers would simply adjust their reports to what the experimenter is asking for. It is rather consistent with Levelt's second proposition [32]. This proposition states that, for binocular rivalry, strengthening the stimulus to one eye does not affect the dominance duration of that eye but rather decreases the dominance duration of the other eye. If it is assumed that intention increases the perceptual strength of the target percept, then the current data conform to Levelt's second proposition. A similar effect of intention, although smaller, can be observed for binocular rivalry: selective attention only decreases the unattended eye dominance duration [30].

Absence of Correlation across Modalities

An important debate about visual bistability concerns the possibility of a common, top-down neural mechanism as the cause of alternations for all ambiguous stimuli [1, 8, 9, 28]. A common mechanism should introduce subject-specific biases irrespective of the stimulus [13, 22]. The number of switches [13], proportion of grouped
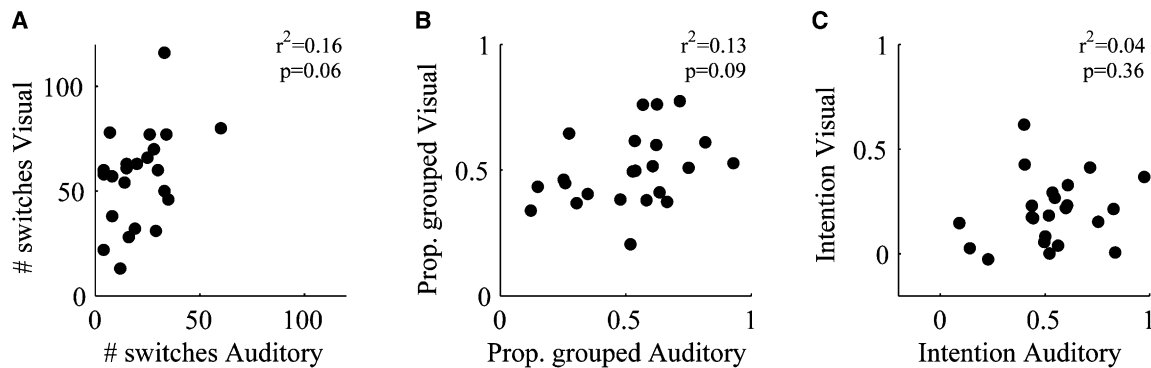
Figure 3. Absence of Correlation between Subject-Specific Measures across Modalities

(A) The number of perceptual switches in the visual modality is plotted as a function of the number of switches in the auditory modality, for the neutral task. Each point represents an individual observer (n = 23). The number of switches is not correlated across modalities.

(B) The relative amount of time where the stimuli are perceived as grouped is compared for both modalities, for each individual observer, in the neutral task. There is no idiosyncratic tendency to favor a grouped or split interpretation across modalities.

(C) The magnitude of the effect of volitional control is compared across modalities. The effect was quantified by subtracting the proportion of grouped percepts between the group and split intentions, for each observer. The magnitude of the effect of volitional control is uncorrelated across modalities.

percept, and effect of volitional control [30] were compared for each subject across the two modalities in the present data. Intersubject variations were large on all of these measures (Figure 3) so they can potentially reveal subject-specific biases. There was a weak, nonsignificant correlation for the number of switches (Figure 3A) indicating no bias to switch quickly or slowly irrespective of sensory modality—unlike the strong correlation observed between different visual bistable stimuli [13, 22]. The proportion of grouped percept was also uncorrelated across modalities (Figure 3B). Finally, the amount of effective volitional control was estimated by subtracting the proportion of grouped percepts between the group and split intentions, for each observer (Figure 3C). This measure was unrelated across modalities. Observers who were better at controlling their auditory percepts were not necessarily better at controlling their visual percepts (Figure 3C, bottom right). For all three measures investigated, idiosyncratic biases did not carry over between visual and auditory bistability.

Auditory Streaming as a Bistable Percept

Auditory streaming determines whether we assign a sequence of sounds to one or more sources. Whereas streaming usually reflects physical reality, such as when more than one person talks at the same time, it can also be fooled, for instance when two interleaved musical melodies are produced by a monophonic instrument. With the ABA… stimulus that we used, there is an irresolvable ambiguity as to how many streams should be perceived. This leads to spontaneous alternations between percepts of one or two streams when the stimulus is heard for a prolonged period of time [4]. In addition, we have shown that these alternations share many features with visual bistability [1]: percepts of one stream versus two streams are mutually exclusive, their duration follows a lognormal distribution with short-term independence and no long-term trend, and volitional control has an influence on but does not abolish alternations. Based on these strong similarities, we propose

that auditory streaming can be considered as an instance of perceptual bistability.

The bistable nature of auditory streaming has not been recognized before. Anstis and Saida [33] reported a "marked long-term trend over time toward auditory segregation" and concluded that streaming was not comparable to visual bistability for which no such trend is observed. They used 30 s long stimuli, however, and most experimenters used even shorter presentation times. The longer observation periods chosen here (240 s), together with the analysis methods normally applied to visual bistability, lead on the contrary to the conclusion that after the first percept, the steady-state of the temporal dynamics of auditory streaming is purely stochastic with no long-term trend (Figure 1A).

This provides an alternative framework to interpret the long-term build-up of streaming documented by numerous studies [34]. A bias for an initial grouped percept that lasts longer than subsequent ones was observed here (in the two modalities, possibly due to the asymmetry between grouped and split percepts). When such an initial grouped bias is combined with random phase duration, averages across listeners and/or repeats will exhibit a gradual increase in the proportion of split reports. The subsequent purely bistable nature of phase alternations then produces a plateau corresponding to the steady state probabilities of the percepts. These two features are fully consistent with characteristics of the build-up of streaming, when considering average measures [3, 34]. Our results suggest that, additionally, measures of temporal dynamics [5] could provide valuable new tools in the investigation of auditory streaming.

Models of Perceptual Bistability

Current accounts of visual bistability emphasize low-level competition of features [10, 12], high-level competition of representations [27], or top-down attentional selection mechanisms [1, 28]. The question arises as to which of those theoretical frameworks is able to account for both visual and auditory bistability.

We observed strong similarities between bistability in the two sensory modalities. A first possibility is that both phenomena are controlled by a common, high-level switching mechanism, as has been hypothesized for various kinds of visual bistability [13]. By using fMRI with auditory streaming stimuli, Cusack [19] registered activation in the intraparietal sulcus correlated with the subjective experience of split percepts. As the intraparietal sulcus is likely involved in crossmodal integration [35], it could contribute to bistability in both modalities.

We failed to observe, however, consistent observer-specific biases across modalities. Strong biases would be expected if a single top-down selection mechanism were the sole determinant of the auditory and visual bistability. Another possibility is that some mechanisms of competition between percepts are distributed across modalities but share common functional principles. In the visual domain, a canonic brain architecture of mutual inhibition between populations of neurons coding for various attributes could explain the similarities between different types of bistability [21]. Inhibition has also been proposed as a functional building block for auditory scene analysis [36]. Distributed competition, as a general computational process, would be useful to resolve perceptual ambiguities irrespective of sensory modality.

Neurophysiological Evidence for Distributed Competition

The hypothesis of distributed competition is consistent with findings of neural correlates of the perception of ambiguous visual stimuli at different levels of neural processing. By means of fMRI, correlates of competition have been observed in V1 for binocular rivalry [37–39] as well as other types of visual bistability [40, 41]. Competition between interpretations is also reflected, however, in neuronal populations that code for the specific attributes that are competing: the human fusiform face area and the parahippocampal place area for binocular rivalry between faces and houses [42], or areas involved in motion processing for rivalry between motion stimuli [43]. Single-unit recordings in awake macaques also demonstrated correlations with perceptual alternations at different level of the visual cortex [44], specifically in area MT for moving stimuli [45] or in the temporal cortex for more complex objects [46].

Similarly, neural correlates of auditory streaming have been observed at different processing stages. Recordings in primary auditory areas with the ABA… stimulus showed that units with receptive fields centered on the A tones displayed a reduced response to the B tones when split percepts were more likely. This was observed in the primary auditory cortex of awake macaque monkeys [16, 17] and its equivalent in the starlings' forebrain [20]. A qualitatively different correlate was found via magnetoencephalography [18]. The split percepts were associated with larger long-latency potentials (P1m and N1m) for the B tones. These potentials are thought to originate from nonprimary auditory areas, the lateral Heschl's gyrus, the planum temporale, and the superior temporal gyrus. The current data on the neurophysiological bases of bistability in the visual and auditory modalities are thus consistent with a distributed competition hypothesis, although the respective contributions of the various stages remain to be elucidated.

Implications for Models of Auditory Scene Analysis

Most models of streaming are based on adaptation, starting from the auditory nerve and brainstem [47] up to auditory cortex [17]. Micheyl et al. [17] found that neural responses to ABA… sequences decrease with presentation time, but with different time constants for A and B tones. The time when responses to B tones fell below a fixed spike-count threshold predicted accurately the average build-up of streaming observed for human subjects. Within the framework of bistability, such a multisecond habituation mechanism could account for the specific characteristics of the first perceptual switch (Figure 1A). It would be of interest to extend the adaptation model to account for the dynamics of spontaneous alternations in the stochastic steady-state of streaming. Temporary reversals of the habituation process should then be observed. When the neural data become available, models of visual bistability that include mutual inhibition can provide inspirations to explain these dynamic effects [2].

Distributed or "integrated" competition at different levels of the central nervous system has recently been proposed by Cusack as a model of auditory scene analysis [48]. This approach can accommodate a range of behavioral and neural data, in addition to having desirable computational properties (R. Cusack, 2005, Soc. Neurosci., abstract). Here we have shown that auditory and visual bistability share many features and that a distributed competition hypothesis is consistent with this finding. Bistability is a means to highlight mechanisms normally used to achieve stable perceptual organization. A potentially useful principle to resolve perceptual ambiguities could be the existence of competition mechanisms, based on adaptation and mutual inhibition, at multiple neural processing stages.

Experimental Procedures

Auditory Stimuli
The auditory stimuli consisted of 4 min long sequences presented over headphones. A high-frequency pure tone A alternated with a low-frequency pure tone B, in an ABA… pattern. The frequency of A was 587 Hz and that of B was 440 Hz (5 semitones difference). The duration of each tone was 120 ms. The silence '…' that completed the ABA… pattern was also 120 ms long, thus making the A tones isosynchronous. Listeners initially adjusted the loudness of the tones to a comfortable level, which was maintained constant during the experiment.

Visual Stimuli
The visual stimuli consisted of two rectangular-wave gratings presented through a 4° radius circular aperture. The gratings comprised thin dark stripes (duty cycle = 0.3, spatial frequency = 0.5 cycle/deg) on a lighter background and appeared as figures moving over the background. The intersection regions were darker than the gratings (multiplicative transparency). The gratings were moving at 1.2°/s in directions 120° apart. A red fixation point over a 1° circular gray mask was added in the middle of the circular aperture and subjects were instructed to fixate this point throughout stimulus presentation.

Procedure
Observers were instructed to report their conscious perception of each stimulus continuously during stimulus presentation. They started with auditory presentation and were asked to decide whether they heard one or two streams. A third, "indeterminate" response type was available if they heard something else or were not sure about their perception at a given instant. Responses were

collected via three buttons on a computer keyboard. A response indicated by a button press was held until a subsequent button press. In the first run, subjects were simply instructed to pay attention to the stimulus (neutral task). In the subsequent two presentations, they were instructed to try to hear either a one-stream percept (group task) or a two-stream percept (split task) in random order of presentation. Judgments with visual presentation of plaids were then performed, with an identical procedure and the three different tasks (neutral, group, split). Judgments were collected continuously at a sampling rate of 20 Hz. The default response when each run started was "indeterminate."

23 observers participated in the experiment (average age: 23) with no self-reported hearing problem and normal or corrected-to-normal eyesight. They gave informed consent to participate to the experiments.

Statistical Analyses

A detailed description of all statistical analyses is provided in the Supplemental Data. To check whether the switching rate between percepts was stable over time, the first seven perceptual phases were extracted from each trial of the neutral task. A planned comparison showed that for both the auditory and visual modalities, the first phase had a longer duration than subsequent ones. With the first phase excluded, best-fitting linear trends indicated no significant drift up or down. In order to test whether the distribution of phases followed a lognormal distribution, we transformed the data from all three tasks onto a log scale and performed an analysis of variance. The distribution of residuals of the ANOVA was not statistically different from a normal distribution (Kolmogorov-Smirnov test). Distribution of normalized phases for auditory and visual stimuli in the neutral task were compared with a Kolmogorov-Smirnov test, which exhibited no significant difference. The independence of successive phase durations was assessed on the distribution of correlations between normalized log-phases, for each subject. The effects of intention were estimated on the proportion of the total time spent reporting the grouped percept and on the average phase duration of the split and grouped percept after transforming phase durations to their natural logarithm and excluding the first and last percepts. Repeated measures ANOVAs were performed on these values with the variable "task" and "modality" (Figure 2A) or "task" and "percept type" (Figures 2B and 2C) as independent factors. Effects of intention on the duration of percepts were estimated by post-hoc analyses.

Supplemental Data

Supplemental Data include three figures, five tables, and Supplemental Experimental Procedures and can be found with this article online at http://www.current-biology.com/cgi/content/full/16/13/1351/DC1/.

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