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ScienceDirect

Hearing Research 229 (2007) 204–212

Hearing Research

www.elsevier.com/locate/heares

Research paper

Neural and behavioral correlates of auditory categorization

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Received 30 August 2006; accepted 28 October 2006
Available online 8 January 2007

Abstract

Goal-directed behavior is the essence of adaptation because it allows humans and other animals to respond dynamically to different environmental scenarios. Goal-directed behavior can be characterized as the formation of dynamic links between stimuli and actions. One important attribute of goal-directed behavior is that linkages can be formed based on how a stimulus is categorized. That is, links are formed based on the membership of a stimulus in a particular functional category. In this review, we review categorization with an emphasis on auditory categorization. We focus on the role of categorization in language and non-human vocalizations. We present behavioral data indicating that non-human primates categorize and respond to vocalizations based on differences in their putative meaning and not differences in their acoustics. Finally, we present evidence suggesting that the ventrolateral prefrontal cortex plays an important role in processing auditory objects and has a specific role in the representation of auditory categories.

Keywords: Categorization; Rhesus macaque; Audition; Prefrontal cortex

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Categorization is a natural and adaptive process that is seen in all animals. While there is a great deal of variability within and across stimuli, animals typically ignore some sources of variation while treating other sources equivalently. For any given situation, we may decide, consciously or not, to attend to a more limited range of information. For example, when a person speaks, the voice carries information about gender, age, emotion, and semantic content. If the speaker is alarmed and is yelling “Fire!”, the gender and the age of the speaker may not carry any meaning at the time even though such information is available. In other situations, however, the gender or the age of the speaker may carry significant information. In a more ethological example, non-human animals are capable of identifying and categorizing other animals as predator or prey.

The advantage of categorization is that it allows humans and non-human animals to respond efficiently to novel stimuli (Freedman et al., 2001, 2002; Miller et al., 2002; Shepard, 1987; Spence, 1937) as well as to form groupings and divisions of their perceptions that may not be present in the external world (Miller et al., 2003). Of course, this capacity to adapt to novel events depends on the animal’s ability to register these events with existing internal representations. For instance, when we see a new model Corvette, we can access the category of “car” without having to identify and determine the function of each of its individual components. By associating this new exemplar with the established category, information that has been learned previously about this category becomes available. These representations can then be used to make decisions about the world and respond to it appropriately.

Categorical representations provide a means to mentally grasp, manipulate, reason, and respond adaptively to objects in our environment, a hallmark of goal-directed behavior. If goal-directed behavior can be thought of as a process that transforms sensory signals into actions, the computations that form the intermediate steps of this transformation involve categorical representations (Ashby and Berretty, 1997; Grinband et al., 2006). These computations are further modulated by context, motivation, and other factors.

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doi:10.1016/j.heares.2006.10.010

These examples are just a few of those that illustrate how crucial categorical representations are to adaptive behavior. In this paper, we review categorization and the factors contributing to categorization with an emphasis on auditory categorization in human and non-human primates. We also discuss neurophysiological studies that relate to categorical processing. Finally, we present directions in which future work on auditory categorization should pursue.

1. Types of categories

Any given stimulus (object) can be a member of several different categories depending on what rules are used to process it at a given time. These different categorical levels are often thought of as hierarchical in that categories at the top of the hierarchy are the most general and those at the bottom are the most specific. At the top of the hierarchy are "superordinate" categories, the most general. "Basic-level" categories are less general; these categories are the terms that people commonly use when encountering an object. At the bottom, are "subordinate" categories. For example, Lassie can be categorized as an animal, a dog, or a collie. The superordinate category would be "animal", the basic level category would be "dog", and the subordinate category would be "collie". Using another example, Handel's Messiah can be categorized as "music" (superordinate), "classical music" (basic), or "baroque-period music" (subordinate). Importantly, these different categories are not equipotent in the sense that they require different amounts of neural processing: we are typically faster and more accurate in categorizing objects into basic level categories than superordinate or subordinate categories (Rosch et al., 1976). Also, the level at which an object is categorized depends on previous experience and knowledge: someone with musical expertise might, at the basic level, categorize Handel's Messiah as baroque music or even as an oratorio (Gauthier et al., 1999; Marschark et al., 2004).

Different hypothetical frameworks can be used to describe the relationship between an object's membership in basic and more superordinate categories. One framework posits that superordinate categories contain a set of features that belong to all of the members of the more basic category (Damasio, 1989; Devlin et al., 1998; Martin et al., 2002; Rosch et al., 1976; Smith et al., 1974). For instance, the basic level category of "dog" might contain descriptors like "has fur", "has wet nose", "has four legs", "breathes", "is mobile", "can reproduce on its own", etc., whereas the superordinate category of animal contains descriptors "breathes", "is mobile", "can reproduce on its own", etc. An alternative view is that the properties of a basic-level category are not omitted from the superordinate category but are represented as more abstract variable values in this higher-order category (Macnamara, 1982; Macnamara, 1999; Prasada, 2000).

2. Perceptual categories

Perceptual similarity is one of the key elements that determine a stimulus' categorical membership (Boyton and Olson, 1987, 1990; Doupe and Kuhl, 1999; Eimas et al., 1971; Kuhl and Miller, 1975; Kuhl and Padden, 1982, 1983; Lasky et al., 1975; Liberman et al., 1967; Miyawaki et al., 1975; Sandell et al., 1979; Streeter, 1976; Wyttenbach et al., 1996). Perceptual categories are based on the physical attributes of an object. For example, male and female voices can be categorized as such by attending to the pitch of the voice, with female voices characteristically having a higher pitch than those of males. In another example, listeners can perceive different speech signals as belonging to the same phonemic category, or viewers can perceive different visual signals as being members of the same color category.

One prominent feature of perceptual categories is that they are often accompanied by categorical perception. In categorical perception, a subject's perception of a stimulus (object) does not vary smoothly with changes in the physical properties of the stimulus (object) (Ashby and Berretty, 1997; Liberman et al., 1967; Miller et al., 2003). In other words, stimuli or objects on one side of the categorical boundary are treated similarly, despite relatively large differences in their physical properties. At locations near the category boundary, small changes in an object's properties can lead to large changes in perception.

A classic example of categorical perception is the categorization of speech units into phonetic categories (Holt, 2006; Kuhl and Padden, 1982, 1983; Liberman et al., 1967; Lotto and Kluender, 1998; Mann, 1980). In a seminal study, Liberman and colleagues (1967) created morphed versions of two different phonemes and asked subjects to report the phoneme that they heard. In morphing, two prototypes (e.g., two phonemes) are chosen and then a (linear) mapping based on the physical features of the prototypes is calculated. Morphed stimuli are ones that lie along this mapping. A "50%" morph then would lie halfway along the mapped continuum between the two prototypes, whereas a "25%" morph would lie a quarter of the way along the continuum. Liberman et al. found that as long as subjects were presented with a morphed stimulus that contained more than 50% of a phoneme prototype, the subjects reliably perceived that stimulus as the prototype. That is, even though the presented stimuli varied smoothly in their physical features, subjects perceived the presented stimuli as being either one of the two phoneme prototypes.

Even though some perceptual categories have sharp boundaries, the locations of the boundary are malleable. For instance, the perception of a phoneme can be influenced by the phonemes that come before it (see Fig. 1). When morphed stimuli that are made from the prototypes /da/ and /ga/ are preceded by presentations of /al/ or /ar/, the perceptual boundary between /da/ and /ga/ shifts (Mann, 1980). Subjects more often perceive the morphed stimuli as /da/ when it was preceded by /ar/. In contrast,

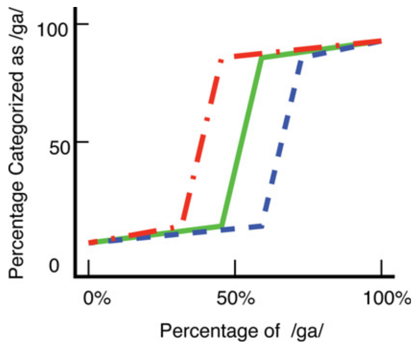

Fig. 1. Schematic of the categorical perception of a continuum of /da/ and /ga/ phonemes. For points along the *x*-axis, 0% refers to a prototypical /da/ and 100% is a prototypical /ga/. Intermediate points are morphed versions of /da/ and /ga/. The green line schematizes the normal perception of this continuum. The red line schematizes the perception of the phonemes when preceded by /al/, whereas the blue line schematizes the perception of the phonemes when preceded by /ar/. When phonemes along the /da/–/ga/ continuum are preceded by /al/ the categorical boundary shifts toward /ga/. In contrast, when phonemes along the /da/–/ga/ continuum are proceeded by /ar/, the categorical boundary shifts toward /da/. This figure is adapted from data by Mann (1980), Lotto et al. (1997), and Holt (2006). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

when the morphed stimulus was preceded by /al/, subjects perceived the morphed stimulus as /ga/.

The perception of phonemes can also be influenced by non-speech stimuli (Holt, 2006; Lotto and Kluender, 1998). When tones whose frequencies match the third formant frequency of /al/ or /ar/ precede presentations of morphed stimuli of /da/ and /ga/, the perceptual boundary shifts in a manner similar to that seen when these morphed stimuli are preceded by the actual /al/ or /ar/ phonemes (see above) (Lotto and Kluender, 1998). Interestingly, the non-speech stimuli may have a greater impact on the perception of /da/ and /ga/ than do the speech stimuli (Holt, 2006).

The perceptual categorization of phonemes is not strictly a human behavior, though other organisms may use different rules to categorize these stimuli. In one study, rhesus macaques were trained on a go/no-go task to respond to the presentation of a /da/ stimulus, and withhold responses to either /ba/ or /ga/ (Kuhl and Padden, 1983). After training was complete, the monkeys participated in the go/no-go task using morphed stimuli made from combinations of /da/, /ba/, or /ga/ instead of the prototypes. Like human subjects, the responses of the monkeys suggested that they perceived the morphed stimuli categorically (Kuhl and Padden, 1982, 1983). Comparable results were found with chinchillas as well (Kuhl and Miller, 1975, 1978). Finally, like humans, the perceptual boundary of these phonemes can be influenced by preceding stimuli: when /da/ and /ga/ stimuli are preceded by /ar/ and /al/, the perceptual boundaries of Japanese quails are shifted (Lotto et al., 1997) (see Fig. 1). Thus, the manner in which perceptual categories are coded may be similar across a wide variety of animal species.

3. Abstract categories

Categories are not only formed based on the perceptual (physical) features of stimuli. Categories can also be based on more abstract information. An abstract category is one in which a group of arbitrary stimuli are linked together as a category based on some shared feature, a functional characteristic, or acquired knowledge. For instance, despite vast physical differences, "hammer", "band saw", and "pliers" are all members of the "tool" category. Similarly, a combination of physical characteristics and knowledge about their reproductive processes allow us to categorize "dogs", "cats", and "killer whales" in the category of "mammals". However, if we were to use other types of knowledge to form a category of "pets", dogs and cats would be members of the pet category but killer whales would not.

Non-human animals can also categorize stimuli into abstract categories. Monkeys that have participated in laboratory-based operant training can categorize objects as being animals or non-animals (Fabre-Thorpe et al., 1998) or as trees or non-trees (Vogels, 1999) to name just a few. The capacity to represent even more abstract categories, such as ordinal number (Nieder et al., 2002; Orlov et al., 2000), is present as well. Although these studies provide important insight into how abstract categories are built, their generalizability to more ethological condition is limited by the use of artificial stimuli.

Behavioral studies that have used more ethological stimuli have shown that non-human primates may form categories "spontaneously". That is, they form categories in the absence of laboratory-based operant training. A classic example is the categorization of food-related species-specific vocalizations by rhesus monkeys (Gifford et al., 2003; Hauser, 1998; Hauser and Marler, 1993a,b). In rhesus monkeys, a vocalization called a "harmonic arch" transmits referential information about the discovery of rare, high-quality food. A different vocalization called a "warble" also transmits the same type of referential information: the discovery of rare, high-quality food. Importantly, while both harmonic arches and warbles transmit the same type of information, they have distinct spectrotemporal properties. In contrast, "grunts" transmit a different type of information (the discovery of common, low-quality food) and are acoustically distinct from harmonic arches and warbles.

Despite these acoustic differences, rhesus categorize these food-related calls based on their referential information and not their acoustic features. When participating in a habituation-discrimination task, the monkeys do not discriminate between vocalizations that transmit the same referential information (i.e., harmonic arches and warbles) even though these vocalizations have different acoustic features. In contrast, the monkeys do discriminate between vocalizations that transmit different types of referential information (i.e., grunts versus warbles/harmonic arches). That is, rhesus perceive harmonic arches and warbles as if they belong to a single functional category (based on referential information and not based on acoustics) and treat grunts as a second, different category.

The formation of abstract acoustic categories is seen in other monkey species. Female Diana monkeys categorize and respond similarly to a male Diana monkey or a crested guinea fowl eliciting leopard-alarm calls (Zuberbuhler, 2000a,b; Zuberbuhler and Seyfarth, 1997). Diana monkeys also form across-species categories with putty-nose monkeys based on the ability of putty-nose monkeys to provide vocal warnings of eagles (Eckardt and Zuberbuhler, 2004). These observations suggest that Diana monkeys form abstract categorical representations of vocalizations independent of acoustics and the species generating the signal.

Other broad functional categories exist in non-human primate vocalizations. Vervet monkeys produce three unique alarm calls for three different predators: a snake, a leopard, and an eagle (Seyfarth et al., 1980). These calls elicit different patterns of species-specific behaviors. Specifically, when they hear an eagle-alarm call, vervets scan the sky for visual cues of the airborne predator, and/or run to locations that provide overhead coverage. However, when they hear a snake-alarm call, vervets stand up and scan the ground. Finally, when vervets hear a leopard-alarm call they run up the nearest tree while scanning the horizon. Additionally, rhesus macaques produce four different submissive screams: tonals, arched, noisy, and pulsed (Gouzoules et al., 1984). These screams are produced when the signaler is being aggressed by other rhesus. The different calls are produced based on who is aggressing the rhesus and the type of aggression that is occurring (Gouzoules et al., 1984).

4. Neurophysiological representations of categories

In this section, we review two cortical areas that appear to play an important role in the formation of categories and using categories to guide adaptive behavior: the temporal cortex and the prefrontal cortex, respectively (Ashby and Spiering, 2004; Freedman et al., 2001, 2002; Hung et al., 2005; Kreiman et al., 2006; Miller, 2000, 2002, 2003).

To establish a context for this section, let us consider an important model of auditory, as well as visual, function (Rauschecker, 1998; Ungerleider and Mishkin, 1982). Namely, auditory processing can be broken down roughly into two functional streams: a "dorsal" pathway that processes the spatial attributes of a stimulus (*where is the sound?*) and a "ventral" pathway that processes the non-spatial attributes (*what is the sound?*) (Hackett et al., 1999; Pandya and Barnes, 1987; Rao et al., 1997; Rauschecker, 1998; Romanski et al., 1999a,b). The auditory spatial pathway originates in the caudomedial belt region of the auditory cortex, whereas the non-spatial pathway originates in the anterolateral belt region of the auditory cortex. Indeed, neurons in the caudomedial belt of the auditory cortex respond more selectively to the location of an auditory stimulus than anterolateral neurons, whereas anterolateral neurons respond more selectively to different exemplars of monkey vocalizations than caudomedial neurons (Tian et al., 2001). In addition to the belt region, the spatial dorsal pathway includes the posterior parietal cortex and the dorsolateral prefrontal cortex, both of which respond to visual and auditory stimuli (Cohen et al., 2005; Stein and Meredith, 1993; Ungerleider and Mishkin, 1982). The non-spatial ventral pathway is defined by a series of projections from the anterolateral belt to the ventrolateral prefrontal cortex. This anatomical parcelization of auditory function is not unique to non-human primates: In humans, there are several lines of anatomical (Galaburda and Sanides, 1980; Rivier and Clarke, 1997; Tardif and Clarke, 2001), neurophysiological (Alain et al., 2001; Anourova et al., 2001; Baumgart et al., 1999; Bremmer et al., 2001a,b; Bushara et al., 2003, 1999; Cusack et al., 2000; Deouell and Soroker, 2000a; Deouell et al., 2000b; Griffiths et al., 1998; Hart et al., 2004; Maeder et al., 2001; Patterson et al., 2002; Rämä et al., 2004; Scott et al., 2000; Vouloumanos et al., 2001; Warren and Griffiths, 2003; Warren et al., 2002; Zatorre et al., 1992), and neuropsychological (Clarke et al., 2000) evidence suggesting that distinct pathways process different attributes of an auditory stimulus (Warren and Griffiths, 2003). The functional segregation of these two processing streams is unclear since recent data suggests that, like the visual system, there is considerable crosstalk between the two pathways (Cohen et al., 2004; Ferrera et al., 1992, 1994; Gifford et al., 2005a; Sereno and Maunsell, 1998; Toth and Assad, 2002).

While the auditory cortex has traditionally been thought to be involved in feature extraction (Mendelson and Grasse, 1992; Middlebrooks et al., 1980; Shamma et al., 1993; Theunissen et al., 2004; Versnel et al., 1995), more recent work has suggested that neurons in the auditory cortex are involved in computations beyond simple feature extraction and may instead play an important role in the computations underlying the representation of auditory objects (Nelken et al., 2003). Consistent with this hypothesis, numerous studies have shown a role for the primary auditory cortex and other regions of the superior temporal gyrus in the categorization of phonemes (Guenther et al., 2004; Husain et al., 2005; Poeppel et al., 2004). For example, neuroimaging data indicate that the left and right superior temporal gyri are modulated when subjects are asked to categorizes syllables with varying voice-onset times as either /ba/ or /pa/ (Guenther et al., 2004; Husain et al., 2005; Poeppel et al., 2004). Interestingly, while both the left and right superior temporal gyri were activated during this task, the left hemisphere was consistently more active than the right during the categorization task. Electrophysiological studies in the auditory cortex of non-human primates and cats also show a neural correlate of voice onset time (Eggermont, 1995; Steinschneider et al., 1994).

Why is it harder to discriminate between exemplars that are in the "middle" of a category than it is to discriminate between exemplars that lie near the border? One potential

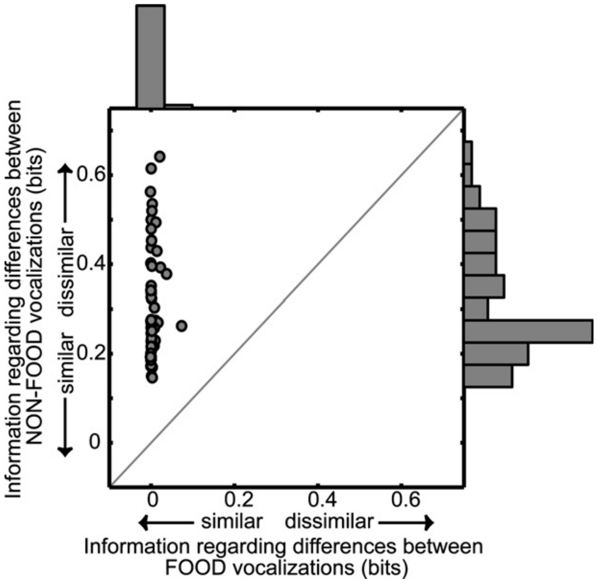

Fig. 2. Distributions of category information quantifying the similarity of the spike trains of vPFC neurons elicited by different categories of species-specific vocalizations. On a neuron-by-neuron basis, the amount of categorical information generated from the food vocalizations (x-axis) and from the non-food vocalizations (y-axis). The solid grey line represents the expected relationship if the neurons had the same amount of category information. The top histogram shows the marginal distribution of the food-vocalization information values. The histogram to the right shows the marginal distribution of non-food-vocalization information values. (See Cohen et al., 2006 for more in-depth analysis of this data.)

mechanism may relate to the distribution of neural resources. Following behavioral training, more neurons are activated in the auditory cortex during the discrimination of sounds that lie near the boundary than during the discrimination of sounds that lie in the center of the category (Guenther et al., 2004). Thus, discrimination may be primarily limited by the number of active neurons. This type of reorganization that may be analogous to the redistribution of neural tuning properties following other types of training (Recanzone, 1998; Recanzone et al., 1993).

In addition to its involvement in the categorization of elements of speech, the auditory cortex also appears to play a vital role in the categorization of more abstract qualities, such as the direction of frequency-modulated tones (Ohl et al., 2001). In the Ohl study, gerbils were trained to categorize frequency-modulated tones as “upward” or “downward”, independent of the starting frequency, the ending frequency, or the rate of the frequency modulation. While the gerbils were involved in the task, epidural evoked potentials were recorded from multiple sites over the auditory cortex. An analysis of these recordings indicated that during early training sessions, neural activity reflected the acoustical properties of the frequency-modulated tones. However, as training progressed and the gerbils learned the categorization rule, neural activity reflected the categorical membership of the frequency-modulated tones, independent of their properties.

In addition to the auditory cortex, recent work from our group has suggested a role for the ventrolateral prefrontal cortex (vPFC) in categorization (Cohen et al., 2006; Gifford et al., 2005b). These studies have suggested a role in the spontaneous categorization of food-related vocalizations based on the information that they transmit and not their acoustic properties.

As discussed above, rhesus categorize harmonic arches and warbles into one category (high-quality, rare food) and grunts (low-quality, common food) into a separate category. Using an oddball paradigm (Näätänen and Tiitinen, 1996), we found that the activity of vPFC neurons was not modulated by transitions between presentations of food vocalizations that transmitted the same referential information, even though the vocalizations had significantly different acoustic structures. vPFC activity, however, was modulated by transitions between presentations of food vocalizations that conveyed different types of referential information. These neurons were also not modulated by transitions betweens spectrally distinct bands of noise. These data suggested that, on average, vPFC neurons are modulated preferentially by transitions between presentations of food vocalizations that belong to functionally meaningful and different categories.

In a second, related study, we tested further the categorical nature of vPFC activity (Fig. 2). Consistent with categorical processing, we found that the vPFC neurons responded similarly to different vocalizations that transmitted information about different types of food quality (i.e., high-quality and low-quality food). However, vPFC neurons responded differently to vocalizations that transmitted information about non-food events. Importantly, this difference in response patterns cannot be attributed wholly to differences between the acoustics of the food and non-food vocalizations: the acoustic variability in the four food vocalizations was comparable to the variability in the six non-food vocalizations. We also found that vPFC neurons responded similarly to different vocalizations that transmitted information about high-quality food, low-quality food, and high-quality or low-quality food. These observations are consistent with the hypothesis that vPFC neurons respond to food and non-food vocalizations based on their category membership but do not differentiate between categories of food quality.

The prefrontal cortex is also involved in the categorization of learned (visual) categories (Freedman et al., 2001, 2002). In an elegant series of studies, Freedman and colleagues training rhesus monkeys to categorize exemplars of dogs and cats. Two important results emerged from this body of work. First, single-unit recordings obtained while the monkeys were categorizing the stimuli indicated that prefrontal activity mirrored the categorical choices of the monkeys. Second, by manipulating the category boundary along arbitrary dimensions, it was shown that the categorical nature of the neural responses is plastic and dependent on the categorical rule.

What is the difference between the categorical representations in the prefrontal cortex and earlier cortical areas such as the temporal cortex (i.e., the inferior temporal cortex [visual] and superior temporal gyrus [auditory]) (Freedman et al., 2003; Guenther et al., 2004; Hung et al., 2005; Husain et al., 2005; Poeppel et al., 2004)? One hypothesis is that since the prefrontal cortex is interconnected with virtually all sensory and motor cortical systems, and specifically with the temporal cortex (i.e., superior temporal gyrus [auditory] and inferior temporal cortex [visual]), an animal's behavior is guided flexibly by the categorical representations in the prefrontal cortex (Miller, 2000, 2002). That is, categorical information in the prefrontal cortex is critical for both the selection and retrieval of task-relevant information as it relates to the rules of an ongoing task (Asaad et al., 2000; Ashby and Spiering, 2004; Badre et al., 2005; Bunge, 2004; Bunge et al., 2005).

Consistent with this hypothesis there are marked differences between the responses of neurons in the prefrontal and temporal cortices during categorization tasks. For example, response of prefrontal neurons tend to vary with the rules mediating a task or the behavioral significance of stimuli, whereas responses in the inferior temporal cortex tend to be invariant to these variables (Ashby and Spiering, 2004; Freedman et al., 2003). Also, neurons in the prefrontal cortex tend to reflect a stimulus' membership in a category more than its physical properties, whereas neurons in the inferior temporal cortex tend be better correlated with their physical properties than prefrontal neurons (Freedman et al., 2003). Finally, in a recent human neuroimaging study (Bunge et al., 2005), activity in the left ventrolateral prefrontal cortex was modulated by the rules of a task during the cue and delay periods of match/non-match task, whereas the temporal cortex was modulated during the cue period but not the delay period. This differential effect was thought to reflect prefrontal cortex interactions with the temporal cortex to retrieve semantic information. Similar results have been found in single-unit recording studies: prefrontal cortex neurons encoded category information during a delay and test period whereas inferior temporal cortex neurons only encoded category information during the sample period (Freedman et al., 2003).

5. Future directions

In this review, we have discussed the behavioral and neural manifestations of categorical processing with an emphasis on categorical representations of auditory stimuli. We have discussed how the prefrontal and temporal cortices are involved in the processing of categorical information in both the auditory and visual domain, and how these areas are highly connected. While a significant body of research investigating categorical processing exists, there still remain many questions to be answered. Below, we highlight two future research avenues that we think are important for a more complete understanding of categorical processing.

First, if in fact the prefrontal cortex is involved in the processing of rule information and retrieval of category information, it brings up an important question: where is category information stored? At this time, there is no clear answer to this question, especially in the auditory domain. Work in the visual system suggests that categorical information may be stored in the inferior temporal cortex (Ashby and Spiering, 2004; Hung et al., 2005; Matsumoto et al., 2005; Muhammad et al., 2006), which is involved in processing visual objects such as faces (Afraz et al., 2006; Ashby and Spiering, 2004; Ungerleider and Mishkin, 1982). If this is true, then auditory categories may be stored in analogous areas that are involved in auditory-object formation and representation (Nelken et al., 2003). By correlating neural activity in these earlier auditory areas with an animal's responses during a categorization task, we can begin to understand where category information is formed and stored in the cortex.

Second, there is relatively little research on how multimodal stimuli are categorized. In many instances, auditory stimuli and visual stimuli provide complementary information (Ghazanfar and Schroeder, 2006). This is true of communication signals (Partan and Marler, 1999; Stein and Meredith, 1993). For instance, in humans, speech perception is enhanced when auditory information is combined with visual information (Calvert et al., 1997; McGurk and MacDonald, 1976; Sumby and Pollack, 1954). Similarly, rhesus monkeys are sensitive to the correlations that exist between the production of a vocalization (an auditory signal) and the facial expression (a visual signal) that accompanies the vocalization. Thus, a fundamental function of neural processing may be to integrate auditory and visual stimuli that provide complementary information (Ghazanfar and Logothetis, 2003; Ghazanfar et al., 2005; Hauser and Akre, 2001; Hinde and Rowell, 1962; Maestripieri, 1997; Partan, 2002; Partan and Marler, 1999; van Hooff, 1962). Are similar processes and areas involved in the categorization of visual and auditory stimuli when presented as one or are new areas of the cortex engaged to process these multimodal stimuli (Ghazanfar and Schroeder, 2006)? Since our world is full of multi-modal sensory information, it will be important to investigate how we combine information from multiple domains into a single coherent signal.

Acknowledgements

We thank Anne Krendl and Emily Cross for helpful comments on the preparation of this manuscript. Y.E.C was supported by grants from the Whitehall Foundation, NIH, and a Burke Award.

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